# SOCIAL AND EMOTIONAL INFLUENCES ON HUMAN DEVELOPMENT: PERSPECTIVES FROM DEVELOPMENTAL NEUROSCIENCE

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# SOCIAL AND EMOTIONAL INFLUENCES ON HUMAN DEVELOPMENT: PERSPECTIVES FROM DEVELOPMENTAL NEUROSCIENCE

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EDITORIAL
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# Editorial: Social and Emotional Influences on Human Development: Perspectives From Developmental Neuroscience

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**Keywords: developmental science, neuroscience, emotion, social processes, developmental theory**

**Editorial on the Research Topic**

**Social and Emotional Influences on Human Development: Perspectives From Developmental Neuroscience**

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The relevance of emotional and social processes in human development is a central focus in developmental psychology (for an overview see Eisenberg, 2006). Developmental psychology has examined which kind of emotional and social processes play a prominent role in particular phases of development and how their relative impact changes over the life-span. For example, attachment theory has highlighted the role of caregiver-child interaction in the development of emotion regulation capacities during early childhood (cf. Cassidy and Shaver, 2016). Adolescence is known as a period of heightened sensitivity toward peer influences (e.g., Steinberg, 2008). Subjective well-being in the elderly is related to the quality of their social contacts (Pinquart and Sörensen, 2000). Overall, an examination of the developmental significance of particular emotional and social processes has led to a more comprehensive understanding of human development.

Additionally, in the last decades psychology has experienced an increased use of methods derived from neuroscience. More recently, developmental researchers have also started to employ neuroscientific and psychophysiological methods in their empirical investigations. This paved avenues for novel ways to address pertinent research questions. Moreover, this provided novel insights that could not have been obtained with classical research methods. Recent years have also seen an increased employment of neuroscientific methods to explore emotional and social processes, giving reasons to establish new subdisciplines such as *Social Neuroscience* or *Affective Neuroscience*. These topics are also new territory for developmental psychology. This Research Topic brings together novel, cutting-edge neuroscientific research on the impact of emotional and social processes on human development. It highlights the benefits of neuroscientific and psychophysiological methods for fostering our understanding of the role social and emotional processes play during different phases of human development.

## SOCIAL INFLUENCES ON DEVELOPMENT

A central focus of many articles has been the social nature of human development. Three studies explored how infants process social stimuli (others' actions and voices) by means of electroencephalography (EEG). Bache et al. combined eye-tracking and EEG to explore how 10-month-old infants process the crawling movement of a same-aged child. Analyses showed differences in sensorimotor mu rhythm between continuous and non-continuous movements. Langeloh et al. explored by means of EEG how 12- to 14-month-olds process usual and unusual actions. They found that the reduction of mu power in frontal regions in response to unusual actions was context dependent, indicating that different social contexts affect how the brain process actions. Zinke et al. employed auditory event-related potentials (ERPs) in 3-month-olds and reliably dissociated components related to short- and long-term memory while the infants were processing familiar and unfamiliar voices.

In their opinion article, Pletti et al. evaluated whether measures relying on pupil dilation allow to discern the motivations underlying early prosocial behavior. They conclude that previous findings do not support claims that early helping is based on intrinsic altruism, but rather on a social motivation to interact with others.

Three further studies explore the role of attachment in human development. Kungl et al. examined preschool-aged children by means of ERPs and found that foster care children show higher arousal to the faces of strangers than control children. Leblanc et al. demonstrate longitudinal associations between early attachment security at 15 months and brain morphometry, mainly gray matter volumes, at 10–11 years. Finally, a longitudinal study by Herd et al. demonstrates the mediating role of inhibition in the interplay of stressful life experiences and secure relationship quality in adolescence.

In their integrative review, Reynolds and Roth discuss empirical findings on the development of attentional biases to faces in the light of current theoretical considerations. Bolenz et al. review the use of computational models to study reinforcement learning under influence of social information throughout development.

Addressing social cognition in autism, a neurodevelopmental condition, Sommer et al. report differences between a group of autistic adults and a comparison group only on the neural, but not on the behavioral level in a false belief task.

## EMOTIONAL AND MOTIVATIONAL INFLUENCES ON DEVELOPMENT

Three articles examined emotion-cognition interactions during development using pupillary responses, thought to be linked to activation of the noradrenergic system, and ERPs. Hoehl et al. examined attentional biases to threatening stimuli in 6-month-old infants. Pupillary dilation indicated that these biases are likely due to increased arousal and thus hint at an evolved preparedness for developing fear to ancestral threats. Chronaki et al. investigated processing biases related to emotional faces in 6 to 11-year-old children using ERPs. They found that in children with elevated symptoms of anxiety and depression, neural responses to angry faces were increased mostly at later, evaluative processing stages supporting cognitive models of threat perception. Hering et al. studied the influence of emotional material on prospective remembering in younger and older adults. While they found no age-differences on the behavioral level, ERPs revealed that emotional material had differential influences on ongoing processing in younger and older adults, hinting at a negativity bias in younger, but a positivity bias in older adults.

Finally, several articles also looked at motivational aspects and their potential influence on cognitive development. In their review, Kray et al. compared how monetary, cognitive, and social incentives are processed and whether they modulate decision-making and cognitive control during adolescence. Similarly, Ferdinand and Czernochowski reviewed motivational influences on the development of performance monitoring and cognitive control across the adult lifespan. Both reviews highlight the contribution of ERPs on identifying motivational influences on cognitive processes and the usefulness of fMRI to examine the brain substrates underlying these processes. Schmitt et al. provide ERP evidence showing that older adults invest more cognitive resources in preparatory control processes when potential gains are at stake.

## CONCLUSION

In sum, this Research Topic not only assembles cutting edge work in social and emotional developmental psychology. The explicit discussion of benefits and limitations of neuroscientific methods also offers an overview on potential applications and benefits of these methods in research on social and emotional development.

## AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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ORIGINAL RESEARCH
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# 10-Month-Old Infants Are Sensitive to the Time Course of Perceived Actions: Eye-Tracking and EEG Evidence

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Research has shown that infants are able to track a moving target efficiently – even if it is transiently occluded from sight. This basic ability allows prediction of when and where events happen in everyday life. Yet, it is unclear whether, and how, infants internally represent the *time course* of ongoing movements to derive predictions. In this study, 10-month-old crawlers observed the video of a same-aged crawling baby that was transiently occluded and reappeared in either a temporally *continuous* or non-continuous manner (i.e., *delayed* by 500 ms vs. *forwarded* by 500 ms relative to the real-time movement). Eye movement and rhythmic neural brain activity (EEG) were measured simultaneously. Eye movement analyses showed that infants were sensitive to slight temporal shifts in movement continuation after occlusion. Furthermore, brain activity associated with sensorimotor processing differed between observation of continuous and non-continuous movements. Early sensitivity to an action's timing may hence be explained within the internal real-time simulation account of action observation. Overall, the results support the hypothesis that 10-month-old infants are well prepared for internal representation of the time course of observed movements that are within the infants' current motor repertoire.

**Keywords: EEG, eye-tracking, sensorimotor simulation, action perception, occlusion, memory, real-time**

## INTRODUCTION

Infants possess a remarkable ability to predict future events. This has been demonstrated in various domains such as visual expectation (Canfield and Haith, 1991; Adler et al., 2008), social interaction (Adamson and Frick, 2003; Striano et al., 2006), action perception (Hunnius and Bekkering, 2010; Rosander and von Hofsten, 2011), and object tracking (Rosander and von Hofsten, 2004). Predicting when and where events occur is indispensable to understand and smoothly coordinate one's behavior with others' actions in everyday life (cf. Hommel et al., 2001). However, it is unclear whether infants actually rely on real-time processing of observed actions when predicting their future trajectory. As a consequence, the cognitive and neural processes of such real-time representations remain poorly understood.

Transient occlusion of ongoing movement is a frequently used paradigm to investigate predictive abilities and their neural implementations. According to this research, both *mnemonic* processes (Wilcox and Schweinle, 2003; Keane and Pylyshyn, 2006; Bosco et al., 2012; Springer et al., 2013) and *sensorimotor* processes (e.g., Graf et al., 2007; Southgate et al., 2009; Elsner et al., 2013) have been advocated to assist movement observation. Studies on *object motion* suggest that infants linearly extrapolate the ongoing trajectory of observed movement (e.g., von Hofsten et al., 1998). Linear extrapolation corresponds to working *memory* operations (e.g., Baddeley and Hitch, 1974; Pelphrey and Reznick, 2002) maintaining an internal representation of the target movement during occlusion that can be matched following the reappearance to generate predictions. In line with this assumption, infants need to plan and control their eye movements based on previously collected information in order to match pre- and post-occlusion input (Bennett and Barnes, 2003; Rosander and von Hofsten, 2004; Springer et al., 2013; Kwon et al., 2014; Bache et al., 2015).

While object motion usually follows linear trajectories with continuous velocity human movement is non-linear with changes in velocity and path. Linear extrapolation may hence not be an optimal approximation of human trajectories. Infants have been shown to render precise predictions about observed *human actions*, such as transporting a ball into a basket (Green et al., 2014). Here, predictions may be derived from *internally simulating* the observed action in sensorimotor areas of the brain as if performing the action oneself (Flanagan and Johansson, 2003; Falck-Ytter et al., 2006; Rosander and von Hofsten, 2011). In line with this assumption, initial evidence in infants suggests that *sensorimotor* processes support the internal representation of spatiotemporal aspects of human action, including predictive functions (Southgate et al., 2009, 2010; Stapel et al., 2010, 2016).

It remains unclear whether infants' processing of human movement recruits *real-time* representations employing simulation, memory, or both. Here, we consider representations as a neural pattern of stimulus coding that maintains stimulus properties as a close analog to the original sensory input in order to integrate previous and newly incoming stimulation (Hebb, 1949/2009).

Transient occlusion allows manipulating the temporal structure of on-going movement so that the post-occlusion trajectory does not reflect a time-matching continuation of the pre-occlusion movement. Applying such a paradigm, behavioral studies in adults pointed out that the processing of observed actions is running parallel to the actions' time course (e.g., Graf et al., 2007). However, previous studies also suggested that delayed and forwarded manipulations may not be processed similarly. More precisely, adults judged the continuation of a human action after a transient occlusion to be continuous when it was in fact slightly delayed, while they judged the continuation to be on time when it was in fact slightly forwarded (e.g., Sparenberg et al., 2012). Infants could recognize temporal shifts only if extreme jumps forward in time were presented (Wilcox and Schweinle, 2003; Bremner et al., 2005), while they could readily detect an one-second delay in their mothers' interaction (Striano et al., 2006). To further explore how infants process the time course of human action, delayed *and* forwarded movements need to be contrasted with continuous movement.

The present study aimed to investigate infants' sensitivity to the time course of human action. Specifically, 10-month-old crawlers watched a same-aged crawling baby that was transiently covered from sight. Following the occlusion, the movement was either continued in a time-matching manner (i.e., no time shift, resulting in continuous movement continuation) or in a non-matching manner (i.e., time shift, resulting in delayed or forwarded movement continuation) relative to the pre-occlusion movement stream (Graf et al., 2007). Due to limits in attention span, infants were randomly assigned to one of two experimental groups watching either *continuous* and *delayed* (i.e., Delay group) or *continuous* and *forwarded* movements (i.e., Forward group) within a single experimental session.

To capture mnemonic and sensorimotor contributions to movement processing, eye movements (via eye-tracking) and rhythmic neural activity (via electroencephalography, EEG) were measured simultaneously. Eye movements have been associated with both mnemonic (e.g., Keane and Pylyshyn, 2006) and sensorimotor processing (e.g., Elsner et al., 2013) and therefore provide a rather indirect measure of cognitive processes. Rhythmic neural activity may provide a complementary view. Specifically, *mnemonic functions* are assumed to be reflected in *frontal theta*[1] modulations (Jacobs and Kahana, 2010; Saby and Marshall, 2012; Lisman and Jensen, 2013; Bache et al., 2015), and *sensorimotor simulation* is assumed to be reflected in *central alpha* modulations (also labeled sensorimotor, rolandic or mu rhythm; Cochin et al., 1999; Muthukumaraswamy et al., 2004; Marshall et al., 2011; Bache et al., 2015).

Only if the ongoing movement was processed in real-time while it was hidden during occlusion, could a time-matching continuation be distinguished from a non-matching one following occlusion (cf. Graf et al., 2007). Hence, infants' sensitivity to the time course of movements would be reflected in differences in tracking and neural patterns following occlusion, whereas there should be no differences prior to and during the occlusion. With regard to *eye-tracking*, we hypothesized that the tracking of the target's reappearance position would be more accurate (i.e., landing on mid to front parts of the target) and more consistent (i.e., less variable across infants) in time-matching continuations (Bennett and Barnes, 2003). In contrast, the reappearance position would be overshot (i.e., landing in front of the target) in delayed continuations, and undershot (i.e., landing behind the target) in forwarded continuations, and tracking would be overall less consistent in both non-continuous continuations. With regard to *EEG*, we hypothesized that *frontal theta* activity would be elevated more when processing non-matching than when processing time-matching continuations because temporarily stored representations during occlusion would not match the reappearance position following occlusion (Orekhova et al., 1999; Kwon et al., 2014). Secondly, *central alpha* activity was expected to decrease more (i.e., indicating increased

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[1] Please note that beside mnemonic functions frontal theta rhythms have also been associated with cognitive control, action monitoring, and error processing (e.g., Cavanagh and Frank, 2014; Cohen, 2014 for recent overviews). But given the current task design, those functions are beyond the scope of the present study.

processing, Hanslmayr et al., 2012; Werkle-Bergner et al., 2014) in non-matching than in time-matching continuations because real-time simulation during occlusion should result in a prediction error relative to the actual reappearance position following occlusion (Kilner et al., 2007; Stapel et al., 2010).

# MATERIALS AND METHODS

## Participants

Participants were recruited from a database of parents interested in participating in infant studies at the Max Planck Institute for Human Development, Berlin. Infants were invited at 10 months of age (±10 days) according to the following criteria: *(a)* the infant was born at term (week of gestation $\geq$ 37, birth weight $\geq$ 2500 g), *(b)* to the parents' knowledge, the infant had no visual impairments nor current health issues, and *(c)* according to the parents, the infant was capable of crawling on hands and knees with her/his stomach lifted but not yet able to walk. Parents were encouraged to bring their own notes about their children's motor development to fill in a short checklist in the lab. The experiment was approved by the Institute's Ethics Committee.

A total of 99 10-month-old infants were tested. Twelve infants were not considered for further preprocessing as they did not crawl a distance of 1.5 m in the lab at least once ($n = 4$) or were too fussy to be properly tested following preparation for EEG and eye-tracking ($n = 8$). For *eye-tracking analysis*, 14 further infants were excluded because (a) the calibration failed ($n = 3$), (b) the trigger information was missing in the recorded data ($n = 6$), (c) the measurement failed due to technical issues ($n = 4$), or (d) fewer than 10% of the actually watched trials were free of artifacts ($n = 1$). Furthermore, for the *EEG analysis*, 37 further infants were excluded because they did not produce enough artifact-free EEG data (at least 10 trials per condition; $n = 30$) or the measurement failed due to technical issues ($n = 7$).

Thus, the final eye-tracking sample consisted of **32** infants in the Delay group and **31** infants in the Forward group, and the final EEG sample comprised **24** infants in the Delay group and **25** infants in the Forward group. **Tables 1**, **2** provide descriptive information on the final samples for eye-tracking and EEG analysis, respectively. **Figure 1** illustrates which trials of both eye-tracking and EEG data were contributed to the analysis within the final samples. Note that not all infants provided data in both measures, and artifact-free trials were contributed randomly throughout the test session. As a result, eye-tracking and EEG data were analyzed separately (cf. Stapel et al., 2010).

**TABLE 1 |** Descriptive information on eye-tracking sample.

| | Delay group ($N = 32$) | | Forward group ($N = 31$) | |
|---|---|---|---|---|
| | ***M*** | ***SD*** | ***M*** | ***SD*** |
| Number of boys/girls | 20/12 | | 15/16 | |
| Age in days[1] | 298.2 | 5.8 | 301.2 | 6.1 |
| Week of gestation at delivery | 39.8 | 1.3 | 40.3 | 1.0 |
| Birth weight in grams | 3385 | 390 | 3606 | 373 |
| Onset age in months[2] | | | | |
| Crawling | 8.0 | 1.1 | 7.9 | 0.9 |
| Sitting | 7.6 | 1.2 | 7.1 | 1.5 |
| Standing | 8.5 | 0.9 | 8.2 | 0.9 |
| Number of trials[3] | | | | |
| Continuous movement | 13 | 8.8 | 11 | 7.5 |
| Time-shifted movement[4] | 11 | 8.2 | 11 | 8.3 |

*M, mean; SD, standard deviation. Participants were randomly assigned to one of the two experimental groups (i.e., Delay group vs. Forward group). [1]300 days equals 10-month birthday. [2]According to parents' report. [3]Available for analysis after preprocessing. [4]Delayed in the Delay group and forwarded in the Forward group. In the Delay group, one child had not yet mastered sitting independently, another pulling up in a standing position; in the Forward group, one child had not yet mastered sitting independently and two children were not yet able to pull themselves up in a standing position. Exceptions were not the same children and thus not excluded. Mean age (t = −2.2, p = 0.033) and birth weight was lower in the Delay group (t = −2.3, p = 0.025); no further differences were found (t < −1.9, p > 0.051). EEG and eye-tracking samples (see also* ***Table 2****) did not differ (t < 1.5, p > 0.150) except for the number of trials (t = 3.4, p = 0.001) due to varying inclusion criteria for eye-tracking and EEG data.*

**TABLE 2 |** Descriptive information on EEG sample.

| | Delay group ($N = 24$) | | Forward group ($N = 25$) | |
|---|---|---|---|---|
| | ***M*** | ***SD*** | ***M*** | ***SD*** |
| Number of boys/girls | 9/15 | | 12/13 | |
| Age in days | 296.8 | 5.6 | 301.0 | 5.8 |
| Week of gestation at delivery | 39.5 | 1.5 | 40.0 | 1.0 |
| Birth weight in grams | 3327 | 373 | 3569 | 318 |
| Onset age in months | | | | |
| Crawling | 8.0 | 1.1 | 8.1 | 0.7 |
| Sitting | 7.6 | 1.1 | 6.9 | 1.6 |
| Standing | 8.5 | 0.7 | 8.5 | 0.7 |
| Number of trials | | | | |
| Continuous movement | 21 | 7 | 19 | 8 |
| Time-shifted movement | 20 | 9 | 21 | 8 |

*Information is shown in analogy to* ***Table 1****. In the Delay group, two children had not yet mastered sitting independently, another child pulling up in a standing position; in the Forward group, one child had not yet mastered sitting independently and two children were not yet able to pull themselves up in a standing position. Exceptions were not the same children and thus not excluded. Age (t = −2.6, p = 0.014) and birth weight (t < −2.5, p = 0.018) were lower in the Delay group; no further differences were found (t < −1.8, p > 0.075).*

## Stimulus Material and Procedure

Participants repeatedly watched a video of a same-aged baby crawling in front of a light gray background (2480 ms; *pre-occlusion phase*). The baby's movement was transiently occluded by a full-screen black occlusion (500 ms; *occlusion phase*) and then immediately continued (1000 ms; *post-occlusion phase*). Hence, each trial lasted for 4000 ms. The video, however, was 4500 ms long, allowing to manipulate the movements' timing. We choose to present an intransitive movement, that is a movement not directed at an apparent object or goal, in order to avoid confounds with object knowledge or object saliency. To avoid lateralization of brain activity, each video was presented

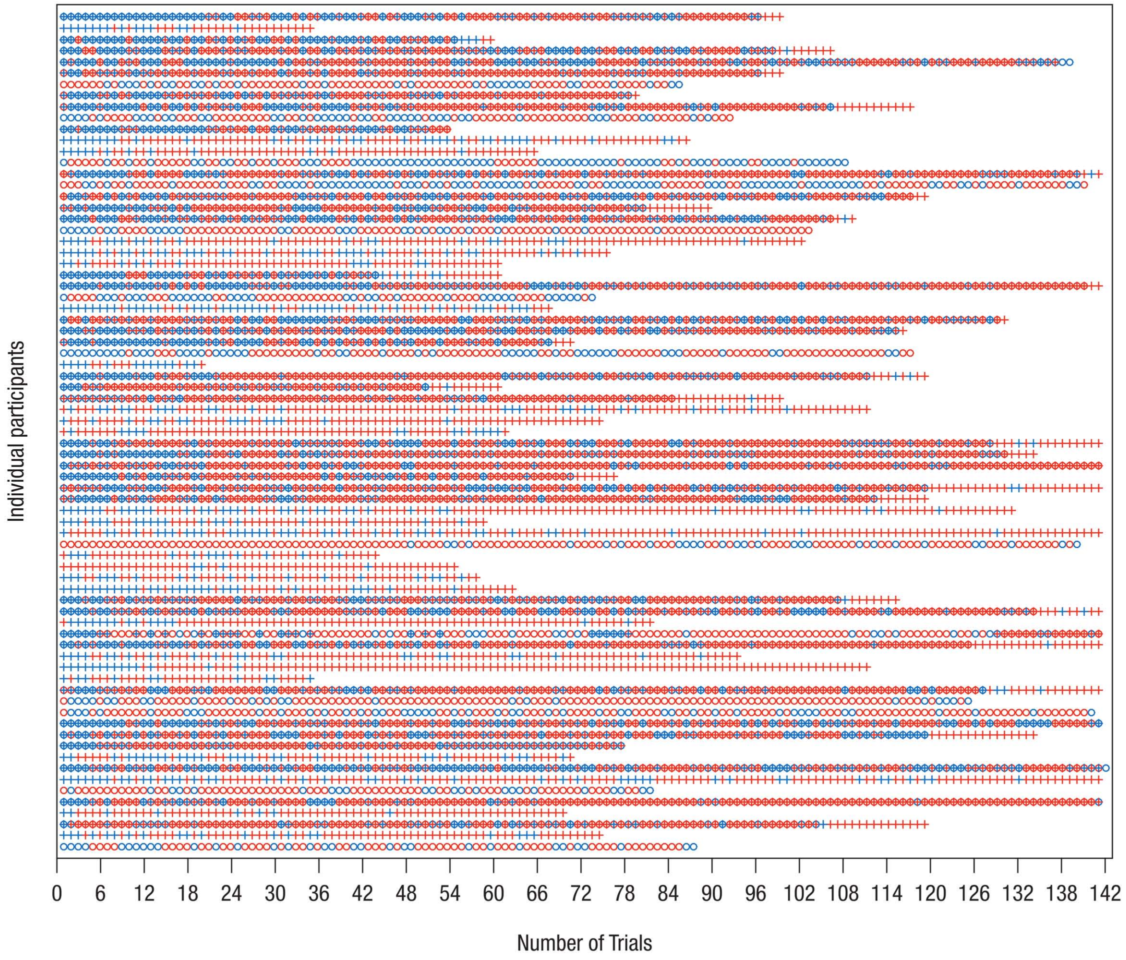

**FIGURE 1 |** Distribution of trials included in analysis of EEG and eye-tracking data. On the *y*-axis, each row represents one data set/participant; only participants who were included in the final samples are shown. The *x*-axis shows the chronological trial number, tick marks spaced according to blocked presentation of conditions. Blue – trial available for analysis; red – trial not available for analysis. Circle – EEG data, Cross – eye-tracking data. Note that not for all data sets measurement of both EEG and eye-tracking was possible. It is apparent that infants contributed trials to the final analysis more or less randomly. Therefore, separate analyses of eye-tracking and EEG measures were performed.

from both left to right and right to left (i.e., flipped versions of the original video). On the *x*-axis of the monitor, the stimulus (i.e., crawling baby) was on average 279 pixel (ranging from 207 to 315 pixel) wide and moved with an average speed of 3° visual angle per second (see **Figure 2** for an illustration of the stimulus material).

In a between-subjects design, participants were randomly assigned to one of two experimental groups: In the Delay group, *continuous* and *delayed* movements were shown, while in the Forward group, *continuous* and *forwarded* movements were presented. To achieve continuous and non-continuous (i.e., delayed or forwarded) movements, the starting time in the video footage was varied. More precisely, during pre-occlusion, non-continuous trials started either 500 ms earlier (i.e., at 0 ms in forwarded conditions) or 500 ms later (i.e., at 1000 ms in delayed conditions) as compared to the continuous trials (i.e., at 500 ms). However, following the occlusion (i.e., 500 ms), the movement was always continued at 3000 ms in the video footage. In other words, during occlusion, the video footage was paused in delayed trials (i.e., 0 ms elapsed), fast-forwarded in forwarded trials (i.e., 1000 ms elapsed), and continued in real-time in continuous trials (500 ms elapsed). Therefore, in non-continuous trials, the post-occlusion movement did not match a natural continuation of the pre-occlusion movement, but resulted in a forwarded (i.e., 500 ms too early) or a delayed (i.e., 500 ms too late) time course of the movement. Notably, the visual input slightly varied during pre-occlusion phases, while it was identical during occlusion and post-occlusion phases. Within each trial, time manipulation could only be detected following occlusion. This design ensured that differences between conditions during occlusion and post-occlusion could not be attributed to visual differences but reflect the manipulation of the movements' time course.

Stimuli were presented using a customized program written in Microsoft Visual C++ (Microsoft Corporation, Redmond,

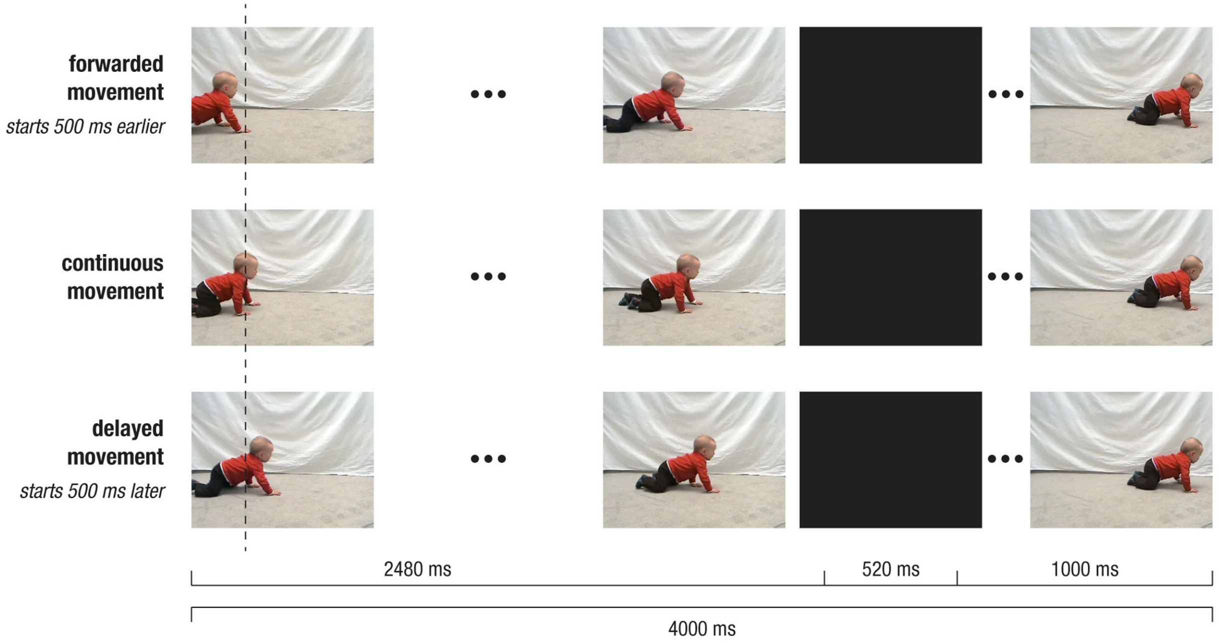

**FIGURE 2 |** Depiction of stimulus design. Screenshots of crawling movement at pre-occlusion, occlusion, and post-occlusion phases, for continuous movement **(Middle row)**, forwarded movement **(Upper row)**, and delayed movement **(Lower row)**. Note that, during pre-occlusion, the starting time in the video clip depended on the experimental condition: The continuous movement started at 500 ms, the delayed movement at 1000 ms and forwarded movement at 0 ms. Therefore, movement positions slightly differed across conditions as indicated by the vertical dotted line. Following occlusion, the video was always continued with the same frame in the video (i.e., at 3000 ms), and therefore the visual input was identical across conditions.

WA, United States). Each trial was preceded by a centered fixation object (i.e., colored pictures of toys; duration of 800 – 1300 ms) on gray background. Conditions were presented in blocks of six trials, because rapid learning over trials has been reported (see Henrichs et al., 2014). The order of blocks was quasi-randomized such that blocks with the same condition and movement direction were never repeated successively. Participants were randomly assigned to one of two predefined block orders per experimental group. The stimulus presentation was controlled by an experimenter; depending on infants' attention and compliance up to 24 blocks (i.e., 144 trials) were presented. The experiment was conducted in an acoustically and electromagnetically shielded room. Experimental sessions were video-recorded in time-synchronized split-screen images including a frontal and lateral view of the infant as well as a running and a condition trigger for coding infants' behavior *post hoc* (Interact; Mangold International GmbH, Arnstorf, Germany). The lighting conditions were kept comparable across participants. The infant sat on the parent's lap in a BabyBjörn® baby carrier facing a 20.1" monitor (dimensions: 40.8 cm × 30.6 cm, visual angle ≈ 29° × 22°) at a distance of approximately 80 cm (for more detailed information on the experimental procedure, see Bache et al., 2015). Despite restricting infant's position, sitting distance could range from 60 to 90 cm when infants leaned forward or backward. In our set-up, the size of one pixel (0.051 cm) equals 0.037° visual angle for an ideal sitting distance.

## Data Acquisition

### Eye-Tracking Data

#### *Recording*

Eye movements were recorded continuously using an EyeLink 1000 remote system eye-tracker (SR Research, Ottawa, ON, Canada), which allows for free head movements. The eye-tracking camera including the infra-red source was permanently positioned centrally below the presentation monitor. Participants were seated 55 cm from the recording eye-tracking camera. The camera recorded the corneal relative to the pupil reflection of the left eye at a frequency of 250 Hz in terms of raw gaze positions in pixel.

The infants' head position was tracked using a small sticker on their forehead that allowed accounting for head movement of up to 100 cm/s. Infants' position relative to the head box of the eye-tracker was checked using the camera image before the experimental procedure started. The data were filtered online using the second stage of the built-in heuristic filter (Stampe, 1993) which reduces noise in the data by a factor of 4 to 6 (according to the EyeLink manual). The average accuracy of the eye-tracking system is 0.5° visual angle for an ideal participant (i.e., sitting still with minimal head movements and generating a perfect calibration), as reported by the providing company, which would approximate to a 0.07 cm area at the viewing distance of 80 cm in the present experiments.

Following EEG preparation and prior to stimulus presentation, a five-point calibration procedure on a gray background was performed in the following order: center, upper center, lower center, left center, right center. The calibration target was a dancing rabbit in a square shape (96 × 96 pixel, approximately 4.9 $cm^2$ on the monitor and 3.5° visual angle from the sitting position) accompanied by an attractive sound. An experimenter pushed a button to accept the gaze position if it was on the target position. The central position was repeated at the end as an estimate of accuracy. Calibration was only accepted if it was reported to be 'good' by the recording software (i.e., average error $< 1°$ visual angle) and if the overall pattern of gaze positions matched the target's positions according to the experimenter's evaluation. If the calibration was not accepted, it was repeated until it was satisfying. If calibration could not be obtained, the experimental procedure was continued, but the participants' eye-tracking data were discarded from analysis.

#### *Preprocessing*

Ideal preprocessing of eye-tracking data should yield data that represent artifact-free and task-relevant eye movement. Yet, in infant studies, raw eye-movement data are typically only preprocessed in terms of detecting saccades or fixations by applying built-in algorithms of the eye-tracking system at hand (e.g., Gredebäck and Melinder, 2010). Recently, Wass et al. (2014) demonstrated that data quality affects fixation detection to such an extent that the interpretation of the results is put into question – even when a satisfactory calibration outcome is achieved. Moreover, comparing common categorization algorithms, it has been shown that results for fixations and saccades vary to such an extent that automated categorization may not always return meaningful results (Komogortsev et al., 2010; see Wass et al., 2013, for calculation of data quality *post hoc*).

In order to avoid classification artifacts and to account for data quality, raw gaze positions (i.e., $x$- and $y$-value in pixel per measurement unit) were visually inspected using a custom-made graphical user interface (GUI, see Supplementary Material) in MATLAB 7.10.0 (MathWorks Inc., Natick, MA, United States) to detect trials with *measurement errors* (i.e., noisy or no data, e.g., following gross movement, substantial changes in body/head position, or changes in the eyes' lubrication) and *compliance failure* (e.g., gazing away from or staring blankly at the monitor; see Haith, 2004; Schneider et al., 2008; Wass et al., 2014). More precisely, raw data were segmented into 3400 ms long epochs from −2200 ms to 1200 ms relative to the onset of occlusion. The first and last 300 ms of each trial were discarded from analysis because (a) following stimulus onset, infants reoriented from the centered fixation object to the stimulus movement starting on either the left or right side of the monitor, and (b) approaching stimulus offset, infants' attention frequently terminated. The extracted segments were displayed neutral with respect to condition, movement direction, and test session to avoid confounding influence. The stimulus dimensions (i.e., $x$- and $y$-values in pixel) for each video-frame were derived using OpenCV[2] by defining the color contrast separating colored stimulus and grayish background. Stimulus dimensions were included in the GUI to map gaze positions to actual stimulus position. Only trials with less than 50% missing data (incl. data points beyond the monitor) were considered for inspection.

Each trial was visually scanned by a trained rater (CB) according to the persistent or repeated presence of the following exclusion criteria: (a) missing gaze positions, gaze positions outside and/or on the borders of the monitor shortly before, during, and/or following the occlusion in order to make sure that transitions were actually perceived, (b) noisy and/or broken data resulting from technical error, (c) prolonged stationary data points reflecting blank stares without following of the stimulus movement. In principle, trials could be associated with more than one criterion. Missing or outlying data points at the beginning and end of the trial were not regarded as an exclusion criterion. Trials that were identified as being of poor quality were discarded from further analyses (see Supplementary Material). In ambiguous trials, video-recordings of the experimental session were used to inform the decision.

Following visual inspection, the percentage of trials available for eye-tracking analysis was calculated relative to the number of trials that the infant had actually watched during stimulus presentation, based on behavioral coding of video-recordings. Only data from infants providing at least 10% artifact-free trials were considered for further analyses.

#### *Analysis of gaze positions over time*

As the movement was mainly evolving on the horizontal axis across time, only raw gaze positions (in pixel) on the x-dimension (Gx) were used. Within subjects, gaze positions were averaged per condition for each measurement point (i.e., every 4 ms). Data for movement from right to left were flipped, so all trials were available in the left-to-right direction. Data on either the $y$- and/or $x$-axis that were outside of the monitor's dimensions were considered missing, and this was also applied to the corresponding gaze position on the other axis. Missing values were discarded before averaging.

The analysis focused on infants' gaze behavior in reaction to the moving stimulus. However, it is difficult to quantitatively determine gaze relative to moving objects based on raw gaze positions. To relate gaze and stimulus position, the midpoint of the minimal and maximal $x$-value of the stimulus dimension per video frame (see Preprocessing) was determined as mean stimulus position (in pixel). Due to the biological characteristics of crawling (i.e., stretching and flexing of extremities), the stimulus dimensions vary from frame to frame and thus the mean stimulus position over time does not represent a linear movement (see black dotted line in **Figure 3A**). Following, at each measurement point, the respective mean stimulus position was subtracted from the raw gaze position, resulting in a difference score that reflects the *distance* between gaze position and stimulus position. Thus, if infants were looking at the front parts of the stimulus target (i.e., baby's hands and head), the resulting scores would be positive (and vice versa). Resulting difference scores were averaged for each measurement point per condition within each participant.

For statistical analysis, within subjects, the *mean distance* as well as the *variance in distance* between gaze and stimulus

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[2] http://opencv.org/

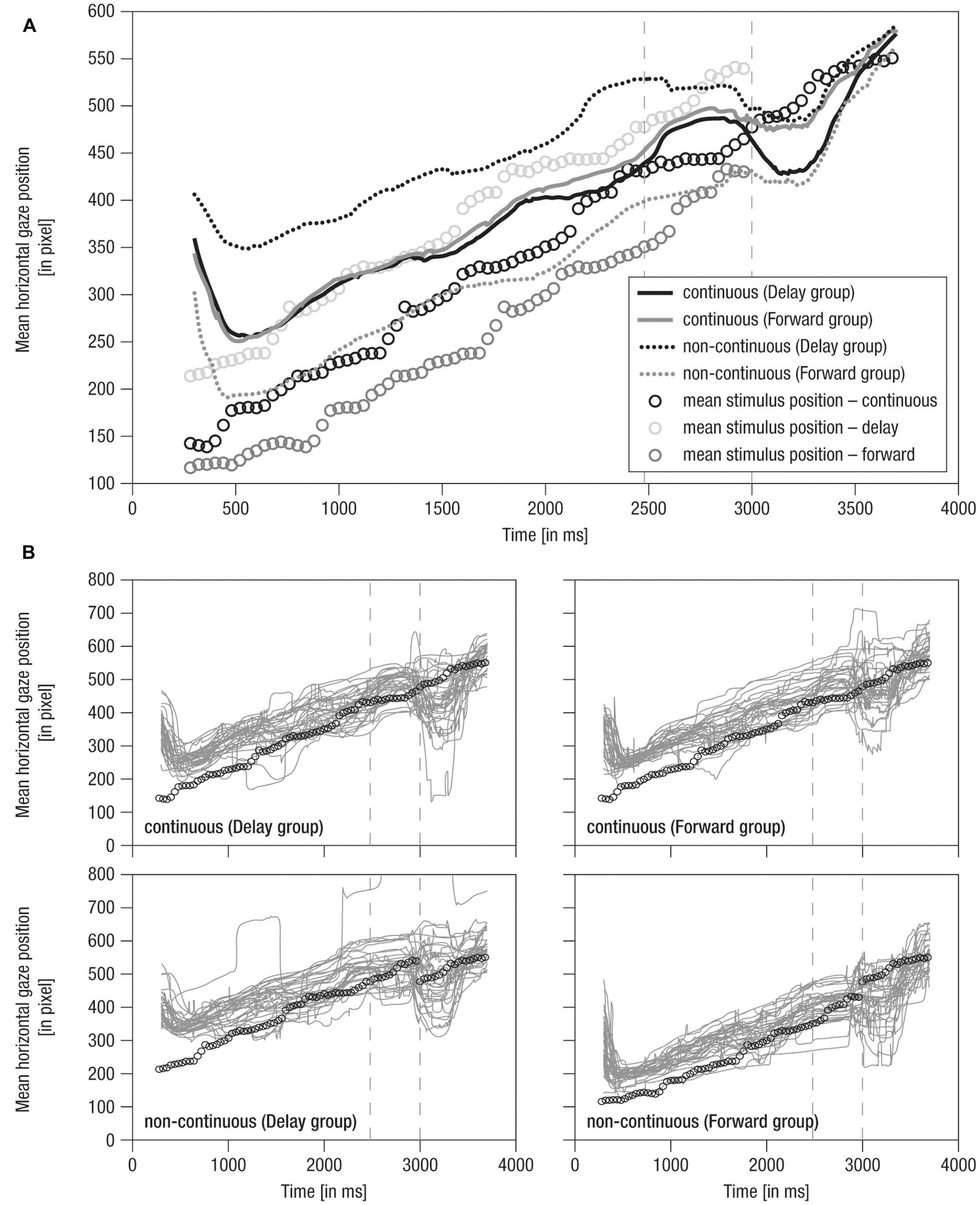

**FIGURE 3 |** Mean horizontal gaze positions over time. **(A)** Grand averaged horizontal gaze positions over time. Lines: Solid – continuous, Dotted – non-continuous movement, Black – Delay group, Gray – Forward group, Vertical dashed – occlusion on- and offset. **(B)** Single averaged horizontal gaze positions over time (gray). Note that circles indicate mean stimulus position over time for the respective condition. Prior to occlusion, circles are horizontally shifted by ± 500 ms due to stimulus design. Gaze positions in continuous conditions match because the stimulus was identical. As the stimulus was not visible during occlusion (i.e., 2480–3000 ms), here, circles indicate imaginary continuation of the movement. Following occlusion (i.e., 3000–4000 ms), only circles for the continuous condition are plotted as the stimulus was identical in all conditions.

position were calculated for each trial across predefined 500 ms time windows for each phase of the trial (i.e., the last 500 ms of the pre-occlusion, the 500 ms of the occlusion, and the first 500 ms of the post-occlusion phase), and resulting means and variances, respectively, were averaged per condition. The two measures reveal different aspects of viewing behavior: Mean distance represents the average gaze position relative to the target position, and was thus taken to reflect tracking *accuracy*. Variance in distance represents the average fluctuation in tracking behavior, and was thus taken to reflect tracking *consistency* (i.e., whether tracking was rather consistent or random across infants).

## EEG Data

### *Recording and pre-processing*

Electroencephalography was recorded continuously with a BrainAmp DC amplifier (BrainProducts GmbH, Gilching, Germany) from 32 active electrodes (actiCap by BrainProducts) inserted into a soft elastic cap according to the 10–20-system (EASYCAP GmbH, Herrsching, Germany). During recording, the right mastoid electrode served as reference and the left mastoid was recorded as an additional channel. Ground was placed at location AFz. Impedances were kept below 20 kΩ during preparation. The EEG was recorded with an analog pass-band of 0.1 to 250 Hz and digitized with a sampling rate of 1000 Hz.

Prior to EEG-preprocessing, based on behavioral coding of video-recordings, trials were discarded if infants (a) did not attend to the total duration of stimulus presentation and (b) produced limb movement that could be seen as part of imitative crawling (i.e., limb movements involving movement of the joints wrist, elbow, shoulder as well as knee and hip). The latter criterion was chosen because we were interested in brain activity related to action observation but not to imitation. Furthermore, using Vision Analyzer 2 (Brain Products) for visual inspection, EEG trials were discarded which comprised broken channels or extreme/untypical artifacts (i.e., extensive movements). To this end, remaining EEG data were segmented into 4700 ms long epochs (from −2700 to 2000 ms relative to the onset of occlusion). Subsequent preprocessing and analyses were conducted using the FieldTrip (developed at the F.C. Donders Centre for Cognitive Neuroimaging, Nijmegen, The Netherlands[3]; Oostenveld et al., 2011) and custom-made routines operated in MATLAB 7.10.0 (MathWorks Inc., Natick, MA, United States).

Data were cleared of stereotypic artifacts using Independent Component Analysis (ICA; Jung et al., 2000). Specifically, ICs representing eye blinks, saccades, muscle activity, or instrumental noise were visually identified and discarded from further analysis by a trained rater (CB). To this end, all selected segments across all conditions were concatenated within subjects, filtered (high pass 1 Hz, low pass 100 Hz, 6th-order Butterworth-filter), and subjected to an extended infomax ICA (Bell and Sejnowski, 1995). A DFT-filter as implemented in FieldTrip was used to suppress line-noise. Decisions for rejection were based on integrated information from the ICs topography, power spectrum, event-related potentials (ERPs) as well as individual trials and the distribution of the IC over trials. Rejected ICs were in accordance with previous reports on typical artifacts in EEG data when stimulus presentation elicited eye-movements in a passive viewing paradigm (e.g., Plöchl et al., 2012).

All subsequent analyses were carried out in sensor space, based on the back-projection of the non-artifact ICs. Previously identified broken channels were interpolated after ICA-cleaning; a maximum of three non-neighboring channels were allowed. Cleaned data was re-referenced to the mathematically linked mastoids, filtered (high pass 1 Hz, low pass 30 Hz, 6th-order Butterworth-filter), and segmented into 4000 ms epochs according to the onset of occlusion (−2480 to 1520 ms). For each single trial, the offset was removed by subtracting the average of the total epoch.

Rhythmic neural activity was analyzed by means of fast Fourier transformation (FFT) using an individualized data approach taking idiosyncrasies into account (Nesselroade et al., 2007). That is, we identified the individual peak frequency (IPF) at the individual peak electrode (IPE) in a given electrode cluster and frequency range (Doppelmayr et al., 1998; Werkle-Bergner et al., 2009). In line with the literature, *frontal theta* activity, considered as reflecting mnemonic processing (see Saby and Marshall, 2012 for a review), was defined as oscillatory activity within 4–6 Hz at frontal electrodes F3, Fz, F4, FC1, and FC2 (Orekhova et al., 1999, 2006). *Central alpha* activity, assumed to indicate sensorimotor simulation (for reviews, see Marshall and Meltzoff, 2011; Cuevas et al., 2014), was defined as oscillatory activity within 6–9 Hz at central electrodes FC1, FC2, C3, Cz, C4, CP1, and CP2 (Stroganova et al., 1999; Marshall et al., 2002).

To detect individual peak frequencies, the spectral power distribution between 1 and 20 Hz at each electrode was estimated by means of FFT across all trials and phases (i.e., from −2480 ms to 1520 ms with regard to occlusion onset). Each trial was zero-padded to 10 s and tapered with a Hanning window to achieve a frequency resolution of 0.1 Hz. The power spectra were corrected for the 1/f trend inherent in scalp EEG data to facilitate the detection of spectral peaks (Demanuele et al., 2007; He et al., 2010). When no IPF was detected, the missing values were interpolated with the mean of all detected peaks to preserve comparable samples for the EEG measures. There was one missing value for frontal theta and central alpha each. These missings were not detected in the same participants across EEG measures.

### *FFT analysis*

For analyses of modulations in rhythmic neural activity, *FFT* was performed separately for each phase of the trial (i.e., pre-occlusion, occlusion, post-occlusion). As the phases (i.e., pre-occlusion, occlusion, post-occlusion) of each trial varied in length, the data were again zero-padded to 10 sec prior to FFT calculation, resulting in a common frequency resolution of 0.1 Hz. Power values for each phase of the trial and experimental condition were extracted for each participant at the respective IPF and electrode after averaging across trials within participants. For each condition, data were collapsed across movement directions (i.e., left to right and right to left) to obtain enough trials for statistical comparison. As the distribution of power values was skewed, data were log-transformed prior to the analysis[4].

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[3] http://www.fieldtriptoolbox.org/

[4] Comparable results were obtained in non-log-transformed data after exclusion of outliers (> mean ± 3*SD).

## Statistical Analysis and Qualitative Description

To provide rich information on infants' tracking behavior over the course of the stimulus movement, mean horizontal gaze positions as well as mean horizontal distance in gaze and stimulus positions over time were described qualitatively. In addition, statistical analyses were done using SPSS 15.0 (SPSS Inc., 1989–2006, United States). Specifically, mixed effects repeated-measures ANOVAs with a between-subject factor *Group* (Delay group vs. Forward group) and the within-subjects factors *Phase* (pre-occlusion vs. occlusion vs. post-occlusion phase) and *Time* (continuous vs. non-continuous) were carried out separately for each measure of eye movement (i.e., mean distance, variance in distance) and rhythmic neural activity (i.e., frontal theta, central alpha). Including Phase makes it possible to check that differences in dependent variables occur only after the time-course manipulation was introduced, namely during the post-occlusion phase. Partial eta squared, $\eta_p^2$, is reported as an estimate of the effect size. Greenhouse-Geisser corrections were applied if the assumption of sphericity was violated. As group sizes were equal, ANOVA was assumed to be robust toward violation of the assumption of homogeneity. Significant effects were followed up by separate Bonferroni-corrected ANOVAs or *t*-tests.

# RESULTS

## Eye-Tracking Data

### Qualitative Description of Gaze Positions over Time

Mean horizontal gaze positions over time are shown in **Figure 3**.

1. During the *pre-occlusion* phase, a decrease in horizontal gaze positions until 500 ms after trial onset indicates a slow orientation reaction. When infants were finally 'on' the stimulus, movement was tracked comparably across experimental groups and conditions in close relation to the stimulus position (**Figure 3A**). Note that in the forwarded/delayed conditions the stimulus depicted a movement that started 500 ms earlier/later in the movement sequence than in the continuous conditions, and the crawling infant was thus at slightly different positions across conditions throughout the pre-occlusion phase (see **Figure 2**). Accordingly, gaze positions were about 150 pixels further backward in forwarded (see gray dotted line in **Figure 3A**) and further forwarded in delayed conditions (see black dotted line in **Figure 3A**) compared to continuous conditions.
2. During the *occlusion* phase, general tracking behavior continued in accordance with the stimulus trajectory presented during the pre-occlusion phase. Toward the occlusion offset, the difference between non-continuous conditions reduced about 50 pixels, possibly indicating adaptation to non-matching stimulus reappearance in repeated/block stimulus presentation.
3. At the *post-occlusion* onset, distinct tracking patterns emerged: In the case of continuous movement in the Delay group, infants' gaze positions were reduced for about 50 pixels; that is, infants gazed opposite the movement direction (solid black line in **Figure 3A**). This was followed by catching-up with the stimulus movement (i.e., steep increase in horizontal gaze positions). All conditions were tracked comparably toward the end of the trial (i.e., at 3500 ms at about pixel 550). Note that visual input was identical in all conditions during the post-occlusion phase but did not match the continued time course of the pre-occlusion input in non-continuous continuations (i.e., delayed/forwarded). Hence, infants quickly caught up with the stimulus in response to manipulated continuations.

Notably, the grand averages reflected the individual data (**Figure 3B**) suggesting that tracking was rather consistent across infants. In sum, average raw gaze positions over time indicate that infants were sensitive to manipulations in the timing of observed movements.

### Qualitative Description of Distance in Gaze and Stimulus Position over Time

The average horizontal distance in gaze and stimulus position over time is shown in **Figure 4**.

1. During the *pre-occlusion* phase, both continuous and non-continuous movements were tracked in accordance with the non-linear dynamics of the crawling movement (**Figure 4A**). Specifically, positive scores indicate that infants preferably tracked the front to middle parts of the baby stimulus with decreasing scores (i.e., about 50 pixels over 2000 ms) when approaching the occlusion phase. This may indicate adaptation to the transient full-screen occlusion of the stimulus movement always occurring 2480 ms post-stimulus-onset.
2. During the *occlusion* phase, in continuous conditions, the cyclic tracking pattern was continued, indicating that infants stayed on the stimulus although it was hidden. In contrast, in non-continuous conditions, distance scores distinctively decreased about 100 pixels (i.e., looking opposing the hidden target's implied movement direction) in *delayed* movement (i.e., converging to the reappearance position) and slightly decreased about 50 pixels in *forwarded* movement (i.e., diverging from the reappearance position). Nevertheless, infants were still 'on' the target in non-continuous conditions, yet on mid to rear parts of it. Hence, though movement manipulation could be detected following occlusion, infants apparently expected a certain continuation during occlusion, possibly due to repeated/blocked presentation of conditions.
3. At the *post-occlusion* onset, tracking of continuous and non-continuous continuations differed between the experimental groups: In the *Delay group*, continuous movement resulted in a pronounced decrease in distance scores (i.e., about 100 pixels, thus looking opposite the movement direction) until the gaze was positioned on rear parts of the stimulus, whereas delayed movement

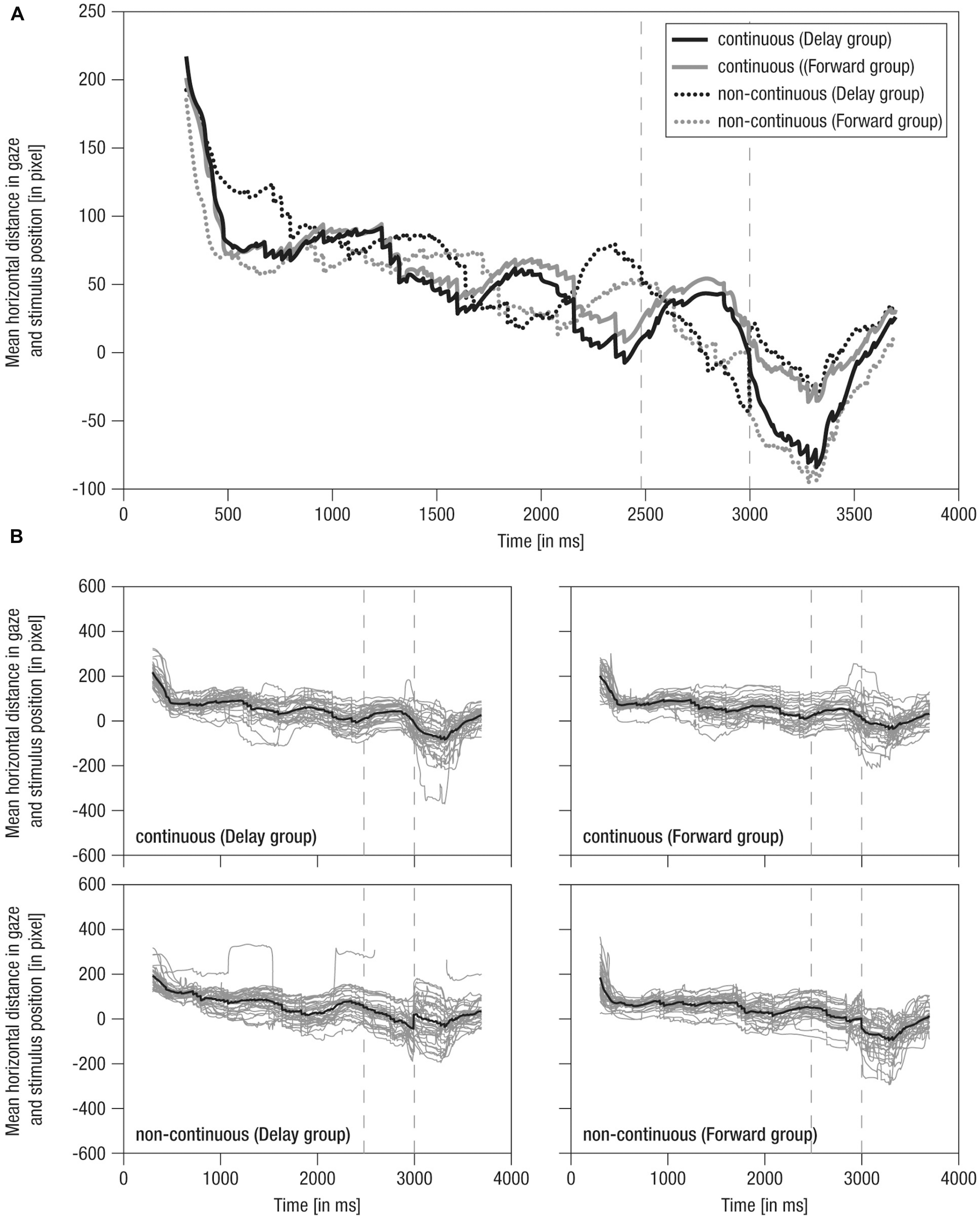

**FIGURE 4 |** Mean horizontal distance between gaze positions and mean stimulus positions over time. **(A)** Grand averaged distance over time. Lines: Solid – continuous, Dotted – non-continuous, Black – Delay group, Gray – Forward group; Vertical dashed – occlusion on- and offset. **(B)** Single averaged distance over time (gray) including respective grand average (black). Note the average stimulus dimensions of 279 pixel.

resulted in a small decrease (i.e., about 40 pixels) until the gaze was positioned at the mean stimulus position. In contrast, in the *Forward group*, continuous movement resulted in only a small decrease (i.e., about 40 pixels) toward the mean stimulus position, whereas forwarded movement resulted in a pronounced decrease (i.e., about 100 pixels) toward rear parts of the stimulus. Hence, continuous movement was apparently not always perceived as time-matching continuation. Finally, following a steep increase in distance scores, all conditions were tracked comparably at about 50 pixels mean distance (i.e., at front parts of stimulus) 700 ms post-occlusion-offset, showing that infants quickly caught up with the actual stimulus movement.

Like mean horizontal gaze positions, grand averages of mean horizontal distance in gaze and stimulus positions were representative of individual data, which were actually highly systematic across conditions and individuals (**Figure 4B**) highlighting that tracking behavior was rather consistent across participants. Overall, these results indicate that infants were able to detect slight temporal shifts in the continuation of transiently occluded movements.

## Statistical Analysis of Mean Distance per Phase

To analyze the *mean distance* as a marker for tracking accuracy in 500 ms time windows before, during, and following occlusion, a mixed effects repeated-measures ANOVA was performed. The results showed a significant main effect of the within-subjects factor (a) Phase [$F_{(1.6,97.9)} = 130.25$, $p = 0.000$, $\eta_p^2 = 0.68$]. Furthermore, there were significant interaction effects for (b) Phase and Time [$F_{(1.6,97.1)} = 4.59$, $p = 0.012$, $\eta_p^2 = 0.07$], (c) Time and Group [$F_{(1,61)} = 10.37$, $p = 0.002$, $\eta_p^2 = 0.15$], and (d) Phase, Time, and Group [$F_{(1.6,97.1)} = 17.1$, $p = 0.000$, $\eta_p^2 = 0.22$]. No further effects were observed ($F < 3.06$, $p > 0.085$). **Figure 5** provides an overview of the results for mean distance and variance in distance.

To evaluate the (d) three-way interaction effect, a total of six paired-sample *t*-tests were performed, separately per levels of Group and Phase. The results showed that, during *post-occlusion*, the *Delay group* tracked continuous movements ($M = -47.88$, $SE = 9.98$) at more rear parts than non-continuous movements [$M = 0.9$, $SE = 13.8$; $t_{(31)} = -3.25$, $p = 0.003$; pre-occlusion: $t_{(31)} = 0.54$, $p = 0.595$; occlusion: $t_{(31)} = 1.51$, $p = 0.142$], whereas the *Forward group* tracked continuous movements ($M = -12.91$, $SE = 10.34$) more frontally than non-continuous movements [$M = -58.18$, $SE = 9.92$; $t_{(31)} = 3.69$, $p = 0.001$; pre-occlusion: $t_{(30)} = 2.1$, $p = 0.03$; occlusion: $t_{(30)} = 2.0$, $p = 0.05$].

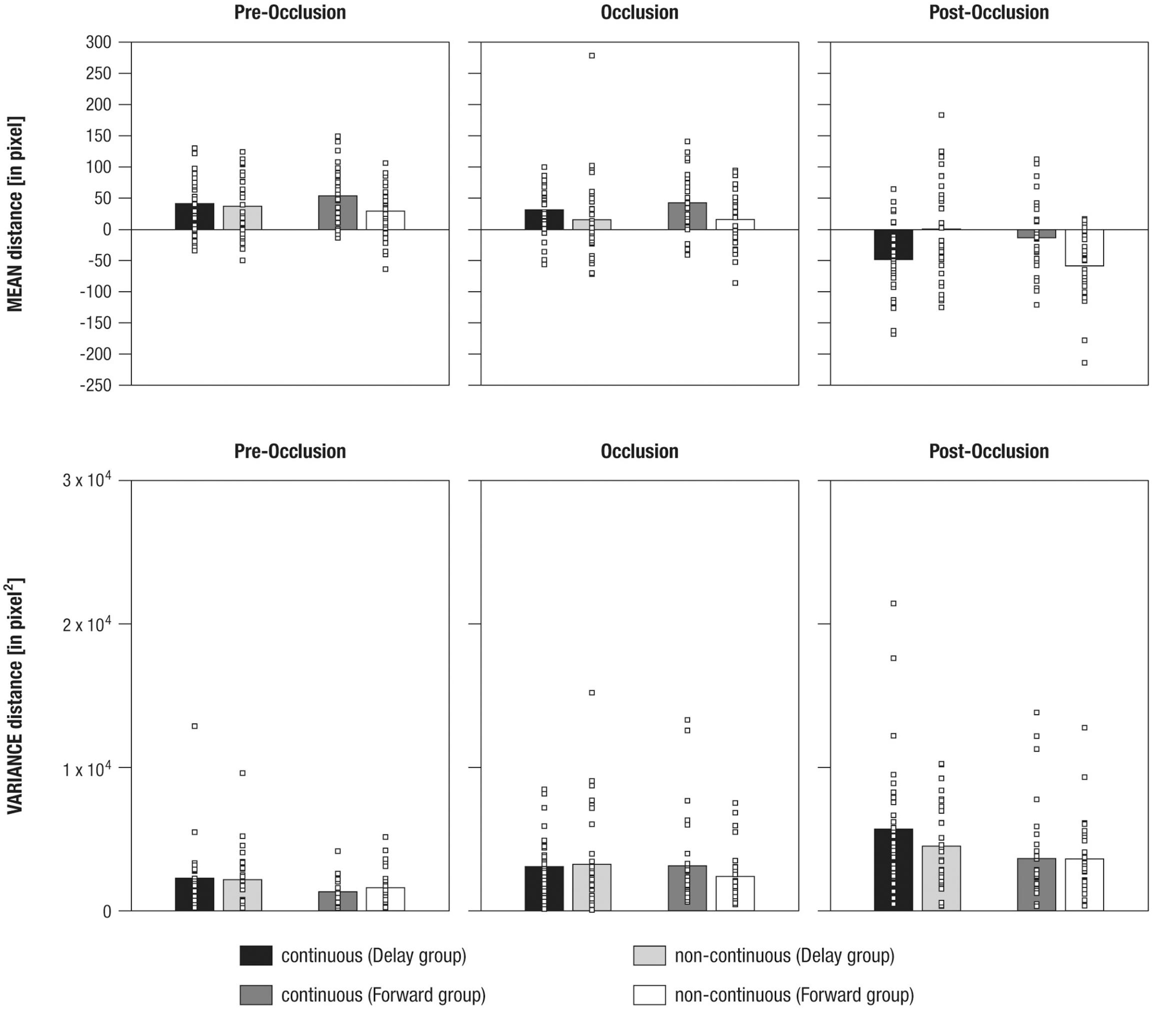

**FIGURE 5 |** Mean differences in mean distance **(Upper panel)** and variance in distance **(Lower panel)** between gaze positions and mean stimulus positions shown separately for experimental conditions (i.e., continuous in the Delay group, continuous in the Forward group, non-continuous in the Delay group, non-continuous in the Forward group), and phases (i.e., pre-occlusion, occlusion, and post-occlusion). Squares indicate single cases to demonstrate the distribution within the sample.

In sum, these results indicate that infants differentiated continuous from non-continuous movements following occlusion. However, as already indicated in the qualitative description of average distance over time (see Qualitative Description of Distance in Gaze and Stimulus Position over Time), continuous movement was apparently not tracked similarly across experimental groups: Corresponding to our hypotheses infants in the Forward group tracked continuous movements more accurately but undershot forwarded continuations. Counter to expectations, infants in the Delay group did not overshoot delayed, but undershot continuous movements.

### Statistical Analysis of Variance in Distance per Phase

To analyze the *variance in distance* as a marker of tracking consistency in 500 ms time windows before, during, and following occlusion, a mixed-effects repeated-measures ANOVA was calculated. This revealed significant main effects of the within-subjects factor (a) Phase [$F_{(1.7,104.2)} = 24.72$, $p = 0.000$, $\eta_p^2 = 0.29$] and the between-subjects factor (b) Group [$F_{(1,61)} = 4.69$, $p = 0.034$, $\eta_p^2 = 0.07$]. No further effects were found (all $F < 2.25$, all $p > 0.110$).

Using paired-sample *t*-tests to follow up on the main effect of (a) Phase indicated that variance in distance was highest during post-occlusion [$M = 4369.1$, $SE = 369.07$; all $t_{(62)} > 4.31$, all $p = 0.000$]. Variance in distance was also higher during occlusion ($M = 2958.11$, $SE = 295.13$) compared to pre-occlusion [$M = 1842.46$, $SE = 189.36$, $t_{(62)} = 3.54$, $p = 0.001$].

To follow-up on the main effect of (b) Group, an unpaired *t*-test showed that variance in distance was higher in the Delay group ($M = 3487.29$, $SE = 314.94$) than in the Forward group [$M = 2611.92$, $SE = 250.87$; $t_{(61)} > 2.16$, $p = 0.034$].

In sum, variance in distance increased due to transient occlusions. In addition, tracking was less consistent overall when infants watched continuous and delayed crawling versus continuous and forwarded crawling.

Taken together, both qualitative and statistical analyses of gazing behavior combine to provide a consistent picture: Results indicate that infants detected slight manipulations of the time course of an observed movement. Specifically, infants watching continuous and forwarded movements produced a tracking pattern consistent with the hypothesis of internal real-time simulation of observed movements during a transient occlusion (Graf et al., 2007). In contrast, infants watching continuous and delayed movements, albeit discriminating both conditions, produced a tracking pattern suggesting that real-time representations were not always precise (enough) or possibly altered by further processing (e.g., learned expectations across repeated presentations).

## EEG Data

### Frontal Theta Activity

To analyze mnemonic contributions to time-course representations, a mixed effects repeated-measures ANOVA was calculated for frontal theta activity. Results showed a significant main effect of Phase [$F_{(1.55,2.06)} = 5.72$, $p = 0.009$, $\eta_p^2 = 0.57$] without evidence for further effects (all $F < 1.41$; all $p > 0.250$). **Figure 6** and **Table 3** provide an overview of the EEG results. Hence, counter to expectations, no differential activation of frontal theta activity was found, indicating that the manipulation of the time course of ongoing movement did not elicit differential demands on memory processes.

### Central Alpha Activity

To analyze contributions from sensorimotor simulation to time-course representations, a mixed effects repeated-measures ANOVA was performed for central alpha activity. A significant interaction effect of Phase and Time occurred [$F_{(1.9,91.5)} = 3.61$, $p = 0.031$, $\eta_p^2 = 0.07$]. No further effects were observed (all $F < 2.14$, all $p > 0.123$).

As also implied by the small effect size, follow-up repeated measures ANOVAs separately per level of Phase, did not yield significant effects (all $F < 2.64$, all $p > 0.110$). From the inspection of results as displayed in **Figure 6** it may be concluded that, during post-occlusion, central alpha activity was lower for *non-continuous* than for continuous movements. Hence, in line with our hypothesis, our findings suggest that the cortical sensorimotor system is involved when infants render real-time simulations of transiently occluded movements that are within their motor repertoire.

# DISCUSSION

This study explored the internal representation of the *time course* of observed movement. To this end, 10-months-old crawling infants watched videos of a same-aged crawling baby that was transiently occluded and reappeared in a time-matching (i.e., continuous) or non-matching (i.e., delayed vs. forwarded) manner. To tap mnemonic and sensorimotor contributions to time-course representations, eye movement and rhythmic neural activity were simultaneously measured. First, the results suggest that sensorimotor functions were recruited more during the perception of non-matching continuations following occlusion. In contrast, there was no evidence for a differential role of mnemonic functions for time-course representations. Secondly, eye movements differentiated between time-matching and non-matching continuations following occlusion indicating a high sensitivity to the movements' time course. In sum, we conclude that 10-month-old infants generate internal movement representations that reflect the timing of observed movements. This corresponds to the internal real-time simulation account of action observation (Graf et al., 2007).

## Eye Movements Are Sensitive to the Time Course of Movements

To investigate infants' sensitivity to the time course of observed movements, we assessed eye-tracking patterns in response to a transiently occluded human movement. Our findings showed that 10-month-old infants distinguished between temporally matching and temporally shifted (i.e., delayed vs. forwarded) continuations following occlusion as demonstrated by differences in the mean distance in gaze and stimulus position.

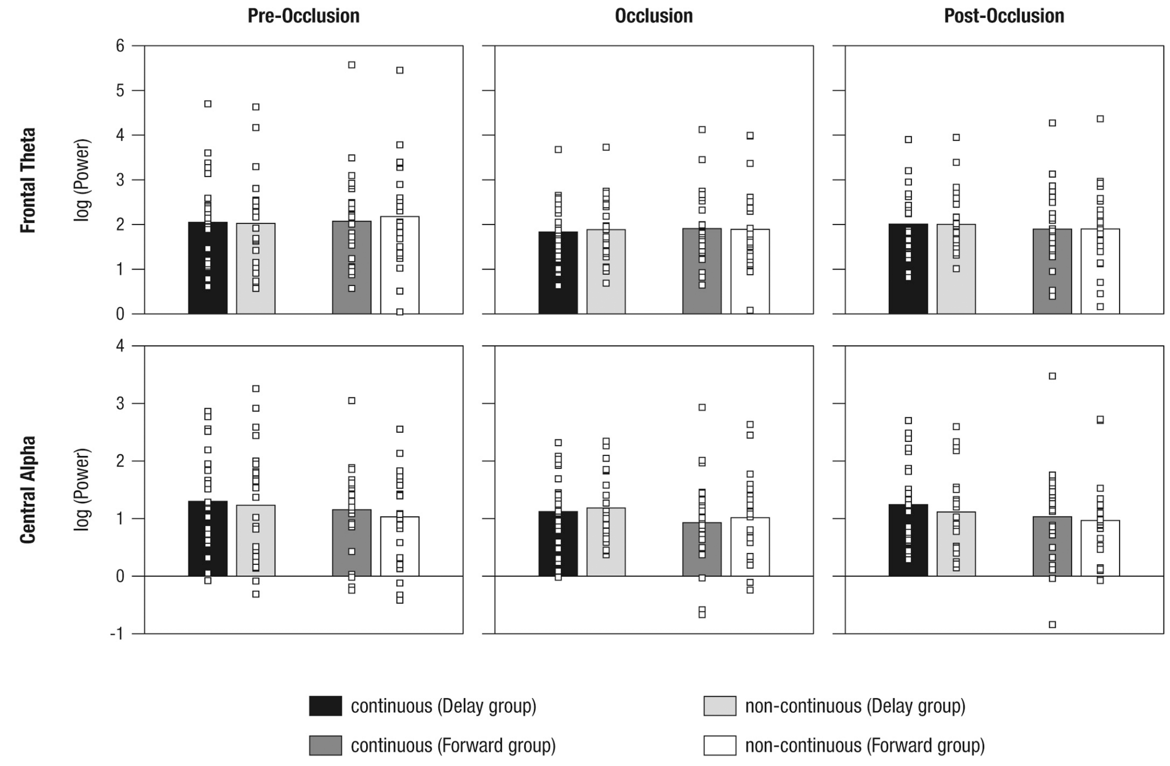

**FIGURE 6 |** Mean power differences between experimental conditions (i.e., continuous in the Delay group, continuous in the Forward group, non-continuous in the Delay group, non-continuous in the Forward group) and phases (i.e., pre-occlusion, occlusion, and post-occlusion) for frontal theta and central alpha activity. Squares indicate single cases to demonstrate the distribution within the sample.

**TABLE 3 |** Descriptives on mean power differences between experimental conditions.

| | | **FRONTAL THETA** | | | |
|---|---|---|---|---|---|
| | | **Delay group (*N* = 24)** | | **Forward group (*N* = 25)** | |
| **Phase** | **Condition** | ***M*** | ***SE*** | ***M*** | ***SE*** |
| Pre-occlusion | Continuous | 2.06 | 0.21 | 2.08 | 0.22 |
| | Non-continuous | 2.04 | 0.21 | 2.19 | 0.23 |
| Occlusion | Continuous | 1.84 | 0.14 | 1.92 | 0.16 |
| | Non-continuous | 1.89 | 0.15 | 1.90 | 0.19 |
| Post-occlusion | Continuous | 2.02 | 0.15 | 1.91 | 0.17 |
| | Non-continuous | 2.01 | 0.15 | 1.91 | 0.18 |
| | | **CENTRAL ALPHA** | | | |
| Pre-occlusion | Continuous | 1.30 | 0.17 | 1.16 | 0.15 |
| | Non-continuous | 1.23 | 0.20 | 1.03 | 0.16 |
| Occlusion | Continuous | 1.13 | 0.14 | 0.93 | 0.15 |
| | Non-continuous | 1.19 | 0.13 | 1.01 | 0.14 |
| Post-occlusion | Continuous | 1.25 | 0.15 | 1.03 | 0.16 |
| | Non-continuous | 1.12 | 0.15 | 0.97 | 0.14 |

*M, mean; SE, standard error of the mean.*

Previous studies have indicated that 4- to 7-month-old infants are largely insensitive to a manipulation in the timing of an object's motion during occlusion, in that temporal violations were only detected in extreme cases (i.e., instantaneous reappearance on the other side of an occluding board; Wilcox and Schweinle, 2003; Bremner et al., 2005). Only at the age of 2 years did toddlers' searching behavior demonstrate an understanding for the relation between time, velocity, and distance when a train went through a tunnel (Möhring et al., 2012). Adults were more accurate in identifying one of multiple moving objects when the objects instantaneously disappeared and reappeared at the position they had vanished or even before that position but not when the objects reappeared at a linearly extrapolated position along their movement trajectory (Keane and Pylyshyn, 2006). Nevertheless, the present study illustrates 10-month-old crawling infants' sensitivity to slight temporal shifts when observing videos of a crawling baby.

We can think of at least three possible reasons why infants in the present study were able to detect temporal changes. First, manipulation in the timing of an object's motion, as carried out in previous infant studies (Wilcox and Schweinle, 2003; Bremner et al., 2005), might be processed differently than manipulation in the timing of a *human action* because body form and dynamics offer rich information on, for instance, changes in velocity or direction (Hernik et al., 2014; Wronski and Daum, 2014). This notion corresponds to studies in adults showing that occluded human actions are internally simulated in real-time (Graf et al., 2007; Parkinson et al., 2012; Springer et al., 2013). Moreover, actions with natural human kinematics have been found to be more accurately predicted than those with artificial ones (Stadler et al., 2012). Similarly, proficient motor experience has been shown to enhance prediction of reappearance positions (Stapel et al., 2016).

Second, previous studies predominantly investigated object motion during the 1st months of life only (e.g., von Hofsten et al., 1998; Wilcox and Schweinle, 2003; Bremner et al., 2005), whereas the present study investigated human motion in 10-month-olds. Though the *developmental trajectory* of time-course representation is poorly understood to date, one may assume that older infants are better at solving temporal shifts in movement (cf Kopp, 2014), irrespective of the observed target.

Third, in most studies, data on infants' gazing behavior are reduced to a selection of putatively relevant aspects, for example, to overall looking time following habituation (e.g., Bremner et al., 2005) or to predictive looking at the end of an observed action (e.g., Henrichs et al., 2014). While the data reduction approach has doubtlessly provided interesting information, it may also have prevented researchers from discovering further early capabilities (see also Roberts, 2004). Here, *rich data* on the gaze progression over time were analyzed, demonstrating 10-month-old infants' spatiotemporal sensitivity while observing continuous and time-manipulated human movement that was within their own motor repertoire.

## Sensorimotor Processing Is Sensitive to the Time Course of Movements

To explore the neural basis of internal real-time processing, we assessed rhythmic neural oscillations related to mnemonic (i.e., frontal theta) and sensorimotor processing (i.e., central alpha) while infants were observing movements that were either time-matching or non-matching following a transient occlusion.

*Frontal theta* activity did not differ between time-matching and non-matching continuations. Thus, we found no evidence that slight time-course manipulations in ongoing movement pose differential mnemonic demands on 10-month-old infants. Frontal theta, as measured here, is thought to implement a neural accumulator (Bland and Oddie, 2001; van Vugt et al., 2012) assisting in maintaining and integrating extracted information across time and space (e.g., Miller and Cohen, 2001; Simons and Spiers, 2003). Correspondingly, it has been shown that, in 10-month-old infants, mnemonic functions support the binding of pre- and post-occlusion movement input into a coherent and unified percept (Bache et al., 2015). The present finding, however, modifies the notion of mnemonic contributions, suggesting that precise temporal representations for movement integration may not be provided by mnemonic functions alone (Wilson, 2001; Coppe et al., 2010).

For *central alpha* activity, we found a significant interaction effect between the timing of movement (i.e., continuous vs. non-continuous) across the phases of the trial (i.e., pre-occlusion, occlusion, post-occlusion). Although it was not possible to discern the direction of the effect in follow-up analyses, inspection of **Figure 6** suggests differences between time-matching and non-matching continuations following occlusion. Central alpha, as observed here, has been associated with sensorimotor simulation during movement observation (Cochin et al., 1999; Muthukumaraswamy et al., 2004; Marshall et al., 2011). Therefore, the present findings indicate sensorimotor involvement in the internal simulation of the timing of human movement. This interpretation is also supported by concurrent findings on eye movements (as described above), suggesting that the non-reliable differences in neural activity may not be due to infants' lacking capabilities to detect differences in movements' time courses.

Behavioral and neuroimaging studies in adults and infants suggest a crucial role of sensorimotor brain areas in timed internal simulation (e.g., Schubotz and von Cramon, 2002; Graf et al., 2007; Southgate et al., 2009; Stadler et al., 2011; Cross et al., 2012; Elsner et al., 2013; Springer et al., 2013; Stapel et al., 2016). Such a predictive function of the motor system may allow reduction of the processing delay in sensory–motor loops, which pose a fundamental challenge to proactive control of perception and behavior (e.g., Blakemore and Frith, 2005; Schubotz, 2007). However, simulating sensorimotor consequences in real-time may not (yet) be fast, stable, or precise enough in 10-month-old crawlers observing a crawling movement (see Wolpert and Flanagan, 2001).

## Further Considerations

Effects of either delayed or forwarded continuations were most obvious when comparing time-matching continuations between the two groups (Delayed and Forwarded). We assumed that, if occluded movement was internally simulated in real-time, infants would undershoot reappearance positions in forwarded continuations and overshoot them in delayed continuations, whereas infants would accurately track reappearance positions in continuous movements. Results showed that infants alternately watching continuous and forwarded movements produced a tracking pattern consistent with this hypothesis. However, infants alternately watching continuous and delayed movements undershot time-matching continuations and overshot delayed continuations. In fact, the tracking patterns of both experimental groups were found to be unexpectedly overlapping (see **Figure 4**): Infants watching continuous and delayed movements tracked the *continuous* movement in a similar way as infants watching continuous and forwarded movements tracked the *forwarded* movement. Vice versa, infants watching continuous and forwarded movements pursued the *continuous* movement in a similar way as infants watching continuous and delayed movements pursued the *delayed* movement. Moreover, tracking was less consistent across infants, when infants watched continuous and delayed continuations in contrast to continuous and forwarded continuations. Note, however, that the variation between conditions is a between subject comparison, i.e., two different groups of subjects performed delayed and forwarded conditions.

Though illustrating infants' remarkable sensitivity to an action's time course, these findings cannot solely be explained in terms of internal real-time processing. We can, however, only speculate as to which processes may have contributed to the pattern of results.

First, the present findings suggest that delayed and forwarded time-shifts in observed human action are not processed similarly (Bremner et al., 2005; Striano et al., 2006). This corresponds to adult studies showing that adults judged the continuation of actions following an occlusion to be continuous when it was in fact slightly delayed while slightly forwarded continuations were judged correctly as forwarded (e.g., Sparenberg et al., 2012). Switching from tracking external motion to internally representing motion may be costly and may thus lead to misaligned internal processing (Sparenberg et al., 2012; see also Mitrani and Dimitrov, 1978). In line with this notion, it is not obvious whether infants in the present study detected delayed continuations as manipulated in time. Future studies are needed to pinpoint the threshold at which time-matching and non-matching continuations are experienced as equal to determine potential *switching costs* early in life.

Second, the present findings may indicate that continuous movements are not always perceived as such (see also Adler et al., 2008). An influence of the stimulus context on action perception may be explained in accordance with *priming* effects (e.g., Pavlova and Sokolov, 2000). For example, when adults first performed a seemingly unrelated motor task (e.g., arm movement) and later observed movements corresponding to the motor task (i.e., arm movement) and non-corresponding (i.e., leg movement), the evaluation of the timing of movement continuations following occlusion was facilitated in corresponding conditions (Springer et al., 2013). Priming during action observation has also been reported in infant populations (e.g., Daum and Gredeback, 2011). From this perspective, non-matching conditions here may have served as the prime altering the processing of the time-matching condition. Future studies may disentangle whether and how time-shifted movements can change the perception of alternately presented continuous movements.

Third, it is possible that expectations based on *learning* across the repeated/blocked presentation of conditions may have contributed to the present results. This may be assumed because infants seem to have adapted their gaze position according to the expected reappearance position when approaching the occlusion offset (see **Figure 4**). Specifically, they looked slightly further back in delayed and slightly further forward in forwarded movements. In addition, following occlusion, there was a tendency to undershoot movements irrespective of the actual condition, which may be interpreted as an overall conservative strategy to stay on the target following a transient full-screen occlusions (cf. Stapel et al., 2016). At the same time, differences in tracking following occlusion suggest that infants did not learn that the stimulus' reappearance position was kept *identical* in all conditions (see Stimulus Material and Procedure). Future studies should clarify whether and how learning may contribute to internal time-course representations when infants observe repetitive human movements.

There was a considerable drop-out on the level of trials and participants in both eye and brain measures. *High attrition rates* of 25–75% are commonly observed in EEG studies with mobile infant populations (see de Haan, 2007; for a meta-analysis see Stets et al., 2012). In eye-tracking studies with infants, drop-out on the level of trials and participants has not been documented consistently. Concurrent preparation of both EEG and eye-tracking reduces potential testing time and challenges infants' compliance (e.g., see number of infants who could not be properly tested in Participants). Furthermore, both methods are sensitive to gross body and head movements that may result in a critical loss of data. In addition, eye-tracking is sensitive to repeated, persistent, and substantial changes in the position of the eyes (due to changes of head and/or body position), and measurement quality decreases over time in head-free recording (Holmqvist et al., 2011). At the same time, multiple repetition of the stimulus material is required for EEG to reduce noise in the signal. Therefore, it seems reasonable to assume comparable drop-out rates for eye-tracking and EEG data, and, potentially, overall higher attrition in simultaneous measurement in comparison to single measurement of either brain or eye data. Furthermore, not all participants can be expected to contribute (enough) data to both measures.

As a *consequence of high attrition*, it was not possible here to directly relate EEG and eye-tracking measures (see also Stapel et al., 2010). Furthermore, it cannot be excluded that attrition was selective for infants who complied better with testing requirements (e.g., Marshall et al., 2009) restricting the generalizability of effects. Moreover, due to infrequent and random contribution of data (see **Figure 1**), a systematic analysis of tracking over time (i.e., within and across blocks) was not conducted, because it would have required reducing the number of available trials and participants substantially.

From a methodological perspective, eye movements elicited during action perception add a source of artifacts to the EEG measurement potentially distorting the results. In adults, it has been shown that eye tracking data measured simultaneously with EEG can be used to identify and correct for those artifacts (e.g., Dimigen et al., 2011; Plöchl et al., 2012). In contrast, in infants, automated approaches to clean EEG of stereotypic artifacts are lacking. Here, we visually identified ICs representing eye movement related artifacts. Even though the ICA produced meaningful results in accordance with the adult literature, we cannot be certain whether artifacts were sufficiently removed in all data because eye and brain data could not directly be related as discussed above.

## CONCLUSION

In this study, an experimental paradigm previously used to investigate internal real-time processing during action perception in adults (e.g., Graf et al., 2007) was successfully adapted and applied to an infant population. We found that 10-month-old crawlers are able to detect slight manipulations of the timing of observed crawling movements as reflected in infants' tracking and neural patterns. This suggests a remarkable sensitivity to spatiotemporal information about external events early in life.

## ETHICS STATEMENT

The study was conducted in the Baby Laboratory at the Max Planck Institute for Human Development, Berlin, Germany. The study was approved by the Institute's Ethics Committee in accordance with the Declaration of Helsinki. Participants were recruited from a database of parents interested in participating in infant studies at the Max Planck Institute for Human Development. Parents gave their written informed consent upon arrival.

## AUTHOR CONTRIBUTIONS

CB, AS, WS, FK, and UL conceived and designed the study, CB collected the data, CB, HN, and MW-B analyzed and interpreted the data, CB drafted the manuscript, all authors revised the work and approved the final version for publication.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fpsyg.2017.01170/full#supplementary-material

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# Reduced Mu Power in Response to Unusual Actions Is Context-Dependent in 1-Year-Olds

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During social interactions infants predict and evaluate other people's actions. Previous behavioral research found that infants' imitation of others' actions depends on these evaluations and is context-dependent: 1-year-olds predominantly imitated an unusual action (turning on a lamp with one's forehead) when the model's hands were free compared to when the model's hands were occupied or restrained. In the present study, we adapted this behavioral paradigm to a neurophysiological study measuring infants' brain activity while observing usual and unusual actions via electroencephalography. In particular, we measured differences in mu power (6 – 8 Hz) associated with motor activation. In a between-subjects design, 12- to 14-month-old infants watched videos of adult models demonstrating that their hands were either free or restrained. Subsequent test frames showed the models turning on a lamp or a soundbox by using their head or their hand. Results in the hands-free condition revealed that 12- to 14-month-olds displayed a reduction of mu power in frontal regions in response to unusual and thus unexpected actions (head touch) compared to usual and expected actions (hand touch). This may be explained by increased motor activation required for updating prior action predictions in response to unusual actions though alternative explanations in terms of general attention or cognitive control processes may also be considered. In the hands-restrained condition, responses in mu frequency band did not differ between action outcomes. This implies that unusual head-touch actions compared to hand-touch actions do not necessarily evoke a reduction of mu power. Thus, we conclude that reduction of mu frequency power is context-dependent during infants' action perception. Our results are interpreted in terms of motor system activity measured via changes in mu frequency band as being one important neural mechanism involved in action prediction and evaluation from early on.

**Keywords: EEG, infants, action perception, action understanding, mu frequency, mirror neuron system**

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## INTRODUCTION

From birth on, infants take part in social interactions. These interactions with others are essential for the development of social-cognitive skills (Striano and Reid, 2006). An important ability trained in such interactions is to predict another person's behavior and to react accordingly. This ability comprises that if the prediction turns out to be wrong (prediction error), the corresponding representation is updated appropriately (Kilner et al., 2007). Even though it is well established that the underlying action understanding starts developing early in life (Gredebäck and Daum, 2015), many open questions regarding its mechanisms remain. In the current study, we present evidence that motor activation in the mu frequency band is involved in infants' action processing in the context of unknown objects and that infants take into account visible action constraints when evaluating actions on unknown objects.

Action understanding consists of both the ability to predict and to evaluate others' actions (Gredebäck and Daum, 2015). The ability to *predict* what others will do next has been observed from 6 months on. By this age, infants show predictive eye movements to a target location of a goal-directed action involving everyday objects (e.g., phone or cup). In the second half of their 1st year, they predict more general action goals such as putting a ball into a bucket or bringing food or a cup to another person's mouth (Falck-Ytter et al., 2006; Gredebäck and Melinder, 2010; Hunnius and Bekkering, 2010). The ability to *evaluate* actions has also been observed from 6 months on. Action evaluation is usually measured following the execution of an either expected or unexpected action (Gredebäck and Daum, 2015). Looking time studies demonstrate that infants look longer at actions with unexpected changes in the goal of a directional action (e.g., Woodward, 1998; Reid et al., 2007). Measuring pupil dilation in response to usual vs. unusual actions offers another method to gain insight into infants' action evaluation. Pupil dilation usually follows after attention grabbing or unusual events (Libby et al., 1973). Gredebäck and Melinder (2010) found that 6- and 12-month-old infants' pupils dilated in response to unusual feeding actions (e.g., spoon with food put to the hand). Hence, we already know that infants predict and evaluate another person's behavior indicating a quite elaborate action understanding that emerges during the 1st year of life. Behavioral imitation studies provide yet another approach to examine infants' action understanding, but are often used with slightly older children (e.g., Gampe et al., 2016). Interestingly, behavioral studies show that infants do not imitate every action they observe. They do so selectively depending on characteristics of the model, such as his or her reliability (Zmyj et al., 2010), group membership (Buttelmann et al., 2013) or external factors such as situational constraints (Gergely et al., 2002).

Gergely et al. (2002) investigated how infants imitate another person's action according to efficiency and situational constraints. The authors found that 14-month-old infants were more likely to imitate an unusual head-touch action (i.e., turning on a lamp using the head) when the model's hands were free compared to when her hands were occupied by holding a blanket. Gergely et al. (2002) concluded that this is because infants evaluated actions according to their efficiency or rationality in the given situation (Gergely and Csibra, 2003). This finding was replicated using similar paradigms and designs, and by testing even younger age groups (Schwier et al., 2006; Buttelmann et al., 2008; Zmyj et al., 2009; Gellén and Buttelmann, 2017). In particular, Zmyj et al. (2009) showed that 12- but not 9-month-old infants considered non-voluntary physical restraints (i.e., model's hands tied to the table) when imitating unusual head-touch actions. However, divergent interpretations relating infants' selective imitation behavior to more basic attention processes or motor resonance (i.e., to map others' actions onto one's own motor repertoire) have been brought forward (Paulus et al., 2011a,b; Beisert et al., 2012; but see also Buttelmann and Zmyj, 2012; Buttelmann et al., 2017).

Thus, in the present study, we measured infants' neural responses when observing head-touch actions similar to the original paradigm by Gergely et al. (2002) in order to investigate possible neural mechanisms, particularly the role of motor activation during the observation of unusual actions. In contrast to previous imitation studies, we did not focus on behavioral responses (i.e., imitation rates) as dependent variable, but rather explored the role of motor activation in infants' brains. The rationale of this approach is that selective motor activation during action observation is likely to be involved in action understanding, as action understanding is shaped by action skills. In particular, Hunnius and Bekkering (2014) found that any progress in motor development is typically associated with improved action understanding, resulting mainly from actively experiencing motor actions (see also Sommerville et al., 2005). This is in accordance with results that suggest that 10-month-olds' motor actions develop ahead of their ability to predict action outcomes (Rosander and von Hofsten, 2011). In addition, Stapel et al. (2016) showed that infants who were experienced crawlers but not yet walkers were more accurate in predicting crawling actions than walking actions in an eye-tracking experiment (see also the eye-tracking study by Bache et al., 2017).

These studies suggest that one of the functional mechanisms underlying action understanding is the mirror neuron system (MNS). Mirror neurons discharge during both action observation and action execution (Rizzolatti et al., 2001; Rizzolatti and Craighero, 2004). Thus, observed actions seem to activate motor processes or schemas in the observer's brain that would also be activated if the person executed the action themself (Prinz, 1997). Consequently, this motor system might be highly relevant for action prediction and evaluation (Wolpert and Flanagan, 2001; Prinz, 2006; Kilner et al., 2007).

One neural marker indicating motor activation and activation of the MNS during action observation and execution is the mu rhythm in the electroencephalogram (EEG) across central electrode sites. Mu rhythm activity has been examined in adults (e.g., Muthukumaraswamy et al., 2004; Lepage and Theoret, 2006) and in infants (e.g., van Elk et al., 2008; Southgate et al., 2009; Stapel et al., 2010; Marshall and Meltzoff, 2011; Cuevas et al., 2014). It is measured in the standard alpha frequency band (for adults at about 8–13 Hz and for infants at about 6–9 Hz) and is thought to reflect sensorimotor cortical activation (for a meta-analysis on EEG mu rhythm, see Pfurtscheller and Da Silva, 1999; Pineda, 2005; Fox et al., 2016). In particular, a suppression or desynchronization in the mu frequency band is associated with motor activation during action observation and execution. The decreasing mu power with movement onset indicates a decrease in neuronal synchrony reflecting the processing of movement-related information. Thus, mu rhythm is often interpreted as a neural correlate representing a link between action perception and production (Muthukumaraswamy et al., 2004).

Several infant studies suggest that the infant central mu rhythm is analogous to the adult mu rhythm (Marshall and Meltzoff, 2011). Southgate et al. (2009) demonstrated stronger mu desynchronization for observation and execution of reaching actions relative to baseline in 9-month-old infants. A second study showed similar results and reported stronger mu desynchronization in response to a reaching hand in a grasping posture even when the action outcome was not visible (Southgate et al., 2010). Thus, mu desynchronization additionally reflects infants' prediction of the motor program of an anticipated action. Furthermore, significantly stronger mu desynchronization compared to baseline was found in 14-month-olds for the observation and execution of button presses in a live EEG paradigm (Marshall et al., 2011).

Mu desynchronization in infants seems to depend on active experience and, thus, on whether or not an action is already in the infants' motor repertoire (van Elk et al., 2008; Gerson et al., 2015). In this line, spectral power in the 7–9 Hz frequency band was more suppressed in 14- to 16-month-olds for the observation of crawling compared to walking (van Elk et al., 2008). This effect was highly related to infants' own crawling experience in that more experienced crawlers showed stronger mu desynchronization. In addition, mu desynchronization was sensitive to bidirectional action-effect associations (of sounds and rattles) in 8-month-olds (Paulus et al., 2012). In sum, this branch of research indicates that motor activation measured by mu desynchronization depends on experience with stronger reduction of mu frequency power occurring for more familiar or trained actions.

In addition, mu desynchronization can be related to generating action predictions (Stapel et al., 2010; Saby et al., 2012). Stapel et al. (2010) found stronger mu desynchronization on fronto-central and mid-frontal channels in 12-month-olds in response to extraordinary actions (e.g., lifting a cup to the ear) compared to ordinary actions (e.g., lifting a cup to the mouth). The authors interpreted this result by applying the theory of predictive coding (Kilner et al., 2007): According to this theory, the MNS forms predictions about another person's action given an assumed goal. The MNS constantly checks whether the predicted action goal still matches what is being observed. For unusual action outcomes, like putting a cup to the ear, there is a mismatch between prediction and observation. Consequently, a new prediction has to be generated and this results in stronger motor activation (Gardner et al., 2015).

To summarize, analyzing mu frequency band power allows us to investigate infants' action processing. While studies on infants' own action experiences reported increased motor activation when observing more familiar actions, studies manipulating action outcomes found that unexpected outcomes elicit a stronger mu desynchronization than expected outcomes. Thus, the mu frequency seems to be involved in both motor resonance depending on action experiences and on action prediction. However, previous research predominantly investigated mu frequency power in response to actions with familiar objects (e.g., a cup or food). This offers us a unique opportunity to study the cognitive processes during infants' observation of head-touch actions with novel objects as used in previous behavioral studies on selective imitation. In particular, reduced mu power during unusual head-touch actions (compared to hand-touch actions) would speak for the induction of a prediction error while watching these actions in the absence of situational constraints. On the other hand, stronger mu suppression in response to hand actions would argue for the role of previous motor experience in processing these actions, since infants much more frequently manipulate objects with their hands.

Thus, this is the first study investigating the neural mechanisms underlying the observation of an unusual head touch in adaptation to paradigms previously used in imitation studies (Gergely et al., 2002; Zmyj et al., 2009). Here, we explored possible neuronal mechanisms that might have influenced selective imitation demonstrated in previous studies. In addition, we aimed to elucidate whether these neural mechanisms are sensitive to the action context or not (cf. Zmyj et al., 2009). To examine infants' neural processing, we designed an EEG study measuring context-dependent motor system activity via mu frequency power during infants' perception of different action outcomes. In a between-subjects design, 12- to 14-month-olds watched short video sequences of models demonstrating that their hands were free (hands-free condition) or restrained (hands-restrained condition). Subsequent test frames showed the same model turning on a lamp or soundbox using either their head or their hand. We intended to explore whether there were differences in mu power between processing of head- and hand-action outcomes in the hands-free condition and whether mu power varied depending on situational constraints in the hands-restrained condition.

We hypothesized that if prediction error and updating (cf Kilner et al., 2007; Stapel et al., 2010) take place when infants observe others using their head rather than their hand to manipulate an object, then reduced mu power on central channels in response to head actions compared to hand actions should occur in the hands-free condition. In the hands-restrained condition, we expected the opposite result pattern if infants incorporate situational factors while predicting and evaluating action outcomes (i.e., reduced mu power in response to hand compared to head actions). If motor experience influences mu frequency power (van Elk et al., 2008; Gerson et al., 2015), then lower mu power indicating motor resonance in response to familiar hand actions compared to less familiar head actions should be demonstrated in the hands-free condition and possibly also in the hands-restrained condition. If infants do not take into account context information, then results should be similar in both the hands-free and the hands-restrained condition.

## MATERIALS AND METHODS

### Participants

The final sample consisted of 22 12- to 14-month-old infants (11 girls, *M* = 13 months 2 days, *SD* = 23 days, age range = 12 months 5 days – 14 months 24 days) in the hands-free condition and 20 infants (9 girls, *M* = 12 months 25 days, *SD* = 22 days, age range = 12 months 1 day – 14 months 29 days) in the hands-restrained condition. Infants were recruited from a midsized

German city and surrounding areas. They were from middle-class background, born full-term (37–41 weeks of gestation), Caucasian and without any known neurological problems. In addition, 32 infants were tested but excluded from the final sample due to fussiness (i.e., infants showed too many movement artifacts or started crying before being presented with the required number of trials), another 39 infants failed to provide 10 artifact-free trials per within-subjects condition, in 4 additional infants contact of the reference electrode was not satisfactory (i.e., very spiky signal of all electrode channels) and in two sessions technical and experimental errors occurred. This attrition rate is within the typical range for infant EEG studies of 50–75% (e.g., DeBoer et al., 2007; Stets et al., 2012). The loss of participants mainly resulted from 12- to 14-month-olds' difficulty to sit motionless during the presentation of multiple trials, as it is required for acquiring valid EEG data. There is no indication for a systematic distortion of our sample. Informed verbal and written consent were obtained from each participant's parent before conducting the experiment. Infants received a certificate with their photo for participation. Experimental procedures were approved by the ethics committee of Friedrich Schiller University in Jena (reference 3752-04/13).

## Stimuli

Infants were presented with video clips and photographs showing adult models performing head or hand actions (adapted from Gergely et al., 2002; Zmyj et al., 2009). Two different types of videos were used: To establish context and motivation at the beginning of the experiment, infants watched two pre-demonstration videos showing a female or male adult sitting at an empty table demonstrating that the hands were free or restrained by turning them. Each participant watched both videos in randomized order regarding sex of the model and situational constraints.

Following the pre-demonstration videos, each trial of the demonstration-phase videos illustrated the action context depicting one of four models (two males, two females) sitting at a table with a touch light in front of them. Subsequent test frames depicted action outcomes. In the hands-restrained condition (adapted from Zmyj et al., 2009), the model's hands were tied to the table with duct tape and could not be moved freely. In the hands-free condition, a line of duct tape was visible on the table but the model's hands were free. In both conditions, subsequent test frames showed a model turning on a lamp using either their hand or their head (see **Figure 1**). The model did not establish eye contact with the observer during the whole experiment. In half of the trials, a round lamp (12 cm diameter) mounted on a black box (27 cm × 20 cm × 6 cm) was illuminated while the model was touching it (cf Meltzoff, 1988). To increase infants' attention toward the presentation, in the other half of trials a toy-squeezing sound was generated while the model was touching a blue and green soundbox (13 cm × 13 cm × 11.5 cm) (in accordance with Buttelmann et al., 2007). The sound was presented with a maximum intensity of 75 dB.

In the test frames, the model was presented on screen with a width of approximately 9.13 cm (visual angle of 9.49°) and a height of 10.34 cm (visual angle of 10.74°) measured from head to table. The touch light was presented with a size of 4.6 cm × 8.4 cm (visual angle of 4.79° × 8.73°) and the soundbox with a size of 4 cm × 4.5 cm (visual angle of 4.17° × 4.69°). Test frames were adjusted to each other with Adobe Photoshop CS4 extended in terms of brightness and contrast (all $ps > 0.05$). **Figure 1** depicts example trials in which the model turns on the light or produces a sound by using either his or her hand or head in both conditions.

## Procedure

Infants were tested individually in a quiet, dimly lit room. The testing area was separated from the rest of the laboratory by dark blue colored room dividers. Infants sat on their parent's lap in front of a 75 Hz 19-inch stimulus monitor with a viewing distance of 55 cm. Parents were instructed not to interact with the infant during data collection. In both the hands-free and hands-restrained condition, the experiment consisted of one block of a maximum of 120 trials. This block comprised 60 trials illustrating a hand touch and 60 trials illustrating a head touch. The videos were displayed in semi-randomized order via the software Presentation (Neurobehavioral Systems, Albany, CA, United States) with the constraint that the same modality (light/sound), gender (male/female) or outcome (hand touch/head touch) were not presented three times consecutively and that all 16 possible test pictures (light/sound, head touch/hand touch, for each of the four models) were displayed within the first 48 trials. To avoid confounding effects of the first observed action, action outcomes (head and hand touch) were counterbalanced between participants in the first trial of each condition.

**Figure 1** shows an exemplary stimulus trial sequence. At the beginning of the trial, a central attractor was presented for an average of 1000 ms to catch infants' attention. The subsequent video sequence depicted the model showing that the hands were free or restrained by wiggling for 5000 ms. After that, a blank screen was presented for a random period between 800 and 1000 ms. Lastly, the test frame representing hand- or head-action outcomes was presented for 1500 ms. Each trial lasted 8500 ms leading to a maximum total testing time of 17 min. Short breaks could be taken after the end of a trial, when the infant became tired or fussy. The session ended when the infant no longer attended to the screen. EEG activity was recorded continuously and infants were video-recorded throughout the experiment for offline coding of looking behavior and movements.

## EEG Recording and Analyses

Electroencephalogram was measured by a 32-channels ActiCap system (Brain Products, Gilching, Germany) with 32 active silver/silver chloride (Ag/AgCl) electrodes arranged according to the 10–10 system. Horizontal and vertical electrooculograms were recorded bipolarly. Impedances were controlled at the beginning of the experiment and accepted when below 20 kΩ. Sampling rate was set at 250 Hz. Electrode signals were referenced to the right mastoid electrode and amplified via a BrainAmp amplifier.

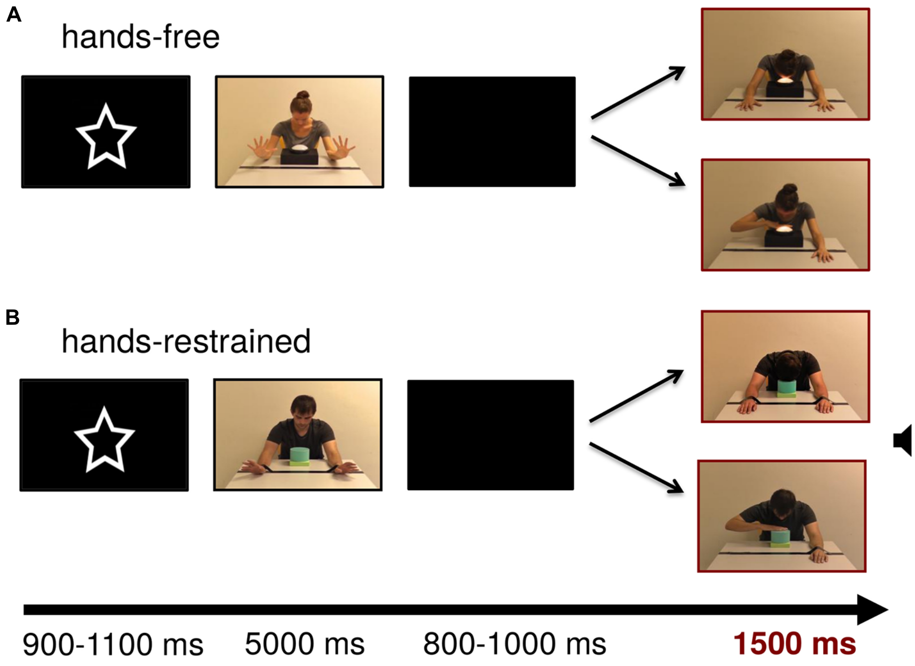

**FIGURE 1 |** Stimulus examples of lamp and sound modality for **(A)** hands-free and **(B)** hands-restrained condition. Persons appearing in this figure consented to the publication of these images.

## EEG Preprocessing

Electroencephalogram data were first processed by using BrainVision Analyzer 2 (Brain Products, Gilching, Germany) and further analyzed in Fieldtrip (Oostenveld et al., 2011). Raw data were filtered off-line with a 0.3–30 Hz band-pass filter to remove frequencies not related to cortical processes of interest. Data were then re-referenced to the average mastoids (TP9, TP10). Data were automatically excluded if the amplitude of the analyzed channels exceeded a voltage threshold of 200 μV within a 200 ms interval. Thus, data including gross motor movements were rejected from final analysis by this automatic artifact rejection algorithm. Data were then segmented into epochs of waveforms that comprised 200 ms before stimulus onset of the test frame, demonstrating a head touch or a hand touch, through 1500 ms following stimulus onset. Infants' looking behavior was video-coded offline. Only trials in which infants did not blink and paid attention to the whole presentation of the test frame, showing head- and hand-action outcomes, were included in further analyses. In addition, videos were coded for more subtle movements of infants, such as hand or head movements that resembled actions performed by the video models in our stimuli (i.e., pressing a button by hand or by head or similar actions, like reaching or pointing) (cf Marshall et al., 2011). An independent rater, blind to hypotheses, coded infants' movements during all observed action outcomes. An additional coder rated 25% of the videos from each condition (hands-free and hands-restrained). A high degree of inter-rater reliability was found between 758 measurements with an average measure intraclass correlation (ICC) of 0.840. To ensure that motor activation related to the target actions (head touch and hand touch) was equivalent between conditions (hands-free and hands-restrained) and within conditions, we conducted a mixed analysis of variance (ANOVA) with the between-subjects factor *condition* (hands-free, hands-restrained) and the within-subjects factor *outcome* (target action movement during head-touch outcomes, target action movement during hand-touch outcomes). The ANOVA did not yield a significant main effect of *outcome*, $F(1,40) = 2.394$, $p = 0.130$, or *condition*, $F(1,40) = 0.985$, $p = 0.327$. Likewise, no significant interaction between *condition* and *outcome* was found, $F(1,40) = 2.394$, $p = 0.130$. Overall, infants very rarely performed actions similar to the hand and head touch demonstrated by the video models during the whole experiment ($M = 1.69$ movements, $SD = 1.62$ movements). Thus, significant differences between conditions and/or action outcomes cannot result from differences in infants' movements similar to the presented target actions (hand and head touch). Data were then baseline-corrected using 200 ms prior to the onset of the test frame and finally segmented for hand and head touch in both hands-free and hands-restrained conditions, respectively.

## Frequency Domain Analysis

Artifact-free data segments were submitted to fast Fourier transformations (FFTs). For each segmented test frame (hand or head touch), the power spectral density (PSD) was computed from 0 to 1500 ms relative to the onset of the related stimulus using a Hanning-tapered window of the same length (by applying the 'ft_freqanalysis' function with 'mtmfft' method as implemented in Fieldtrip). Power estimates were calculated for frequencies ($\frac{2}{3}$ Hz bins) between 0 and 124.667 Hz. Grand averages of the FFTs were computed for both hand- and

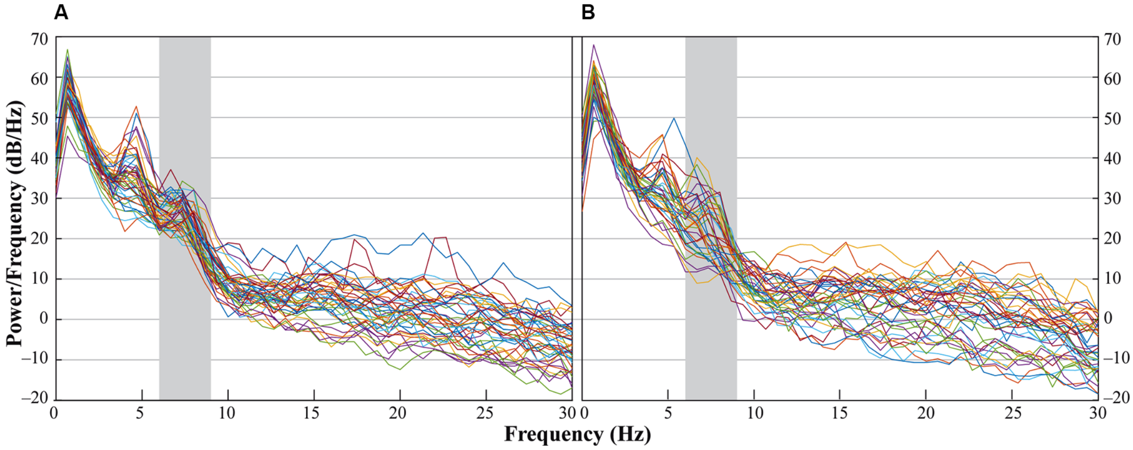

**FIGURE 2 |** Individual power spectra across an average of hand- and head-touch actions and across an average of frontal and central electrodes (F3, F4, C3, C4) for **(A)** hands-free and **(B)** hands-restrained condition.

head-action outcomes in the hands-free and hand-restrained condition.

A minimum of 10 artifact-free trials per outcome was required for an infant to be included in the statistical analyses. In the hands-free condition, each infant contributed 13 to 56 trials ($M = 21.23$, $SD = 9.88$) to the head outcome and 11 to 56 trials ($M = 19.18$, $SD = 9.81$) to the hand outcome. In the hands-restrained condition, each infant contributed 10 to 34 trials ($M = 17.25$, $SD = 5.87$) to the head outcome and 10 to 29 trials ($M = 16.05$, $SD = 5.45$) to the hand outcome. Across conditions each infant contributed 10 to 56 ($M = 19.33$, $SD = 8.36$) valid trials to the head outcome and 10 to 56 valid trials to the hand ($M = 17.69$, $SD = 8.10$) outcome.

In accordance with previous research we analyzed central electrode positions on the left and right hemisphere (C3, C4) to investigate differences in motor activation indicated by mu frequency power (e.g., Paulus et al., 2012). As visual inspection indicated differences between unusual head-touch and familiar hand-touch actions especially on frontal channels and as previous studies also investigated the role of frontal activation in infants' action perception (e.g., van Elk et al., 2008; Stapel et al., 2010), we included lateral frontal channels (F3, F4) into the final analysis. In addition, parietal channels P3 and P4 were included in the analysis in order to exclude the possibility that potential alpha-band effects were widespread across the scalp (including posterior regions) suggesting general arousal rather than involvement of the motor system. Occipital channels (O1, O2) were not selected for comparison to fronto-central electrode positions because channels were too noisy and did not provide enough artifact-free data for valid analyses. For each participant, a dominant mu peak was identified for frontal and central electrodes (F3, F4, C3, C4) between 6 and 9 Hz. Analyses revealed that in the hands-free condition up to 20 infants peaked between 6.7 and 8 Hz in response to the hand touch and up to 19 infants in response to the head touch (see **Figure 2A**). Similarly, in the hands-restrained condition up to 15 infants peaked in response to the hand touch and 15 infants in response to the head touch between 6.7 and 8 Hz (see **Figure 2B**). This is in accordance with previous research on mu frequency in infants indicating that mu frequency band falls between 6 to 9 Hz in infants (Marshall and Meltzoff, 2011) and peaks at about 8 Hz in 1-year-olds (Marshall et al., 2002). Thus, the statistical analyses were conducted across the average power of the 6 to 8 Hz frequency range.

### Statistical Analysis

To investigate overall differences between conditions, data were analyzed by a mixed ANOVA with the between-subjects factor *condition* (hands-free, hands-restrained) and the within-subjects factors *action outcome* (head, hand), *region of interest* (frontal: F3/F4, central: C3/C4, parietal: P3/P4) and *hemisphere* (left, right). Partial eta squared ($\eta_p^2$) or Cohen's $d$ ($d$) are reported as estimates of the effect size. Greenhouse-Geisser correction for non-sphericity was employed if applicable for conservative corrections. Fractional degrees of freedom ($df$) were reported when Greenhouse-Geisser correction was necessary (i.e., when Mauchly's test for sphericity was significant) and applied. The significance level was set at $p < 0.05$ (two-tailed) for all statistical analyses.

## RESULTS

### Hands-Free vs. Hands-Restrained Condition

To compare results between the hands-free and hands-restrained condition, we first computed a mixed ANOVA with the between-subjects factor *condition* (hands-free, hands-restrained) and the within-subjects factors *action outcome* (head, hand), *region of interest* (frontal, central, and parietal) and *hemisphere* (left, right). Analysis yielded a significant interaction between *condition*, *action outcome*, *region of interest*

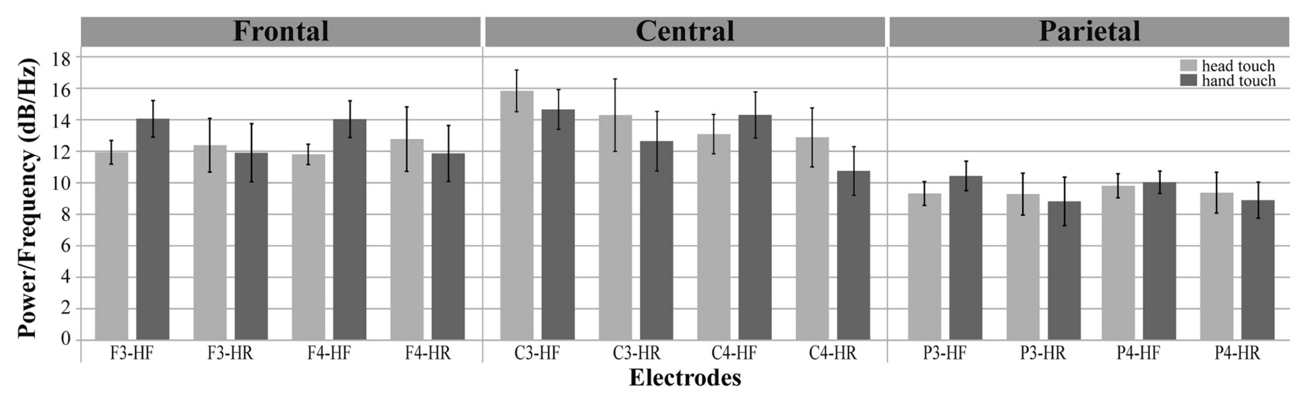

**FIGURE 3 |** Grand average EEG power across mu frequency band (6–8 Hz) for electrodes of interest (F3, F4, C3, C4, P3, P4) in response to hand touch (dark gray) and head touch (light gray) for both hands-free (HF) and hands-restrained (HF) condition. Error bars represent standard errors of the mean.

and *hemisphere*, $F(2,80) = 3.390$, $p = 0.039$, $\eta_p^2 = 0.08$ (for a detailed illustration of main effects and interactions, see Supplementary Table 1). Thus, conditions were further analyzed separately to explain this interaction effect. Mu power of all electrodes of interest (F3, F4, C3, C4, P3, P4) is plotted in **Figure 3**.

## Hands-Free Condition

Infants demonstrated dominant peaks in response to observing head- and hand-action outcomes in the frequencies of interest (6–8 Hz) especially on frontal and central electrodes (see **Figure 2A**). Visual inspection of the grand average FFTs indicated reduced mu power in response to the head touch compared to the hand touch. This tendency was more pronounced on frontal electrodes (see **Figure 4**).

The repeated-measures ANOVA (rmANOVA) revealed a significant interaction of *action outcome*, *region of interest* and *hemisphere*, $F(2,42) = 6.918$, $p = 0.003$, $\eta_p^2 = 0.25$ (for a detailed illustration of main effects and interactions, see Supplementary Table 2). In order to resolve this significant interaction, we conducted three two-way rmANOVAs with the within-subjects factors *action outcome* (head, hand) and *hemisphere* (left, right) for each region of interest. For frontal channels (F3, F4), we found a significant main effect of *action outcome*, $F(1,21) = 8.675$, $p = 0.008$, $\eta_p^2 = 0.29$, indicating that mu power in both frontal electrodes was significantly lower in response to head-touch outcomes ($M = 11.87$, $SD = 2.96$) compared to hand-touch outcomes ($M = 14.05$, $SD = 5.35$) independent of *hemisphere*, $F(1,21) = 0.28$, $p = 0.868$. Analysis of frontal regions did not reveal a significant interaction between *action outcome* and *hemisphere*, $F(1,21) = 0.044$, $p = 0.836$. For central channels (C3, C4), the rmANOVA analysis yielded a significant interaction of *action outcome* and *hemisphere*, $F(1,21) = 7.990$, $p = 0.010$, $\eta_p^2 = 0.28$. *Post hoc* *t*-tests for left (C3) and right (C4) hemisphere compared mu frequency power of hand- and head-action outcomes. On the right hemisphere mu power was slightly lower in response to head-touch ($M = 13.09$, $SD = 5.86$) compared to hand-touch outcomes ($M = 14.31$, $SD = 6.89$). However, it did not reach significance, $t(21) = -1.932$, $p = 0.067$, $d = 0.41$. No significant differences in mu power were found on the left hemisphere, $t(21) = 1.175$, $p = 0.253$. For parietal channels (P3, P4), the rmANOVA did not reveal a significant main effect of *action outcome*, $F(1,21) = 1.076$, $p = 0.311$, *hemisphere*, $F(1,21) = 0.004$, $p = 0.952$, nor a significant interaction between *action outcome* and *hemisphere*, $F(1,21) = 1.869$, $p = 0.186$.

Thus, we found reduced mu power in response to head-touch actions compared to hand-touch actions especially on frontal electrode positions and a tendency for the same effect at the right central electrode site.

## Hands-Restrained Condition

In the hands-restrained condition we investigated whether infants incorporate contextual information while evaluating action outcomes via the motor system measured by differences in mu frequency power. Comparable to the hands-free condition, the majority of infants peaked in response to observing head- and hand-action outcomes in the frequencies of interests (6 – 8 Hz) especially on frontal and central electrodes (see **Figure 2B**). Visual inspection indicated increased mu power in response to the head touch and reduced mu power in response to the hand touch (see **Figure 5**).

We again conducted a rmANOVA with the within-subjects factors *action outcome* (head, hand), *region of interest* (frontal, central, parietal) and *hemisphere* (left, right). There were, however, no significant interactions of *action outcome*, *region of interest*, and *hemisphere*, all $ps > 0.29$. Likewise the analyses did not reveal main effects of *action outcome*, $F(1,19) = 1.601$, $p = 0.221$ or *hemisphere*, $F(1,19) = 0.753$, $p = 0.396$. We only found a significant main effect of *region of interest*, $F(2,27.25) = 15.220$, $p < 0.001$, $\eta_p^2 = 0.45$, indicating that across action outcomes overall mu power was lower at parietal regions ($M = 9.09$, $SD = 5.49$) than at frontal ($M = 12.23$, $SD = 7.60$) and central regions ($M = 12.64$, $SD = 7.79$). In sum, results showed no differences in mu power between head and hand touch in the hands-restrained condition.

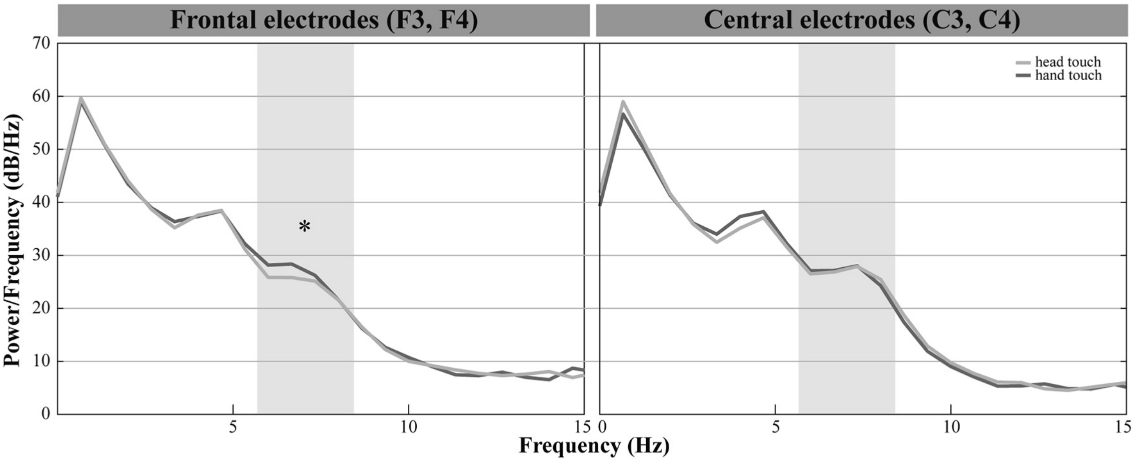

**FIGURE 4 |** Grand average EEG mu power for hand touch (dark gray) and head touch (light gray) for an average of frontal electrodes (F3, F4) and for an average of central electrodes (C3, C4) in the hands-free condition. Asterisks depict significant differences with $p < 0.05$.

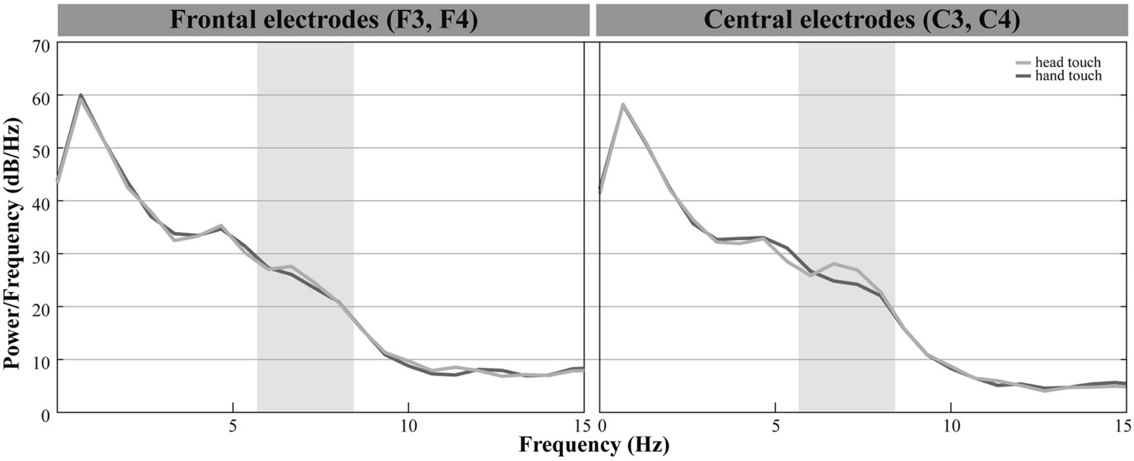

**FIGURE 5 |** Grand average EEG mu power for hand touch (dark gray) and head touch (light gray) for an average of frontal electrodes (F3, F4) and for an average of central electrodes (C3, C4) in the hands-restrained condition.

## DISCUSSION

This study was designed to shed light on the neural mechanisms underlying infants' observation of unusual head-touch actions used previously in selective imitation studies (e.g., Gergely et al., 2002; Gellén and Buttelmann, 2017). For this, we investigated the role of motor activation through measuring differences in mu frequency power. In addition, we aimed to explore whether motor activation during action perception is sensitive to contextual factors. To this end, we adapted a well-known behavioral imitation paradigm (Gergely et al., 2002; Zmyj et al., 2009) to an EEG experiment for the first time: In a between-subjects design, infants were presented with short video sequences of adult models demonstrating that his or her hands were either free or restrained. Subsequent test frames showed the same person turning on a lamp or soundbox using their head or their hand. Results in the hands-free condition revealed that 12- to 14-month-old infants displayed reduced mu frequency power in response to unusual head-touch actions compared to familiar hand-touch actions. Interestingly, in the hands-restrained condition we did not find differences in mu frequency power in response to hand- vs. head-touch actions.

Previous research associated mu desynchronization with motor activation or cortical processing of movement-related activity (Fox et al., 2016). In the hands-free condition, significant changes in mu frequency band in response to the observation of head-touch vs. hand-touch actions were predominantly found in frontal regions (F3, F4). Despite other studies demonstrating changes in mu frequency band on frontal or fronto-central channels (van Elk et al., 2008; Stapel et al., 2010), effects of mu frequency band are often more pronounced on central electrode positions (Marshall and Meltzoff, 2011). Since in our study no significant differences in mu power were found on central channels, an interpretation of our results in terms of alpha power associated with general attention or cognitive control processes unrelated to motor activation may be considered (Marshall et al., 2009; Quandt et al., 2011; Klimesch, 2012).

In adults, tasks-related modulations in alpha power can be associated with two controlled functions of attention, namely selection and suppression. Here, alpha frequency activity is thought to function as an attention filter and a decrease in alpha amplitude reflects a release from inhibition. In addition, alpha-band activity has been suggested to indicate controlled access of a semantic knowledge system (Klimesch, 2012). Alpha desynchronization across the whole scalp was reported in 9-month-old infants in response to objects that were presented after engaging in mutual eye contact vs. no eye contact. Eye contact might have put infants in a receptive state of semantic knowledge acquisition (Hoehl et al., 2014). According to these accounts, infants may have been more attentive in response to the unusual head touch.

However, we found significant differences in alpha power between unusual and familiar actions only on frontal sites (parietal channels did not show the same result pattern). This is in line with previous neurophysiological studies relating changes in frontal alpha rhythm to early states of observational and imitative learning (Marshall et al., 2009; Quandt et al., 2011). Accordingly, brief imitative experience of unfamiliar actions is associated with larger alpha desynchronization on frontal channels (Marshall et al., 2009) independent of the type of training (visual and/or active experience; Quandt et al., 2011). Thus, neural processing of action observation, especially on frontal channels, is influenced by a moderate amount of initial experience with these actions. Neuroimaging literature suggests that this frontal activation for unfamiliar actions reflects dorsolateral prefrontal cortex (DLPFC) activation during an active process of consolidating or forming motor representations of previously unknown actions (Jeannerod, 2006; Vogt et al., 2007). With increasing active experience, activation shifts toward more posterior motor regions for high levels of expertise (Shadmehr and Holcomb, 1997; Calvo-Merino et al., 2005; Kelly and Garavan, 2005). In this view, the reduction in alpha power on frontal channels in response to unusual head-touch actions compared to hand-touch actions may reflect a process of mapping observed movements onto previously created motor memories (Jeannerod, 2006; Marshall et al., 2009).

Finally, we suggest a third explanation for the frontal effects in the hands-free condition based on our hypotheses. If prediction error and updating (Kilner et al., 2007) take place when infants observed an unusual action, we expected reduced mu power in response to unusual compared to familiar action outcomes (Stapel et al., 2010). If motor experience influenced mu frequency power in the present study, lower mu power in response to familiar hand actions compared to unfamiliar head actions was expected (van Elk et al., 2008; Gerson et al., 2015). We found reduced mu power in response to the unusual head touch compared to the familiar hand touch and, thus, propose that infants updated their action predictions via the motor system for action outcomes that violated their prior action expectations (Kilner et al., 2007).

Our neural findings are in line with previous behavioral research on action understanding suggesting that by the age of 6 months infants are able to predict another person's actions (for a similar explanation of the results, see principle of rationality, Gergely and Csibra, 2003). For example, 6-month-olds anticipated action outcomes more frequently for functional compared to non-functional goal-object combinations (e.g., cup to mouth or to ear) or their pupils dilated in response to unexpected feeding actions (Gredebäck and Melinder, 2010; Hunnius and Bekkering, 2010). In addition, our results are in accordance with previous EEG studies on action processing. In the hands-free condition, we replicated the finding by Stapel et al. (2010) that 12-month-olds showed stronger mu desynchronization in response to extraordinary compared to ordinary actions. Further EEG studies demonstrated that even 9-month-old infants discriminated familiar vs. unusual eating actions. Infants responded with an N400-like component only to unexpected action outcomes (e.g., pretzel put to ear) indicating a violation of semantic action context (Reid et al., 2009; Kaduk et al., 2016). Furthermore, infants have been shown to distinguish between disrupted and complete actions in terms of increased frontal gamma band activity or more negative slow wave components (Reid et al., 2007; Pace et al., 2013). However, low-level explanations (e.g., variability in stimulus materials) might have accounted for differences between conditions in previous studies. To sum up, in the hands-free condition reduced mu power in response to the unusual head touch indicates that 12- to 14-month-old infants were able to predict action outcomes after being presented with the action context.

In addition, we investigated whether context information influenced motor activation in the hands-restrained condition. We expected opposite result patterns to the hands-free condition. Accordingly, the head touch did not elicit lower mu power compared to hand touch in the hands-restrained condition. Thus, it seems that infants incorporate situational factors while evaluating action outcomes. This is in accordance with previous behavioral studies suggesting that by 6–12 months of age infants are able to interpret actions as goal-directed and take into account situational constraints (e.g., Gergely et al., 1995; Woodward and Sommerville, 2000; Schwier et al., 2006; Zmyj et al., 2009; Gredebäck and Melinder, 2010). Despite visual inspection indicating differences in mu power especially on central channels, we did not find significant different brain responses between hand- and head-action outcomes in the hands-restrained condition. In line with previous behavioral and imitation studies (Gergely and Csibra, 2003; Schwier et al., 2006; Zmyj et al., 2009), we would have expected infants to discriminate both action outcomes also in this scenario. The predictive coding theory proposes that the MNS functions to recognize and code for goals of observed actions (Kilner et al., 2004, 2007). Infants should have been able to encode both action goals and context-specific information to predict action outcomes and update their predictions in case of prediction error. When observing a model turning on a lamp by hand despite the fact that hands were previously tied to the table, prediction error and prediction updating were expected to take place in response to the physically impossible action.

There are several possible explanations for why we did not find differences between hand and head touches in the hands-restrained condition. First, infants might have not entirely processed the restraining duct tape visually. Second, it might be that infants did not know what to predict when they observed a person whose hands were tied to the table. In this case subsequent action outcomes would have not been evaluated in comparison to prior action predictions (for a similar explanation in word learning by exclusion, see Grassmann et al., 2015). These explanations are rather unlikely, as Zmyj et al. (2009) demonstrated that 1-year-olds imitated selectively depending on the same external physical constraint when presented on a computer screen. Besides, if infants did not recognize our situational constraint at all, results should have revealed similar effects to the hands-free condition. Another explanation might be that infants visually processed the situational constraint but the head touch was still highly salient. This hypothesis is supported by a recent eye-tracking study demonstrating that 14-month-old infants paid a similar high amount of attention to the head touch of a model irrespective of whether or not the model was able to use his or her hands (Buttelmann et al., 2017).

Finally, two different processes might have played a role in the hands-restrained condition: One-year-olds already have numerous experiences with hand-touch actions as they can observe other humans turning on switches resulting in visual (e.g., light) or auditory effects (e.g., sounds) repeatedly in everyday life. Increased experience might have enhanced motor activation at central sites during action observation (van Elk et al., 2008; Cannon et al., 2014; Gerson et al., 2015). In addition, infants might have formed action predictions based on semantic knowledge. Action outcomes that violated these prior predictions might have led to prediction updating and, thus, increased motor activation (Kilner et al., 2007). Both high experience and prediction updating in response to hand actions might have affected mu power at the same time in the hands-restrained condition. Hence, we conclude that motor activation measured via mu frequency band is context-sensitive in the present study. However, effects of experience might have interfered with brain activity based on predictive coding. This is in accordance with an adult study measuring influences of motor experience and conceptual knowledge on brain activity in action perception (Gerson et al., 2017). Here, motor experience and predictions based on conceptual familiarity were experimentally manipulated in a 1-week pre-/post-training design. Results revealed that motor system activity measured via beta power changed in response to both factors in a parallel but distinct way: Increased experience led to increased motor activity whereas increased conceptual information about a previously unfamiliar action led to a relative decrease of motor activity across time. To summarize, results of the hands-restrained condition differed from the hands-free condition in terms of mu power indicating that mu power reflecting motor activation during action observation is context-dependent.

The stimuli used in the present study were based on previous behavioral imitation studies indicating that 12- to 14-month-olds are more likely to imitate an unusual head touch depending on varying situational constraints (Gergely et al., 2002; Zmyj et al., 2009). Our neural findings extend recent behavioral results as we revealed differences in mu power in response to head vs. hand touch dependent on external situational constraints. In addition, our results suggest a neural mechanism underlying previous behavioral findings: Infants might form action predictions and update their predictions for deviating action outcomes via the motor system (Kilner et al., 2007). In accordance with the predictive coding framework, increased motor activation in response to the unusual head touch might reflect the process of updating predictions in case of prediction error. This is in line with research on adults demonstrating increased motor activation in response to deviating or unusual action outcomes (e.g., Manthey et al., 2003; Koelewijn et al., 2008). Motor system activity in adults was even sensitive to the degree of prediction with increased activation in response to highly predictable action outcomes (Braukmann et al., 2017).

The present results highlight the role of motor activation during action perception by utilizing stimuli adapted to previous behavioral studies. However, with the present neurophysiological findings we cannot draw any conclusions regarding the possible effect on infants' imitative behavior. Here, we offer one possible explanation for why infants show increased motor activation in response to unusual actions; this explanation is in accordance with the predictive coding theory. The relation between motor activation and infants' imitation still awaits further clarification.

In sum, the present study revealed a reduction in mu power, which might be related to the motor system, in response to an unusual head-touch action in 12- to 14-month-old infants. Reduced mu power in response to unusual compared to familiar actions may indicate prediction error and updating according to the predictive coding framework (Kilner et al., 2007). This effect was only pronounced in the hands-free condition, suggesting that the motor system activated during action prediction and evaluation is context-dependent. Our neuroscientific findings extend previous behavioral results suggesting that a reduction of mu frequency power is one possible functional mechanism underlying infants' early action understanding.

## ETHICS STATEMENT

This study was conducted in the Baby Laboratory of the Department of Biological and Developmental Psychology at Heidelberg University, Heidelberg, Germany. The study and experimental procedures were approved by the ethics committee of Friedrich Schiller University, Jena, Germany (reference: 3752-04/13) and were in accordance with the Declaration of Helsinki. Participants were recruited from a database of parents interested in participating in infant studies at the Department of Biological and Developmental Psychology at Heidelberg University, Heidelberg, Germany. Parents of all subjects gave written and verbal consent before conducting the experiment.

## AUTHOR CONTRIBUTIONS

ML, DB, SG, SP, and SH conceived and designed the study. ML collected the data. ML and DM analyzed the data. SH was consulted about data interpretation. ML drafted the manuscript. All authors revised the work and approved the final version for publication.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2018.00036/full#supplementary-material

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# Dissociating Long and Short-term Memory in Three-Month-Old Infants Using the Mismatch Response to Voice Stimuli

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Auditory event-related potentials (ERPs) have been successfully used in adults as well as in newborns to discriminate recall of longer-term and shorter-term memories. Specifically the Mismatch Response (MMR) to deviant stimuli of an oddball paradigm is larger if the deviant stimuli are highly familiar (i.e., retrieved from long-term memory) than if they are unfamiliar, representing an immediate change to the standard stimuli kept in short-term memory. Here, we aimed to extend previous findings indicating a differential MMR to familiar and unfamiliar deviants in newborns (Beauchemin et al., 2011), to 3-month-old infants who are starting to interact more with their social surroundings supposedly based on forming more (social) long-term representations. Using a voice discrimination paradigm, each infant was repeatedly presented with the word "baby" (400 ms, interstimulus interval: 600 ms, 10 min overall duration) pronounced by three different female speakers. One voice that was unfamiliar to the infants served as the frequently presented "standard" stimulus, whereas another unfamiliar voice served as the "unfamiliar deviant" stimulus, and the voice of the infant's mother served as the "familiar deviant." Data collection was successful for 31 infants (mean age = 100 days). The MMR was determined by the difference between the ERP to standard stimuli and the ERP to the unfamiliar and familiar deviant, respectively. The MMR to the familiar deviant (mother's voice) was larger, i.e., more positive, than that to the unfamiliar deviant between 100 and 400 ms post-stimulus over the frontal and central cortex. However, a genuine MMR differentiating, as a positive deflection, between ERPs to familiar deviants and standard stimuli was only found in the 300–400 ms interval. On the other hand, a genuine MMR differentiating, as a negative deflection, between ERPs to unfamiliar deviants from ERPs to standard stimuli was revealed for the 200–300 ms post-stimulus interval. Overall results confirm a differential MMR response to unfamiliar and familiar deviants in 3-month-olds, with the earlier negative MMR to unfamiliar deviants likely reflecting change detection based on comparison processes in short-term memory, and the later positive MMR to familiar deviants reflecting subsequent long-term memory-based processing of stimulus relevance.

**Keywords: ERPs, early infancy, familiarity, voice discrimination, long-term memory, MMN**

# INTRODUCTION

Our capacity to effectively interact with our environment relies on our ability to utilize both short-term and long-term memory (Atkinson and Shiffrin, 1968). Short-term memory allows us to process and evaluate the constant stream of information (e.g., sensory input) that we are constantly confronted with when awake. It holds information for a short time period and thereby enables us to filter out important information, e.g., by recognizing if a sound is different, and therefore possibly threatening, from the stream of environmental sounds (so-called change detection). Long-term memory representations, on the other hand, are representations of events or information that we have encountered before and are stored for a longer time (hours to years), usually because of their relevance in guiding behavior (either due to emotional relevance or because they represent environmental regularities). These long-term representations can bias short-term processes by drawing attention to relevant items being held in short-term memory. Recognition processes, especially in the auditory domain, start to develop early during ontogeny (Fagan, 1973; Pascalis and de Haan, 2003; Jabès and Nelson, 2015) possibly connected to a relatively early maturation of several brain regions that are known to subserve memory formation such as the hippocampus (Seress et al., 2001; Huber and Born, 2014). For example, newborns and even fetuses show a preference for their own mother's voice compared to the voice of a stranger (DeCasper and Fifer, 1980; Lee and Kisilevsky, 2014). This suggests that infants form long-term representations of familiar voices and use them to guide the short-term processing of incoming auditory information (like environmental sounds, voices, etc.) to identify their mother.

Event-related electrical brain potentials (event-related potentials, ERPs) have been successfully used in adults and newborns to quantify and dissociate auditory short-term and long-term memory. One of the earliest change detection responses reliably induced by any discriminable change in auditory stimulation is the mismatch negativity (MMN) which is frequently termed Mismatch Response (MMR) in the developmental literature because it can change in polarity in infants (MMR: Cheour-Luhtanen et al., 1996; Cheour et al., 2000; Leppänen et al., 2004; Näätänen et al., 2007). The MMR is thought to reflect a comparison process in short-term memory between the sensory memory traces of a repeated presentation of a (standard) stimulus and the neural trace of an infrequent stimulus (a so-called deviant; Cheour et al., 2000; Näätänen et al., 2007). Interestingly, MMR amplitude, latency, and duration are modulated by familiarity of the deviant stimulus, making it possible to dissociate influences of longer-term memory processes in change detection as well. For example, native language phonemes evoke larger MMRs after fewer repetitions of the standard stimuli than foreign language phonemes (in adults, Näätänen et al., 1997; Huotilainen et al., 2001; and infants, Cheour et al., 1998) and training of auditory discrimination increases the MMR for practiced stimuli (in adults, Atienza and Cantero, 2001; Tervaniemi et al., 2001; Näätänen et al., 2007; and newborns, Cheour et al., 2002; Partanen et al., 2013). These modulations of the MMR are thought to reflect long-term memory-based processing of relevance that occurs in addition to the short-term memory-based change detection processes.

In newborns, a larger, more positive MMR is elicited by a familiar deviant (the voice of the infant's mother) compared to an unfamiliar one (Beauchemin et al., 2011). Interestingly, in that study, both the unfamiliar and the familiar deviant voice elicited an MMR of positive polarity, although the MMR to the familiar deviant occurred earlier and exhibited a larger amplitude than the MMR to the unfamiliar deviant. This suggests that the newborn brain uses similar mechanisms for detecting deviation regardless of whether the deviant stimulus is familiar (and represented in long-term memory) or unfamiliar (with only a short-term representation available). Here, we aimed to extend the findings by Beauchemin et al. (2011) of a modulation of the MMR depending on the familiarity of the deviant to 3-month-old infants (10–18 weeks) who have gained a vast amount of experience with voices and are in a window of unique plasticity in the auditory cortex (synaptogenesis reaches a peak at 3 months, Huttenlocher and Dabholkar, 1997). At this particular age infants are also starting to interact more with their social surroundings supposedly based on the formation of social long-term representations (e.g., the emergence of a social smile). We were particularly interested in whether and to what extent at this age long-term memory-based and short-term memory-based processing of familiar and unfamiliar deviant stimuli, respectively, would already express itself in more dissociable MMR features. Specifically, in addition to a larger, more positive MMR to a familiar deviant reflecting long-term memory-based processing of deviation, we expected to find signs of a negative MMR to unfamiliar deviants, reminiscent of the emergence of a robust MMN during the first post-natal months characterizing short-term memory-based processing of deviation (Kushnerenko et al., 2002; Jing and Benasich, 2006; He et al., 2009).

# MATERIALS AND METHODS

## Participants

Overall, the data of 31 infants (15 females) between 10 and 18 weeks (99.7 ± 2.9 days; range: 74–130 days) were included in analyses. All infants were born singleton at full-term (mean gestational age: 39.8 ± 0.2 weeks) with normal neonatal outcome (birth weight > 2,500 g, mean birth weight: 3,524 ± 83.0 g, mean birth height 51.7 ± 0.4 cm), were healthy according to parental report, and had no severe complications during pregnancy or delivery. All infants had an Apgar score above 9 at 10 min after birth (median 9/10/10 for the 1/5/10 min Apgar score). All infants were breastfeed, some of them partially substituted by formula ($n = 4$). Three additional infants were tested but excluded due to excessive artifacts or extreme fussiness. Parents of participants were recruited via email advertisements across the universities mailing system, flyers, and through mothers who had already participated in another study during pregnancy with their child. Participating families received monetary compensation for their time and effort. The study was part of a larger study focusing on the role of sleep for memory processing in infants and was approved by the ethics committee of the Medical Faculty of the University and University Clinics Tübingen.

## Voices Oddball Task

The oddball paradigm was adapted from a previous study investigating the discrimination of a familiar from an unfamiliar voice in newborns (Beauchemin et al., 2011). Instead of using a single vowel we chose to use the word “baby” as the target stimulus (like in other studies exploring the processing of the mother’s voice in infants, e.g., deRegnier et al., 2000; Mai et al., 2012) because it contains richer acoustic features possibly related to voice discrimination processes than that of a short snippet of a vowel. For each infant, the paradigm consisted of repeatedly presented recordings of the word “baby” (400 ms, ISI = 600 ms) pronounced by three different female speakers: an unfamiliar one (frequently presented “standard” stimulus, 85% of the trials, $n = 510$), the infants’ own mother (infrequently presented “familiar deviant,” 7.5% of the trials, $n = 45$), and a second unfamiliar one (“unfamiliar deviant,” 7.5% of the trials, $n = 45$). The standard and the unfamiliar deviant stimuli for each infant were chosen from a pool of four female voice recordings – allocation of the voices was balanced across participants. Stimuli were presented in a pseudorandomized order using the software Presentation (Neurobehavioral Systems©, Berkeley, CA, United States) with the constraint that every presentation of a deviant had to be followed by at least three standard stimuli in order to facilitate a robust MMR response (Cheour et al., 2000; Beauchemin et al., 2011). Stimulus presentation lasted for a total of 10 min (600 trials in total) and was played to the awake infants. The stimuli were presented binaurally through loudspeakers at a constant sound pressure peaking at ∼75 dB to avoid differences in ERPs elicited by differences in intensity of the stimuli. For recording the task stimuli, infants’ mothers and the four other female speakers were instructed to pronounce the word “baby” with a German pronunciation as naturally as possible while avoiding any emotional connotations. Thus, voice recordings represent instances of non-infant directed speech. The voices were recorded with a portable USB Condenser Microphone (Go Mic by Samson Technologies®) and custom-made pop filter using the software Audacity 2.0.5 for recording and post-processing. Minimal processing was necessary to produce stimuli of comparable length and loudness using noise removal, amplifying, cutting recordings and changing tempo minimally where necessary.

## Sleepiness and Control Variables

To control for possible effects of sleepiness on acute attentional and memory processes, sleep duration in the last 24 h was assessed by asking the mothers (“When and for how long did your child sleep within the last 24 h?”). Additionally, in a subsample of 23 infants, the mothers were asked to judge the infants’ level of sleepiness on a 10-point scale (from 1, “very awake,” to 10, “asleep”) right before starting the voice paradigm.

## Procedure

Infant–mother dyads were screened for eligibility (e.g., no complications during pregnancy or birth, full-term, singleton birth, birth weight > 2,500 g, no known health issues) during a telephone interview. Testing sessions were scheduled individually at a time when infants were expected to be in a calm and alert state. Upon arrival at the laboratory, the infant was given time to adapt to the environment while the experimenter explained the procedure and filled in a questionnaire about sleep, alertness and any deviations from routines on the testing day together with the mother. After giving written informed consent, each participating mother’s voice was recorded to create the individual familiar deviant for the oddball paradigm for each infant, respectively.

Electroencephalography (EEG), electrooculography (EOG), and electrocardiography (ECG) electrodes were applied while the mother distracted the infant or held the infant on her lap. After setting up the EEG recordings and making sure that the infant was in an alert and comfortable state (feeding or changing diaper beforehand, if necessary), the infant was positioned on a diaper changing unit lying down on its back with the head approximately in the middle between two loudspeakers (distance of approximately 45 cm, each). The mother stood in front of the unit and interacted with the infants (e.g., presenting hand puppets, blowing bubbles, changing facial expressions, etc.) to keep the infants calm and alert as has been suggested to be suitable in conducting infant studies (Brannon et al., 2008; Hoehl and Wahl, 2012). They were instructed not to talk to their child or make any kind of noises during the voice paradigm. If the infant was uncomfortable in this position, the mothers alternatively had their infant on their arm during recording, with the position of loudspeakers adjusted accordingly. The oddball paradigm was presented to the awake infant for 10 min and could be paused, if necessary, due to fussiness or changes in alertness (this was the case for two infants). Fifteen infants had slept upon arrival in the laboratory and most of them had been fed ($n = 28$) right before the presentation of the paradigm after the electrode placement.

## EEG Data Collection and Processing

Electroencephalography was recorded using soft Ag/Cl electrodes attached to an infant-suitable cap (EASYCAP GmbH, Herrsching, Germany) at electrode positions F3, Fz, F4, FCz, C3, Cz, C4, Pz, and mastoids, with reference to M2, and Fp2 as the ground. Electrode impedances were mostly below 10 kΩ, but always kept below 20 kΩ (which is considered acceptable for recording infant ERPs, Friedrich and Friederici, 2004; Hoehl and Wahl, 2012). Additionally, EOG recordings included one electrode below the left eye and one at the Fp1 position. Electrophysiological signals were digitized online at a rate of 500 Hz using a standard amplifier (BrainAmps, Brain Products GmbH, Gilching, Germany).

Offline, EEG data was processed using the Brain Vision Analyzer 2.0 Software (Brain Products GmbH, Gilching, Germany). The EEG was re-referenced to linked mastoids (in one participant, the signal from M1 was very noisy, therefore only M2 served as a reference) and filtered between 1 and 30 Hz and a 50 Hz notch filter (following Beauchemin et al., 2011). The signal was segmented into epochs of 1,000 ms from 200 ms pre-stimulus to 800 ms post-stimulus. ERP segments were rejected as artifacted in a channel-specific manner (Fujioka et al., 2011) when (1) a voltage difference $>100\ \mu V$ occurred within 300 ms, (2) a period of low activity (<0.5 μV) was detected for a period >100 ms, (3) absolute amplitudes exceeded ±100 μV, or (4) an ocular artifact was identified using a semiautomatic detection method (based on Independent Component Analysis, Hoffmann and Falkenstein, 2008). Baseline correction was applied using the 200 ms pre-stimulus period. Pz was excluded from further analyses as this channel contained too many artifacts to produce reliable trial numbers in the majority of participants, possibly due to the fact that infants were lying on the back of their heads.

To be included in analyses, electrodes were required to meet a criterion of 10 artifact-free epochs for familiar and unfamiliar deviants, respectively, and 50 artifact-free epochs for the standard stimuli (following recommendations for collecting infant ERP data, DeBoer et al., 2007; Hoehl and Wahl, 2012). This procedure resulted in participants having a differing number of contributing electrodes in their final frontal and central averages. The mean number of included epochs per participant across all electrodes was 278.9 (±17.5, range of 64–488) for the standard stimuli (corresponding to 54.7% of the total number of stimuli presented), 25.8 (±1.1, 10–45; 57.2%) for the familiar deviants and 25.8 (±0.8, 10–42; 57.3%) for the unfamiliar deviants.

## Data Analyses

First, epochs were averaged per condition (familiar and unfamiliar deviants, standard stimuli) for each participant, separately. The MMR was calculated as a difference wave by subtracting, per electrode site and participant, the ERP to the standard stimulus from the ERP to the unfamiliar deviant resulting in the MMR for the unfamiliar voice, and by subtracting the ERP to the standard stimulus from the ERP to the familiar deviant (mother's voice) resulting in the MMR for the familiar deviant (see **Figure 1** for the mean ERP responses for each

**FIGURE 1 | (Left)** ERP responses to the frequent standard stimuli (black lines), familiar deviant stimuli (mother's voice, dotted red/dark gray lines), unfamiliar deviant stimuli (stranger's voice, dotted blue/light gray lines). **(Right)** MMR to the familiar (red/dark gray lines) and unfamiliar (blue/light gray lines) deviant voice stimuli (determined as difference wave forms by subtracting the ERP to standard stimuli). Mean potential responses recorded from the different frontal and central electrode sites are shown for an interval between –200 pre-stimulus onset to 800 ms post-stimulus onset.

condition and the MMRs for each electrode, separately). Based both on visual inspection of the ERP data and findings from previous studies (e.g., Leppänen et al., 1997; Dehaene-Lambertz and Pena, 2001; Kushnerenko et al., 2002, 2007; Háden et al., 2009; see for a review, Kushnerenko et al., 2013) mean amplitude of the MMR was calculated for a 100–200 ms, a 200–300 ms and a 300–400 ms post-stimulus interval. To investigate possible differences between frontal and central electrode sites, F3, Fz, and F4 were averaged in one frontal average, C3, Cz, and C4 were averaged in a central average, for statistical analysis (see e.g., Partanen et al., 2013 for a similar approach of averaging over electrodes). To determine the intervals of a genuine MMR (significant difference between the response to the deviant compared to the standard stimuli), the original ERPs to all types of stimuli were compared in frontal and central electrode sites within the same post-stimulus intervals.

Results are reported as means (±SEM). Statistical analyses relied on repeated measures analyses of variance (ANOVA) with stimulus type, region (frontal vs. central) and post-stimulus interval as within-factors with *post hoc* tests for significant effects (Bonferroni corrected). Partial $\eta^2$ was used to indicate central effect sizes. For the ANOVA, degrees of freedom were corrected using the Greenhouse–Geisser procedure where appropriate. A $p$-value $< 0.05$ was considered significant.

# RESULTS

## Comparison of the Familiar and Unfamiliar MMRs

The mean amplitude (in μV) of the MMR to the familiar deviant was more positive than the MMR to the unfamiliar deviant in general (MMR familiar: 1.58 ± 0.71 μV, MMR unfamiliar: −1.13 ± 0.68 μV; main effect of stimulus type: $F(1,30) = 7.0$, $p = 0.013$, $\eta_p^2 = 0.19$, **Figure 2**). This was also true when looking at the post-stimulus intervals separately: for 100–200 ms [$F(1,30) = 6.0$, $p = 0.020$, $\eta_p^2 = 0.17$], 200–300 ms [$F(1,30) = 5.7$, $p = 0.024$, $\eta_p^2 = 0.16$] as well as 300–400 ms [$F(1,30) = 5.9$, $p = 0.022$, $\eta_p^2 = 0.16$]. Additionally, the mean amplitude of the MMR was more positive in the 300–400 ms interval than the earlier two intervals in general [both $t(30) > 2.7$, $p < 0.03$; main effect of interval: $F(2,60) = 5.3$, $p = 0.008$, $\eta_p^2 = 0.15$].

## Comparison of the Original ERPs

Overall, the mean amplitude of ERP to the familiar deviant was more positive than the ERP to the standard stimuli (main effect of stimulus type: $F(1.5,45.7) = 5.7$, $p = 0.011$, $\eta_p^2 = 0.16$). Importantly, the differences between the stimulus types seemed to depend on the post-stimulus interval [trendwise significant, interval × stimulus type interaction: $F(2.7,81.1) = 2.7$, $p = 0.058$, $\eta_p^2 = 0.08$].

A significant difference between the ERPs to the familiar deviant and standard stimuli, i.e., a robust MMR, was only found in the 300–400 ms post-stimulus interval. In this interval, the mean amplitude of the ERP to the familiar deviant (3.84 ± 0.94 μV) was significantly larger, i.e., more positive, than the mean amplitude of the ERP to the standard stimuli [1.39 ± 0.62 μV, $t(30) = 3.52$, $p = 0.002$, $d_z = 0.63$]. No significant differences in mean amplitude of the ERPs to the familiar deviant and standard stimuli emerged for the 100–200 ms [$t(30) = 1.13$, $p = 0.54$] or the 200–300 ms post-stimulus interval [$t(30) = 1.61$, $p = 0.24$]. Looking at the ERP traces of single infants visually, 29 of the 31 infants descriptively showed some differentiation of the ERP to the familiar deviant from the ERP to the standard, 25 of those as a positive deflection.

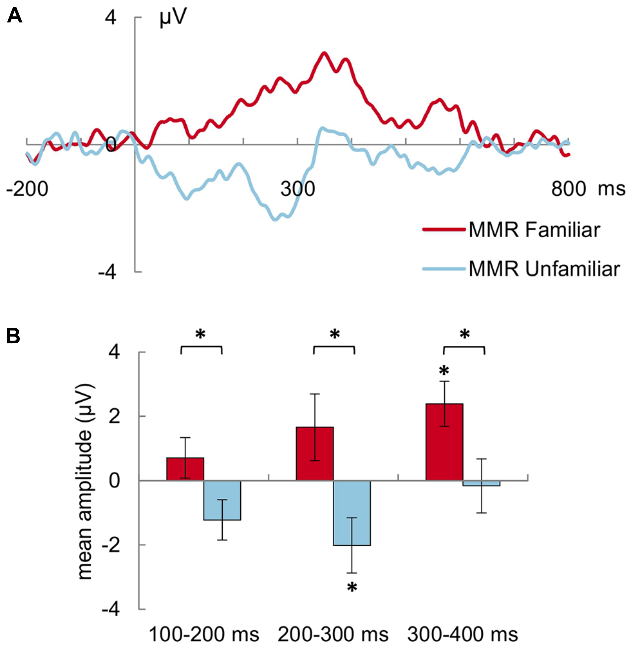

**FIGURE 2 | (A)** Mismatch Responses (MMR) to the familiar (red/dark gray line) and unfamiliar voice (blue/light gray line) averaged across all frontal and central electrode sites and all subjects. (The MMR is determined by the difference between the ERPs to the familiar and unfamiliar deviant, respectively, minus the ERP to the standard voice stimuli.) The mean potential from −200 pre-stimulus onset to 800 ms post-stimulus onset is shown. **(B)** Mean (±SEM) amplitude of the MMR to the familiar (red/dark gray) and unfamiliar (blue/light gray) deviant voices for the 100–200 ms, 200–300 ms, and 300–400 ms latency ranges. Asterisk above brackets indicates $p < 0.05$ for pairwise comparison between MMR to familiar vs. unfamiliar deviants. Asterisk on top of SEM bar indicates significant ($p < 0.05$) MMR, i.e., a significant difference between the ERP to the deviant stimulus as compared to the ERP to the standard stimulus. The MMR to the familiar deviant is more positive than the MMR to the unfamiliar stimulus. Compared with the ERP to standard stimuli, the MMR to familiar deviants expresses itself as significant positive shift in the 300–400 ms post-stimulus interval, whereas the MMR to the unfamiliar deviants expresses itself as significant negative shift in the 200–300 ms post-stimulus interval.

A robust MMR differentiating between the ERPs to unfamiliar deviant and standard stimuli was only found in the 200–300 ms post-stimulus interval. In this interval, the mean amplitude of the ERP to the unfamiliar deviant (1.91 ± 0.96 μV) was smaller, i.e., more negative, than the mean amplitude of the ERP to the standard stimulus [3.96 ± 0.67 μV, $t(30) = -2.36$, $p = 0.05$, $d_z = -0.42$]. No significant differences in mean amplitude of the ERPs to the unfamiliar deviant and standard stimuli emerged for the 100–200 ms [$t(30) = -1.95$, $p = 0.12$] or the 300–400 ms post-stimulus interval [$t(30) = -0.15$, $p = 1.0$]. Descriptively, 26 of the 31 infants showed some differentiation of the ERP to the unfamiliar deviant from the ERP to the standard, 19 of those as a negative deflection.

Additionally, mean amplitudes were generally larger in the frontal electrodes compared to the central electrodes in the 200–300 [$t(30) = 5.13$, $p < 0.001$, $d_z = 0.92$] and 300–400 ms intervals [$t(30) = 4.68$, $p < 0.001$, $d_z = 0.84$] than the 100–200 ms interval [$t(30) = 0.87$, $p = 0.39$; interval × region interaction: $F(2,60) = 13.4$, $p < 0.001$, $\eta_p^2 = 0.31$, main effect region: $F(1,30) = 19.6$, $p < 0.001$, $\eta_p^2 = 0.40$; main effect interval: $F(2,60) = 20.2$, $p < 0.001$, $\eta_p^2 = 0.40$].

## Control Variables

Infants were reported to have slept an average of 13.4 h (±0.4) in the last 24 h which is typical for infants of this age. No major deviations from daily routines were reported, other than two infants who received vaccinations 2 days before testing. For the subsample of infants where mothers were asked to rate their infant's sleepiness, all infants scored $\leq 6$ ($2.8 \pm 0.3$), thus, not very sleepy. Correlational analyses of these control variables with the main dependent measures did not yield any indication that the mean amplitude measures were influenced by infants' age, amount of sleep, or reported sleepiness (all $r < 0.37$, $p > 0.08$, uncorrected for multiple comparisons, there was a weak trend of higher sleepiness to correlated with lower values in the 100–200 ms interval for the familiar MMR and the familiar deviant ERP).

# DISCUSSION

Our study in 3-month-old infants revealed a distinct MMR to unfamiliar and to familiar (mother's voice) deviant stimuli – although this differential pattern has to be interpreted cautiously because of large variance – as well as a significant difference between these responses. Overall, the MMR (calculated as the difference between the ERPs to the deviants and the standard stimuli) was more positive for the familiar compared to the unfamiliar deviant across a large post-stimulus interval of 100–400 ms in frontal and central electrodes. For the familiar deviant (i.e., the mother's voice), a robust MMR (with reference to the ERP to the standard stimuli) expressed itself as a significant positive deflection in the 300–400 ms post-stimulus interval. By contrast, for the unfamiliar deviant, a robust MMR (with reference to the ERP to the standard stimuli) expressed as a significant negative potential deflection in the 200–300 ms post-stimulus interval. Our findings confirm previous work in newborns (Beauchemin et al., 2011) showing that long-term memory-based processing of a familiar deviant voice is associated with a stronger positive MMR compared with responses to an unfamiliar deviant voice. The present study extends those findings in newborns in showing that, at the age of 3 months, processing of unfamiliar deviants is associated with a distinct negative MMR, occurring slightly earlier (200–300 ms) than the positive MMR to familiar deviant voice. Thus, our study shows a reliable dissociation between earlier and later components of the MMR in 3-month-olds, possibly reflecting short-term memory-based change detection processes and subsequent long-term memory-based processing of relevance, respectively.

We found a negative MMR to the unfamiliar deviant, robustly differentiating between the standard and the deviant in the 200–300 ms post-stimulus interval. This negative component probably reflects the early discrimination process that detects change in a stream of repeated stimuli maintained in short-term memory (Näätänen et al., 2007). Thus, it can be considered a precursor of the adult-like MMN. Also, the latency range in which this negative MMR is observed in the 3-month-olds roughly corresponds to that seen in adults, although in adults the MMN might occasionally overlap with the earlier N1 component (Näätänen et al., 2007; Duncan et al., 2009). The negative MMR to the unfamiliar deviant may suggest a more mature and adult-like response to the unfamiliar compared to the familiar stimuli. The reason why the negative component was not prominent in the MMR to the familiar deviant (although it clearly was discriminated) is probably the strong positive MMR in the subsequent 300–400 ms post-stimulus interval, which extends into the earlier interval. This suggests that the cognitive processes linked to the two MMR components are partly running in parallel.

In contrast to the negative MMR to the unfamiliar deviant, we found a positive MMR to the familiar deviant which robustly differentiated between the standard and the deviant in the 300–400 ms post-stimulus interval. This positive component likely reflects a recognition process that evaluates the relevance of the detected stimulus based on a comparison with long-term memory representations. It can be considered a precursor of the adult early P300 which has been related to a switch from automatic to attentional processing (e.g., Polich and Kok, 1995; Polich, 2007). This kind of relevance evaluation might be the basis of infants showing a preference for their own mother's voice very early during ontogeny (DeCasper and Fifer, 1980; Lee and Kisilevsky, 2014). The existence of a long-term memory-modulated MMR component fits nicely with the notion that familiarity with a voice or phonemes of our native language, as well as trained auditory patterns, influence the magnitude and time course of change detection as reflected in the ERP response (Näätänen et al., 1997, 2007; Cheour et al., 1998, 2002; Atienza and Cantero, 2001; Tervaniemi et al., 2001). It is also in accordance with findings of the majority of MMR studies in newborns which show a frontocentral positive component peaking around 300 ms following deviant stimuli that are more or less familiar to the newborn (Leppänen et al., 1997; Dehaene-Lambertz and Pena, 2001; Winkler et al., 2003). Although our findings are in line with past research, influences of multi-sensory integration may also be present. Specifically, mothers could be seen during the task while the females providing the standard and unfamiliar deviant voices were not present. Nevertheless, influences of multi-sensory integration should be minimal, as mothers did not actually speak during the task, therefore no visual stimulus of the mother's mouth moving was present for the infant to integrate with the sound of the familiar deviant. Furthermore, we cannot directly measure if infants recognized their mother's voice. However, given that infants have previous experience with their mother's voice in unemotional, non-infant directed settings and processing of the voice recordings was kept to a minimum this seems unlikely. Taken together, our findings add evidence to the notion that the polarity of the MMR during infancy is highly sensitive to the familiarity of the deviant stimuli, with unfamiliar deviants producing an earlier negative potential deflection and familiar deviants producing a later positive potential deflection (Hirasawa et al., 2002; Martynova et al., 2003; Cheour, 2007; Beauchemin et al., 2011).

Our findings corroborate the only study thus far that has investigated the influence of familiarity on the MMR in newborns and showed that the MMR to a familiar deviant is more positive than to an unfamiliar one (Beauchemin et al., 2011). In comparison with those findings in newborns where the effect of a more positive MMR to the familiar than unfamiliar deviant concentrated on an early (around 200 ms) and late (around 500 ms) post-stimulus interval, in our 3-month-olds the effect starts earlier and is robustly observed over a broader 100–400 ms post-stimulus interval. These differences might partly reflect maturational changes, i.e., shortening of latencies and changes in scalp distribution over the course of infancy and childhood (Jing and Benasich, 2006; Cheour, 2007). Furthermore, our 3-month-olds show a reliable early MMR of negative polarity to the unfamiliar voice, which was not present in the newborns. The newborns, instead, showed a late positive MMR also to the unfamiliar deviant (with reference to the standard stimuli) which reached significance only after 400 ms. The emergence of an early negative MMR to the unfamiliar deviant in our 3-month-olds, thus, might reflect the emergence of effective short-term memory-based processing of stimulus deviation and is in accordance with longitudinal studies showing that a robust negative MMR starts to appear only after a couple of months (Kushnerenko et al., 2002; Jing and Benasich, 2006; He et al., 2009). In light of the negative polarity of this MMR component, the mechanisms likely differ in quality from those associated with the late positive MMR which in the 3-month-olds (unlike in newborns) appeared to be exclusively related to long-term memory-based comparison processes. The expression of a negative MMR to unfamiliar deviants reminiscent of the MMN in adults in our 3-month-olds might be related to the relatively fast maturation of the auditory cortex during the first months of life (Huttenlocher and Dabholkar, 1997) and also to experience with voices in general and familiar voices in particular during this period. However, it has to be noted that conclusions drawn from the comparison between the present study in 3-month-olds and Beauchemin et al.'s study in newborns remain tentative as the experimental procedures were not exactly the same. Thus, we used longer word stimuli instead of a single vowel and also our babies were awake whereas in the Beauchemin et al.-study the babies were in active sleep during stimulus presentations. These factors *per se* might have systematically changed MMRs in the two studies (Friederici et al., 2002; Otte et al., 2013; but see Cheour-Luhtanen et al., 1996 for no influence of alertness level on the MMR).

Using the MMR as an electrophysiological marker in a voice discrimination paradigm, we reliably dissociated components linked to short-term memory-based from long-term memory-based processing in 3-month-old infants. A robust negative MMR to an unfamiliar deviant in the 200–300 ms post-stimulus interval possibly reflects an earlier change detection process. On the contrary, a robust positive MMR to the familiar deviant (mother's voice) might reflect processing of the relevance of the input utilizing long-term memory representations. Our study, thereby, extends previous findings in newborns showing a robust differentiation between familiar (mother's voice) and unfamiliar deviants with a more refined dissociation between change detection (short-term) and relevance processing (modulation by long-term representations) in 3-month-old infants.

## AUTHOR CONTRIBUTIONS

KZ and JB designed the study. KZ, EB, and JB wrote the manuscript. KZ and LT conducted the study and analyzed the data.

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# Intrinsic Altruism or Social Motivation—What Does Pupil Dilation Tell Us about Children's Helping Behavior?

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Experimental and observational evidence shows that children, from around 18 months of age onwards, perform actions that can be interpreted as "helping." For instance, they hand back fallen objects or want to participate in household activities (e.g., Rheingold, 1982; Warneken and Tomasello, 2006; Brownell, 2011; Carpendale et al., 2015). A growing amount of research is trying to understand the psychological basis behind this behavior (for reviews see Paulus, 2014; Brownell, 2016; see also Warneken, 2015, for an evolutionary perspective). For example, is young children's "helping" due to an interest in the wellbeing of others? Or does it reflect a motivation to interact with other people and to be involved in their actions? In order to understand what drives children's helping, a number of recent studies have used pupil dilation as a measure of children's arousal (Hepach et al., 2012, 2016a,b), concluding that children's motivation to help is intrinsically altruistic. This opinion piece aims at re-examining those findings, suggesting that they are also compatible with alternative explanations.

In the studies discussed here, pupil diameter is measured by means of an eye tracker. Changes in pupil diameter reflect the contraction or dilation of the sphincter and the dilator muscles, innervated (respectively) by the parasympathetic and sympathetic branches of the autonomic nervous system. Changes in pupil dilation (when light conditions are kept constant) thus reflect changes in autonomic arousal (Beatty and Lucero-Wagoner, 2000). The advantage of using pupillometry is that it provides information which cannot be accessed with behavioral measures and a quantitative measure of the psychological processes underlying a certain behavior (Hepach and Westermann, 2016). One drawback of pupil dilation is that it is an unspecific measure of autonomic activation, which might result from a variety of cognitive and emotional processes (Beatty and Lucero-Wagoner, 2000; Sirois and Brisson, 2014). This ambiguity does not (without tight control conditions) allow to infer which psychological process is causing the arousal. Despite this fact, pupil dilation assessments are potentially useful in developmental research: They give a quantitative measure of the psychological processes related to a certain event which is not influenced by shyness or verbal fluency because children are not required to provide an overt response (Hepach and Westermann, 2016). Hepach et al. (2012, 2016a,b) for the first time applied this measure in the context of instrumental helping to assess children's autonomic arousal when perceiving a situation in which someone displays a need for help.

## THE PROSOCIAL AROUSAL HYPOTHESIS

In a series of experiments, pupil dilation was used to measure 2-year-old children's arousal state while observing an adult needing help (for instance, drawing a picture and dropping the crayon they need, or stacking objects and dropping the last one needed to complete a pile). Then, children were either given the opportunity to help or observe someone else helping (Hepach et al., 2012, 2016a,b).

According to the authors, these studies show that:

1 - 2-year-olds show increased arousal after seeing an adult in need of help
2 - The degree of arousal predicts the speed with which children help the adult
3 - The arousal diminishes after the adult has received help, either by the child or by another person, but stays high if the adult does not receive help.

According to a recent review, these results indicate that toddlers have an intrinsic prosocial motivation (Hepach, 2017). The author also considers several alternative explanations for children's helping behavior: social motivation (children might not be altruistically motivated to help, but simply want to interact with the adult); goal contagion (children want to see the action completed because the adult's goal becomes their own); restoration of order (children are motivated to put back displaced objects). All of these alternatives are rejected in favor of the explanation that children are intrinsically motivated to see others helped because they genuinely care for their well-being. The author argues that "*children's motivation to help others is not only intrinsic but also inherently prosocial*" (p. 53), since the arousal "*is the physiological manifestation of children's emotional involvement and the degree to which they occupy themselves with others' unfulfilled needs*" (p. 51).

This conclusion is surprising, because the experiments discussed in the review do not convincingly refute all of the alternative explanations listed above (social motivation, goal contagion, and restoration of order). The author's argument thus relies on the assumption that the arousal measured via pupil dilation has to be prosocial and would thus only arise from other-oriented, altruistic motivation: "*When young children appraise situations in terms of another individual needing help, the increase in elicited internal arousal reflects the measurable degree of their intrinsic motivation to help*" (p. 52). Yet, given the unspecific nature of physiological arousal, which is granted by the author just a few sentences later—"(c)*hanges in pupil size do not appear to indicate the stimulus' valence*" (p. 52)—, using pupil dilation as a direct measure of prosocial motivation is not warranted: Current literature suggests that increase in pupil dilation might indicate increased attention, emotional arousal, cognitive effort such as memory processes, target detection and/or surprise (Bradley et al., 2008; Privitera et al., 2010; Preuschoff, 2011; Laeng et al., 2012; Sirois and Brisson, 2014; Verschoor et al., 2015). These processes are not systematically ruled out in the studies that the review mentions, so assuming that an increase in pupil dilation signals an increase in motivation is a big and hasty step.

## *PRO*-SOCIAL OR SOCIAL?

In lieu of evidence validating pupil dilation as a specific measure of *prosocial arousal*, it is important to consider which predictions alternative explanations make with regard to arousal in the studies presented in Hepach (2017). In the following we take a closer look at three key studies.

First, in one study, 2-year-olds observed an adult drawing a picture and accidentally dropping the crayon from the table (or stacking cans to form a tower and dropping the last item). One group was given the opportunity to help the adult; one group was brought in front of the adult, held back, and saw that the adult was not helped; one group was brought in front of the adult, held back, and observed another person helping. At this point, children who saw that the adult was not helped showed greater pupil dilation than children in the other two groups (Hepach et al., 2012).

This result fits the *prosocial arousal* hypothesis, because an intrinsic altruistic motivation should lead to higher arousal when observing someone in need as opposed to observing the situation being resolved or resolving it oneself. However, it also fits all of the alternative hypotheses: We would expect high arousal when children are faced with an opportunity to join in a contingent interaction (social motivation), to fulfill an agent's goal (goal contagion), or to tie up loose ends (restoration of order), compared to when they can act on their respective motivation or when the opportunity has passed because the situation was resolved by a third party. Furthermore, the greater pupil dilation in the no-help condition could reflect a greater memory load due to keeping in mind the unresolved action.

Second, in another experiment, 2-year-olds observed a scene in which an adult needed help to complete an action because they dropped an object (Hepach et al., 2016a). Children were then given the opportunity to help by picking up the object. Here, the degree of pupil dilation predicted the speed with which the children picked up an object, yet—importantly—not necessarily the needed object. There were 12 objects scattered on the floor, only half of which pertained to the experimenter's activity. There was no difference in pupil dilation between children who picked up a relevant or an irrelevant object first, and pupil dilation predicted action latency independently of object relevance. Moreover, children kept picking up objects after having picked up all relevant ones. Can we still say that they were helping?

Here, the results actually favor the social motivation hypothesis: If children's arousal reflected the motivation to fulfill the experimenter's need, we would expect it (a) to be higher in children that seek out relevant objects first and (b) to predict action latency only for children that pick up relevant objects. Whereas if it would reflect the motivation to engage in a contingent interaction with the experimenter—picking up objects as part of an interactive game—we would expect exactly the pattern of results that emerged in the study. Thus, this study actually provides evidence for the claim that young children's helping behavior is driven by a motivation to interact with others (Paulus, 2014).

Finally, in a third study, 2- and 3-year olds were led to believe that they damaged the experimenter's playground by spilling water on it. Then they got the opportunity to help by handing them a towel. In one condition, they successfully completed the action. In another condition, just as they reached for the towel, another adult took it and handed it to the experimenter. Results showed that children who could not repair the damage showed greater pupil dilation than children who could (Hepach et al., 2016b).

In our opinion, this result represents direct evidence *against* the prosocial arousal hypothesis: While the authors argue that the increased arousal of children who could not repair the damage themselves can be seen as a sign of guilt, which itself would arise from an intrinsic prosocial motivation, this pattern would in fact *not* be expected for a truly intrinsic, other-oriented motivation. If children were only concerned with the experimenter's well-being, their arousal should recede regardless of who provided the help (as actually shown in Hepach et al., 2012). Thus, the result rather speaks for an extrinsic, self-oriented motivation, in which children's arousal is a function of expected (social) consequences for themselves. Moreover, the results can be explained equally well by the social motivation hypothesis: children who could not successfully comply with the experimenter's first request (spilling the water instead of handing it over), may have been particularly frustrated when they could not even perform the second one (handing a towel), which causes increased pupil dilation. Interestingly, most children did not attempt to clean up themselves, but handed the towel to the experimenter instead. This might be an indication that children wanted to participate in a joint task, rather than help by repairing the damage.

To summarize, the pattern of results seems to actually contradict the claim of an intrinsic and altruistic prosocial motivation. Moreover, none of the studies described above allows to rule out the social motivation hypothesis in favor of the prosocial arousal hypothesis.

## ADDITIONAL CONCERNS AND CONCLUSIONS

In addition, it should be noted that each of the studies reported in the review by Hepach (2017) uses new manipulations and analyses, meaning that each single result is never directly replicated. For instance, an increase in arousal from baseline after seeing a person needing help compared to seeing displaced objects is reported only in Experiment 2 of Hepach et al. (2016a), and a correlation between arousal and helping speed only in Experiment 1 of the same paper. It would be desirable to replicate these findings before drawing strong theoretical conclusions[1].

Although prosocial arousal is an intriguing hypothesis, we argue that the results presented in these studies do not warrant strong theoretical conclusions. In particular, they fail to exclude the social motivation hypothesis. This hypothesis is especially compelling if one considers that from early infancy, children are gradually and persistently encouraged to participate in collaborative activities with adults (Rheingold, 1982; Carpendale et al., 2013; Hammond, 2014; Dahl, 2015). Thus, children might be motivated to help because they are used to—and enjoy—taking part in joint tasks with adults. In this view, not only the social interaction in itself would be rewarding, but also the ability to comply with the experimenter's more or less explicit requests (Rheingold et al., 1987).

A second concern is that in most of the studies discussed by Hepach (2017)—as is the case in other studies (e.g., Svetlova et al., 2010)—children received cues from the experimenter, which increased over time. Usually the experimenter would first look at the object they needed, then verbalize their need, and finally explicitly ask children to give them the object. In these studies, only a few children reacted immediately. Most of them required several cues before acting, and some did not help at all. This means that children's helping behavior was elicited rather than spontaneous, which speaks for extrinsic rather than intrinsic motivation.

To conclude, this line of research provides a fruitful and intellectually stimulating contribution to the study of early helping. The work of Hepach and colleagues shows that children pay attention to social scenes and are sensitive to others' requests, which in itself is important information. However, we cannot state that pupil dilation in these studies is due to a genuinely altruistic motivation, rather than a desire to interact with the experimenter, or to comply with her requests. To distinguish between these interpretations, one could add further control conditions, e.g., a condition in which the child has the opportunity to interact without helping, or a condition in which no requests are made to the child. In any case, pupil dilation does not inform us about which particular process is underlying the arousal, which could be related not only to a concern for others, but also to different memory demands, children's excitement to interact with others, or self-referential emotions such as guilt. This should be kept in mind by future studies. Thus, the debate on what motivates children's instrumental helping is still ongoing (Paulus, 2018).

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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[1] A step in this direction has been recently made in Hepach et al. (2017), where a joint re-analysis of data from several studies shows again that pupil dilation predicts acting speed in instrumental helping tasks.

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# Early Adverse Caregiving Experiences and Preschoolers' Current Attachment Affect Brain Responses during Facial Familiarity Processing: An ERP Study

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When being placed into more benign environments like foster care, children from adverse rearing backgrounds are capable of forming attachment relationships to new caregivers within the first year of placement, while certain problematic social behaviors appear to be more persistent. Assuming that early averse experiences shape neural circuits underlying social behavior, neurophysiological studies on individual differences in early social-information processing have great informative value. More precisely, ERP studies have repeatedly shown face processing to be sensitive to experience especially regarding the caregiving background. However, studies on effects of early adverse caregiving experiences are restricted to children with a history of institutionalization. Also, no study has investigated effects of attachment security as a marker of the quality of the caregiver-child relationship. Thus, the current study asks how adverse caregiving experiences and attachment security to (new) caregivers affect early- and mid-latency ERPs sensitive to facial familiarity processing. Therefore, pre-school aged foster children during their second year within the foster home were compared to an age matched control group. Attachment was assessed using the AQS and neurophysiological data was collected during a passive viewing task presenting (foster) mother and stranger faces. Foster children were comparable to the control group with regard to attachment security. On a neurophysiological level, however, the foster group showed dampened N170 amplitudes for both face types. In both foster and control children, dampened N170 amplitudes were also found for stranger as compared to (foster) mother faces, and, for insecurely attached children as compared to securely attached children. This neural pattern may be viewed as a result of poorer social interactions earlier in life. Still, there was no effect on P1 amplitudes. Indicating heightened attentional processing, Nc amplitude responses to stranger faces were found to be enhanced in foster as compared to control children. Also, insecurely attached children allocated more attentional resources for the neural processing of mother faces. The study further confirms that early brain development is highly sensitive to the quality of caregiving. The findings are also relevant from a developmental perspective as miswiring of neural circuits may possibly play a critical role in children's psycho-social adjustment.

**Keywords: ERP, attachment, foster-care, facial familiarity, mother-child relationship, N170, Nc**

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# INTRODUCTION

In the last decades, a growing body of research has focused on the effects of early adverse experiences on neurobiological functioning to explain psycho-social adjustment and later health outcomes (e.g., Pechtel and Pizzagalli, 2011). Pathogenic care puts children at high risk for maladjustment in several developmental domains and increases vulnerability to psychopathological outcomes in later life (e.g., Cicchetti, 2002). When being placed into more benign environments, however, many children are capable of forming secure attachments to their foster parents (Dozier et al., 2001; Stovall-McClough and Dozier, 2004; Cole, 2005; Oosterman and Schuengel, 2008; Ponciano, 2010; Jacobsen et al., 2014, see Caharel et al., 2005 for meta-analytic data). More precisely, attachment security has been found to significantly increase during the first year of placement (Gabler et al., 2014; Lang et al., 2016). Still, foster children have been found to lack an age-appropriate reticence around strangers, also referred to as disinhibited social engagement (Zeanah et al., 2004; Oosterman and Schuengel, 2008; Pears et al., 2010; Van Den Dries et al., 2012; Jonkman et al., 2014; Lawler et al., 2014), which tends to persist despite improvements in attachment security (Chisholm, 1998; Smyke et al., 2002; O'Connor et al., 2003; Rutter et al., 2007; Zimmermann, 2015). Recent evidence suggests that atypical brain activity (i.e., cortical hypoactivation) may be associated with this behavioral pattern (Tarullo et al., 2011; Mesquita et al., 2015). This emphasizes the role of neurophysiological studies when studying effects of early adverse experiences on behavioral development.

The current study follows the assumption that pathogenic care leads to alterations in neural circuits related to psycho-social functioning as biological systems develop in an adaptive response to the social environment (Cicchetti, 2002). Thereby, it focusses on an important aspect of social-information processing (i.e., face processing) and asks how it is affected by early adverse caregiving experiences and current attachment security.

## Theoretical Background: Important Aspects of Face Processing

Inevitably, the processing of faces is an important aspect of any social interaction and numerous studies in infants and children provide evidence that the development of face recognition is highly influenced by early social experiences (see Moulson et al., 2009). For example, several studies could show that infants' regular interpersonal experiences facilitate the processing of faces they are exposed to frequently (e.g., Quinn et al., 2002). Also, the quality of the emotional environment has been shown to affect neural circuits leading to a facial emotion bias in maltreated children (e.g., Pine et al., 2005), and infants from non-abusive households (de Haan et al., 2004; Taylor-Colls and Fearon, 2015). This experience-dependent process allows for individual shaping of the face recognition system with regard to a given social environment (see Greenough et al., 1987; Nelson, 2001).

### Face-Sensitive ERP Components in Infancy and Childhood

Due to its excellent temporal solution, the ERP method is a very practical approach to illustrate how neurocognitive processes in response to faces unfold over time (de Haan et al., 2007). We selected three well-studied components that can reliably be identified in preschoolers, to examine individual differences at different stages in the time-course of facial information processing (see Todd et al., 2008) in children with and without a history of pathogenic care.

### P1

The first face-sensitive ERP component in the temporal sequence of neural face processing, the P1, occurs at occipital electrode sites approximately 100 ms following stimulus onset. It has repeatedly been reported in studies on face processing in infants (de Haan and Nelson, 1999), children (Taylor et al., 2001, 2004; Carver et al., 2003; Todd et al., 2008; Moulson et al., 2009; Mesquita et al., 2015), as well as adults (e.g., Halit et al., 2000; Itier, 2004), and is particularly likely to be sensitive to faces by 4 years of age (Taylor et al., 2001, 2004; Itier, 2004). The P1 might possibly reflect an early stage of facial encoding as it is sensitive to low-level individual differences between faces and non-face stimuli (Rossion and Caharel, 2011). Still, it is suggested that the activation of face representations in the brain does only appear at a later stage reflected by a subsequent negative component, the N170 (Rossion and Jacques, 2012).

### N170

The N170 is an early-latency occipito-temporal ERP component and usually defined as the first negative peak following the P1. There is consistent evidence that the N170 is sensitive to faces as compared to non-face stimuli in adults (for an overview of the N170 "face effect" see Rossion and Jacques, 2012), and, occurring at longer latencies, in children by about 4 years of age (Taylor et al., 1999; Todd et al., 2008; Kuefner et al., 2010).

The N170's sensitivity to facial familiarity still seems to be a topic of debate. However, evidence suggests that personal importance of faces alters the N170 response by the activation of robust representations in the brain that have evolved due to frequent exposure (Caharel et al., 2002, 2005, 2006; Mesquita et al., 2015, but see Eimer, 2000). As an example, the N170 amplitudes was found to discriminate between mother's and random famous faces in adults (Caharel et al., 2005) and between caregiver and stranger faces in children (Todd et al., 2008; Moulson et al., 2009; Dai et al., 2014).

### Nc

Finally, the Nc represents a well-studied ERP component in the face-processing literature. It is prominent in the fronto-central area of the scalp at mid-latencies. It is not specifically related to face-processing, rather does it appear to reflect the allocation of attentional resources in response to salient or interesting stimuli (Courchesne et al., 1981; Nelson, 1994; de Haan and Nelson, 1997; Reynolds and Richards, 2005). Thus, it is of major interest when studying the individual processing of faces that are assumed to vary in salience during the course of development. Indeed, the

Nc component has, too, shown to discriminate between caregiver and stranger faces in infants and preschoolers (de Haan and Nelson, 1997, 1999; Dawson et al., 2002; Carver et al., 2003; Todd et al., 2008; Moulson et al., 2009; Webb et al., 2011).

## ERP Evidence for Individual Differences in Facial Familiarity Processing

### Facial Familiarity Processing and the Developing Infant–Caregiver Relationship

The few ERP studies on facial familiarity processing in children give rise to the assumption that neural correlates of caregiver and stranger face processing clearly relate to important aspects of normative socio-emotional development. The Nc is of major interest as it is associated with attention to face stimulus. Interestingly, older children elicit larger Nc amplitude responses to a stranger's face as compared to the mother's face (Dawson et al., 2002; Carver et al., 2003; Todd et al., 2008; Moulson et al., 2009). Still, these neural correlates are suggested to vacillate frequently during the early years (Swingler, 2008). Interestingly, in infants, increased proximity seeking to the mother is associated with larger Nc amplitudes (heightened attentional processing) to stranger faces (Swingler et al., 2007). Thus, it is proposed that age-related changes in neural response patterns occur in conjunction with the formation of the child-caregiver attachment relationship (see Bowlby, 1982). And it also goes along with the child's attentional focus increasingly shifting from the mother to a broader social world (Carver et al., 2003; Swingler et al., 2007). Even though it has been proposed that social information processing varies as a function of attachment security (Dykas and Cassidy, 2011), however, to our best knowledge there is no study that has related the quality of the attachment relationship to mother and stranger face processing.

### Facial Familiarity Processing in Children from Adverse Rearing Environments

Moulson et al. (2009) collected ERP data from currently institutionalized, never-institutionalized and previously institutionalized children placed in foster care while passively viewing pictures of their primary caregiver's and a stranger's face. First, they found institutionalized children to elicit smaller amplitudes than non-institutionalized children. Although the effect was only consistently present for the early visually evoked potential P1, waveforms indicated that later occipital components (P400, N170) were equally affected. This brain activity pattern is consistent with studies in children from low-SES backgrounds (Kishiyama et al., 2009) and non-ERP studies in children with a history of social deprivation (Otero et al., 2003; Marshall et al., 2004; Tarullo et al., 2011). In conclusion, it is claimed that a lack of an appropriately stimulating environment might lead to persistent cortical hypoarousal (also see Moulson et al., 2009). Second, previously institutionalized children placed in foster care did show some —but not full—recovery regarding the dampened ERP amplitudes to faces. However, there was no effect of timing of intervention on ERP outcomes (Moulson et al., 2009). Third, institutionalized and never-institutionalized children groups did hardly differ in response to the caregiver and stranger faces at later latencies despite their dramatically different caregiving backgrounds. Surprisingly, there were no significant interactions between group and facial type. However, findings were inconsistent across measurement points.

In a recent study, Mesquita et al. (2015) investigated children's facial familiarity processing in a sample of 3- to 6-year-old children currently living in Portuguese institutions. They addressed the non-significant interaction between group and facial type reported by Moulson et al. (2009) and extended the study by taking into account within group variations regarding disordered social behavior. Thereby, they found evidence that children displaying atypical social behavior are more likely than typically functioning children to elicit smaller P1 amplitudes in response to faces. Also, children with inhibited attachment symptoms appeared to elicit larger N170 amplitudes to their caregiver's face. Despite its exploratory nature, Mesquita et al.'s (2015) study suggests that it might not be institutionalization *per se*, but individual attachment related experiences and outcomes that alter children's neural processing of faces.

To conclude, all we know about the impact of adverse rearing environments on facial familiarity processing is based on these two studies. Thus, our knowledge exclusively stems from data assessed in (previously) institutionalized children. Also, associations found between children's behavior and brain activity solely rely on caregiver reports (i.e., Mesquita et al., 2015). Finally, there is a gap in the literature regarding studies that investigate overt attachment related behavioral and neural responses to familiar and unfamiliar persons in children with different family rearing backgrounds.

## The Current Study

Our first major aim was to compare foster children's neural processing of facial familiarity to an age matched control sample. Basic visual functions regarding face processing (as represented by the P1 amplitude response) were found to be impaired in institutionalized children (e.g., Moulson et al., 2009; Mesquita et al., 2015), but it is unclear whether the effect would show in children without a background of institutional rearing, since family and institutional rearing backgrounds clearly differ in terms of deprivation. Thus, we did not necessarily expect the P1 effect to be equally prominent in family reared foster children, still, we tested for the effect to confirm this assumption. In contrast, the N170 has shown to be affected by prolonged exposure to a particular face (e.g., Caharel et al., 2002). Thus, we expected the effect of facial familiarity, especially processing of the (foster) mothers face to vary with foster care status. Regarding the Nc, larger amplitudes relate to enhanced attentional processing of either the caregiver or the stranger's face depending on aspect of socio-emotional development (e.g., Carver et al., 2003; Swingler et al., 2007). Indeed, our previous findings suggest that during social interactions foster children seem to be more affected by a stranger's presence as observed on a behavioral level (Kungl, 2016). Thus, we expected Nc amplitude responses to stranger faces to be larger in foster children as compared to control children.

Our second major aim was to investigate effects of attachment security on facial familiarity processing in foster and control children. As suggested by Spangler and Zimmermann (1999) "including the physiological processes in addition to the psychological processes enables us" to gain further knowledge on "the function of the inner working model with respect to processes that are [...] not expressed through overt behavior." (p. 270). To our best knowledge, the studies conducted by Carver, Swingler, and their research group are the only studies relating changes in the attachment relationship (Carver et al., 2003) and attachment relevant behaviors (Swingler et al., 2007, 2010) to brain responses during mother-stranger face processing. Still, no study has looked at the quality of the attachment relationship as related to ERP data in children neither in high-risk nor in normative samples. Referring to the N170's sensitivity to facial familiarity, and thus, previous exposure to a particular face, we expected the quality of caregiving experiences (indexed by attachment security) to affect facial familiarity processing as early as the N170 time window. Securely attached children are by theory more likely to have frequently engaged in close social interactions, and thus face to face contact. This was expected to result in different N170 amplitude responses to faces. We further aimed to explore if there might be an interaction between foster care status and attachment security on N170 amplitudes. Also, as the attachment system is believed to regulate not only the child's psychological but also physiological processes related to his/her social world (e.g., Spangler and Grossmann, 1993; Spangler and Zimmermann, 1999), the attention drawn to familiar and unfamiliar faces, as represented by Nc amplitude responses, was expected to differ in securely attached children as compared to insecurely attached children.

# METHODS

The current study is part of a larger project named "Attachment and Psychosocial Adjustment of Foster Children: Individual and Social Factors of Influence" (Spangler et al., 2009) that aimed to investigate preschool-aged foster children during the transition into the foster home. A detailed description of the longitudinal study as well as its findings can be found in other publications focusing on the development of attachment (Gabler et al., 2014; Lang et al., 2016) and attachment disorders (Zimmermann, 2015).

The foster group included in the current study forms a regional subsample of the overall study. Importantly, included children did not significantly differ from the rest of the sample regarding age at placement, attachment security, or problem behavior..

The current study reports on data retrieved at one home visit (for assessment of attachment security) and a laboratory visit[1] (for ERP assessment) for both the control and the foster group. Prior to the assessments, informed consent entailing the purpose of the study, anticipated consequences, uses and storage of data as well as the voluntary basis of participation was negotiated with the (foster) mother and a written informed consent form was signed.

## Participants

The final foster sample included in the ERP analyses consisted of 13 foster children (8 male/5 female) and 24 children living in their birth family (10 male/14 female). Nine more children (incl. 3 foster children) were tested but excluded from further analyses due to technical problems ($n = 3$), non-compliance during the application of the electrode cap ($n = 2$), removal of the cap during the experiment ($n = 1$) or an insufficient number of artifact-free trials ($n = 3$).

At the ERP assessment foster children's age (months: $M = 55.62$, $SD = 11.69$) did not differ from control children's (months: $M = 56.58$, $SD = 9.04$), $t_{(35)} = 0.28$, *ns.,* and the time foster children had been living within the foster home was about 20 months ($M = 20.23$, $SD = 5.00$). In control children, attachment security was assessed within a few weeks after the ERP assessment ($M = 1.59$, $SD = 0.84$). In foster children, however, attachment security was assessed at an average of 8 months ($M = 8.15$, $SD = 4.24$) before the ERP assessment resembling the time point of 1 year (months: $M = 12.62$, $SD = 0.91$) after placement in the current foster home. Foster children's age at placement ranged from 15 to 61 months ($M = 33.54$, $SD = 14.10$).

## Measures

### Attachment Security

Children's attachment security was assessed during a 2.5 hrs home visit using the German version 3.2 of the Attachment Q-Sort (AQS; Waters and Deane, 1985, German version: Schölmerich and Leyendecker, 1999). The AQS is a widely used measure in studies with children aged 12–70 months (Ijzendoorn and Bakermans-Kranenburg, 2004). Conducting a series of meta-analyses Van Ijzendoorn et al. (2004) found evidence for the validity of the observer AQS as a measure of attachment. The original version of the AQS (Waters and Deane, 1985) was modified by Waters (1995) and includes 90 items referring to children's secure base and exploratory behavior as well as other aspects like social referencing. These items are individually printed on cards that are then sorted into 9 piles categorizing the child's behavior from "less characteristic" to most characteristic. Subsequently the child's Q-Sort is correlated with a hypothetical criterion sort developed by experts representing the prototypically behavior of a most secure subject (see Waters and Deane, 1985). In the present study, two trained observers separately sorted the Q-Set. Inter-observer reliability was high, $r = 0.70$ (range: $rs = 0.39$–$0.87$). Using a composite of both observers' Q-sets for the analyses enhanced reliability up to $r = 0.82$ as calculated by Spearman Brown formula. For the analysis, attachment security was dichotomized by median split.

### Neurophysiological Data

***Procedure***

The ERP assessment took place at the laboratory visit. Children were carefully instructed and introduced to the procedure in a child-oriented way. An electrode cap (ActiCap, Brain Products, Gilching, Germany)—referred to as being a "luminous magic cap"—was positioned after measuring the vertex and the experimenter injected gel in each electrode. Scalp impedances were indicated by color LEDs at the electrode. They were ideally

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[1] In addition, further behavioral data was collected at the laboratory visit. For an overview see Kungl (2016).

kept below 15 kΩ, however 15–30 kΩ was graded acceptable in some cases. The average scalp impedance was 6.74 kΩ, ($SD =$ 2.83 kΩ) across all participants.

The child was seated in front of a computer screen that was surrounded by a blue shielding to block the child's view of the room. While one experimenter was standing next to the child and led him/her through the session, another experimenter was sitting behind a curtain operating the recording and observing the child via a webcam. Eye movements and interruptions were marked online in the EEG. Children were told they should sit quietly and pay attention to their mother's[2] as well as to a stranger's face, which would be shown on screen in a repeated fashion. A cartoon signaled the end of each block where children received tokens (Sticker) to maintain their motivation. These tokens were to be traded into a present afterwards.

### *Stimuli*

Each child's mother was photographed at their visit to the laboratory. Pictures of their faces were taken against a blue background while sitting in an upright position and looking straight into the camera. Mothers were told to put on a friendly face but not to show teeth while smiling. Photographs were cropped and placed on a gray background layer. All color information was removed and images were adjusted in figure-ground ratio, position, contrast and lightning if necessary. In addition to the familiar face (mother) an unfamiliar face stimulus (stranger) was randomly selected from the pool of stimuli showing the other female participants. Pictures of mothers who wore glasses were always paired together. To maintain a foveal angle of $7.9^\circ \times 6.6^\circ$, and thus, minimizing eye movement picture size on screen was $9 \times 7.5$ cm at a distance of 65 cm.

### *EEG recording*

EEG and EOG data were collected using 30 active electrode channels. Electrodes were placed in standard positions according to the international 10–20 system. EEG was recorded from Fp1, Fp2, Fz, F3, F4, F7, F8, FC6, Cz, C3, C4, T7, T8, CP1, CP2, CP5, CP6, TP9, TP10, Pz, P3, P4, P7, P8, Oz, O1, O2, PO9, PO10. One electrode was placed under the child's right eye and used for EOG recordings. Electrode AFz served as the ground and FCz as the online reference. The signal was continuously recorded with a sampling rate of 250 Hz (BrainAmp amplifier, Brain Products, Gilching, Germany). Stimuli were presented via a second computer using an experiment generating software (Inquisit 3, Millisecond Software, Seattle, Washington). Both computers were interfaced.

### *Assessment of event-related potentials*

*ERP data collection.* ERPs were recorded while children were shown facial images of their mother and a stranger in a counterbalanced manner. Each trial consisted of a 300 ms fixation period during which a small yellow star appeared in the center of the screen followed by the presentation of the face stimulus for 700 ms and a post-stimulus recording period of 600 ms during which the screen was black. The subsequent inter-trial interval varied randomly between 500 and 1,000 ms. The presentation of stimuli was semi-randomized and the frequency of appearance was counterbalanced with 80 trials per face condition (mother, stranger). The experiment consisted of 8 blocks of 20 trials each allowing for small breaks in between blocks.

The average number of artifact-free trials was 38.97 ($SD =$ 13.10) per condition. The number of trials did not significantly differ neither between conditions ($M_{mother} = 37.97$, $SD = 13.93$; $M_{stranger} = 39.97$, $SD = 13.32$), $t_{(36)} = -1.62$, $p =$ ns, nor between groups ($M_{controlgroup} = 41.31$, $SD = 13.79$; $M_{fostergroup} = 34.65$, $SD = 10.9$), $t_{(35)} = 1.50$, $p =$ ns. The number of trials is comparable to other studies using a similar paradigm in this age group (e.g., Carver et al., 2003).

*ERP editing and reduction.* Data was edited offline using BrainVision Analyzer (Version 2.4., Brain Products, Gilching, Germany). First, during raw data inspection intervals were eye movement artifacts occurred were taken out manually. Subsequently, a 0.3–30 Hz filter, and a 60 Hz notch filter (all having a 24 dB/oct gradient) were applied. When necessary bad channels were replaced via interpolation by spherical splines (order of splines = 4). The average number of replaced channels was 0.88 ($SD = 1.66$) across all participants. The continuous data was re-referenced to the average reference and the implicit online reference was reused as channel FCz. After segmenting data by face condition we ran an automatic artifact rejection not allowing for voltage steps of more than 100 μV, differences of two values in one segment of more than 150 μV and/or an amplitude exceeding 100 μV or falling below −100 μV, respectively. Since we showed a fixation cross for 300 ms prior to the actual stimulus we chose the interval from −500 to −300 ms for subsequent baseline correction. This way we ensured, that activity elicited by the fixation cross did not affect the actual baseline. Finally, a grand average for each face condition was calculated. Participants whose data provided less than 15 remaining segments per condition were not included in further analyses.

*ERP measures.* To detect components of interest we drew assumptions based on the literature and visually inspected the grand average waveforms and peak information (amplitude in mV) for each component and subject was extracted. Finally, mean amplitude values of ±1 sampling point around the designated individual peak were exported into the data analysing software SPSS 23.0.

Peak detection was performed automatically. It was informed by inspection of the grand average waveforms and previous literature. The P1, indicated by a positive deflection, was defined as the maximum positive peak at occipital sites (O1/2) occuring between 80 and 220 ms ($M = 167$, $SD = 27$). Furthermore, the N170 was defined as the most negative peak distributed over posterior electrode sites (PO9/10) occurring between 210 and 370 ms after stimulus onset ($M = 307$, $SD = 31$). Finally, in accordance with the literature, the Nc was defined as the second most negative peak at fronto-central electrode-sites after stimulus onset occuring between 280 and 520 ms ($M = 390$, $SD = 27$). Previous studies with young children have found the Nc to be prominent over distributed scalp regions and have included a

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[2] For reasons of simplicity we use the term "mother" in the following. However, for foster children, stimuli were foster mother's faces.

number of electrodes (e.g., Carver et al., 2003; Swingler et al., 2007). In the current study, the Nc was analyzed at the midline (FCz, Cz) as well as the lateral lead pair C3/4. **Figure 1** shows electrode sites representing leads that were included in the analyses.

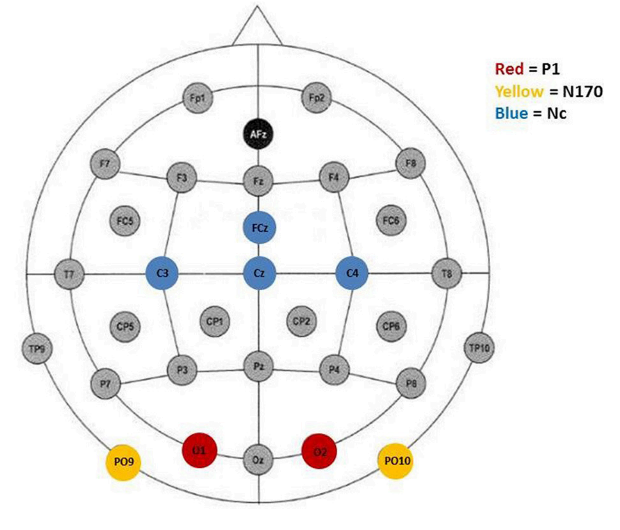

**FIGURE 1 |** Electrode placement according to the 10–20 system. Colored electrode sites represent leads included in the analyses of P1 (red), N170 (yellow), and, Nc (blue).

## Analysis Plan and Statistical Considerations

Differences in foster children and control children as well as effects of attachment security on (foster) children's facial familiarity processing, were analyzed for P1, N170, and Nc separately. Therefore, brain electrical activity in response to mother and stranger faces were separately subjected to a repeated measure design. The ANOVAs were conducted with foster care status (foster group, control group) and attachment (secure, insecure) as the between-subjects factors, and face type (mother, stranger) as the within-subjects factor. Also, hemisphere (for lateral lead pairs) or lead (for midline leads) was added as an additional repeated factor. To investigate whether foster children's (or control children's) brain activity in response to mother and stranger faces may vary as a function of attachment, three-way interaction effects between attachment, foster care status and face type, were considered within the main analyses. As ERP amplitude responses were not correlated with age, and control and foster children did not differ regarding age at the time of the ERP assessment, it was not necessary to include age as a covariate in the analyses. To reveal interaction effects, LSD pairwise comparisons were performed. Note that mean values reported within descriptions of the main analyses (including **Table 2**) are estimated marginal means and standard errors.

# RESULTS

## Attachment Security

Across the total sample attachment security ranged from $-0.10$ to $0.60$ ($M = 0.32$, $SD = 0.19$) with a median of $Md = 0.35$. *T*-Tests showed that there was no difference between foster children and control children regarding attachment security, $t_{(35)} = 0.22$, ns. To compare children scoring high on attachment security with those who were rated less securely attached the total sample was split at the median leading to two groups. **Table 1** shows that the distribution of children assigned to insecure or secure[3] was comparable in foster and control children.

## ERP Responses to Mother and Stranger Faces with Regard to Foster Care Status and Attachment

### P1 Amplitude Responses

For P1 amplitude responses the 2 face type × 2 foster care status × 2 attachment × 2 hemisphere repeated measures ANOVA with P1 amplitude responses as the dependent variable revealed no significant effects, which means that the P1 was unaffected by facial familiarity, neither did foster and control children nor securely attached from insecurely attached children differ regarding P1 amplitude responses to both faces.

### N170 Amplitude Responses

The 2 face type × 2 foster care status × 2 attachment × 2 hemisphere repeated measures ANOVA with N170 amplitude as the dependent variable revealed main effects for face type, $F_{(1,\,33)} = 4.88$, $p = 0.034$, $\eta_p^2 = 0.13$, foster care status, $F_{(1,\,33)} = 7.00$, $p = 0.012$, $\eta_p^2 = 0.18$, attachment, $F_{(1,\,33)} = 6.33$, $p = 0.017$, $\eta_p^2 = 0.16$, but no interaction effects. Regarding the main effect for face type, mother faces elicited larger amplitudes than stranger faces in all children ($M_{mother} = -0.02$, $SE = 1.03.53$; $M_{stranger} = 2.09$, $SE = 1.13$). Regarding the main effect for foster care status mean N170 amplitude responses were larger (more negative) in the control group ($M = -1.87$, $SE = 1.16$) than in the foster group ($M = 3.94$, $SE = 1.57$). **Figure 2** depicts the grand average waveforms for each group in response to mother and stranger faces[4].

For the main effect of attachment, mean values indicated that regardless of face type and foster care status securely attached children elicited larger N170 responses ($M = -1.60$, $SE = 1.41$) than insecurely attached children ($M = 3.12$, $SE = 1.24$). This effect is visualized in **Figure 3**[5]. Also, N170 amplitude responses to both faces were larger on the left ($M = -0.28$, $SE = 1.05$) than on the right hemisphere ($M = 2.35$, $SE = 1.20$).

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[3] Note that we use the terms secure and insecure for children scoring above and, respectively, below the sample median in the AQS attachment security rating. However, this may not necessarily resemble the traditional classification introduced by Mary Ainsworth (e.g., Ainsworth et al., 1978).

[4] Importantly, we are aware that there appears to be a visually evoked potential, probably due to the presentation of the fixation cross starting at −300 ms (see **Figure 2**). The graph indicates that this waveform, which emerged prior to stimulus presentation, differed between both groups. However, regarding the earlier positive peak preceding the N170 the difference between foster and control group was not significant. Thus, it is most likely that the effect is specific to face-sensitive processing represented by the N170 component.

[5] Note that the difference between attachment groups regarding the earlier positive peak preceding the N170 was not significant.

## Nc Amplitude Responses

To investigate our research questions with regard to Nc amplitude responses, two separate analyses were conducted, first, for central lateral leads (C3/C4), and second, for fronto-central midline leads (FCz/Fz). In line with previous literature (e.g., Swingler et al., 2007) lateral leads were analyzed separately to include potential hemisphere effects.

At the central lateral lead pair C3/4 the 2 face type × 2 foster care status × 2 attachment × 2 hemisphere repeated measures ANOVA showed a significant main effect for hemisphere, $F_{(1,\ 33)} = 9.33$, $p = 0.004$, $\eta_p^2 = 0.22$, and a significant interaction between foster care status and face type, $F_{(1,\ 33)} = 6.39$, $p = 0.02$, $\eta_p^2 = 0.16$. Regarding the main effect for hemisphere, mean values were larger on the left ($M = -6.20$, $SE = 0.57$) than on the right hemisphere ($M = -4.66$, $SE = 0.66$). For the interaction between foster care status and face type, **Figure 4** indicated and pairwise comparisons confirmed that at central lateral leads the foster group showed larger Nc responses in the stranger face condition ($M = -6.56$, $SE = 0.92$) than in the mother face condition ($M = -4.86$, $SE = 1.01$), $p = 0.016$, whereas the control group did not significantly discriminate between the two faces at central lateral leads ($M_{mother=}$ $-5.27$, $SE = 0.74$; $M_{stranger} = -5.03$, $SE = 0.67$).

**TABLE 1 |** AQS security score and frequency of securely and insecurely attached children by group in numbers. Pearson's Chi$^2$ test results.

| Attachment group | AQS security score | Foster group | Control group | Total sample | Chi$^2$ | *p* |
|---|---|---|---|---|---|---|
| Insecure | ≤0.35 | 8 | 11 | 19 | 0.83 | ns |
| Secure | >0.35 | 5 | 13 | 18 | | |
| Total sample | | 13 | 24 | 37 | | |

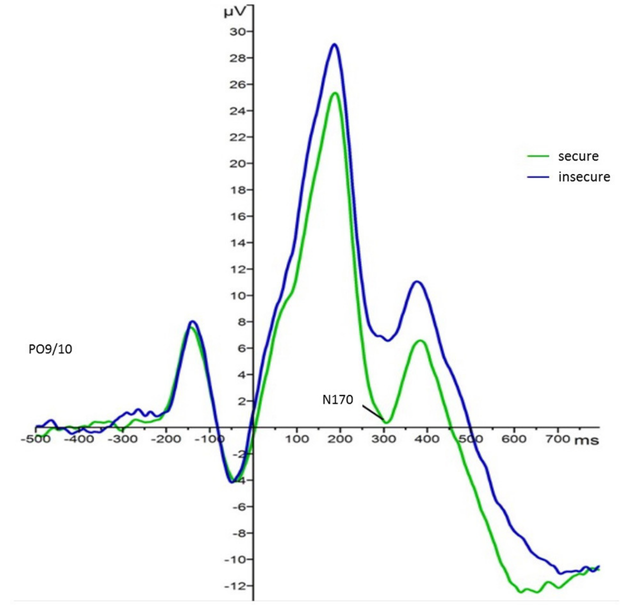

**FIGURE 3 |** Grand average waveforms for N170 amplitude responses (microvolts) in securely (green) and insecurely (blue) attached children collapsed over parieto-occipital electrodes PO9 and PO10, face type, and foster care status.

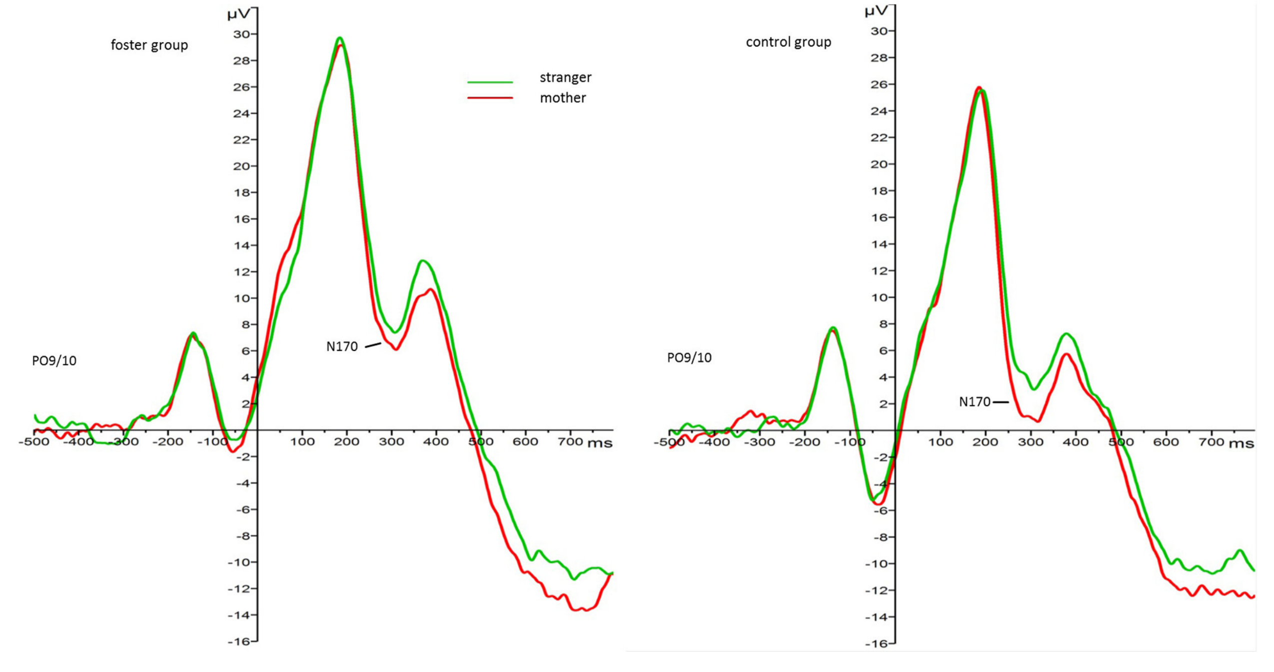

**FIGURE 2 |** Grand average waveforms for N170 amplitude response (microvolt) to mother (red) and stranger faces (green) by foster care status. Collapsed over parieto-occipital leads PO9 and PO10.

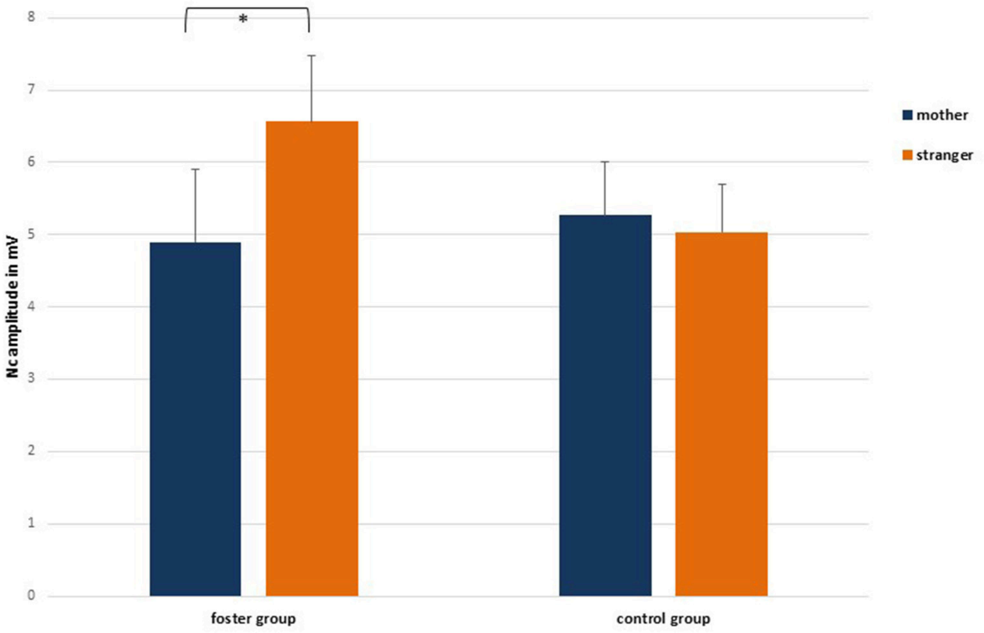

**FIGURE 4 |** Nc amplitude responses in the mother and stranger face condition by group, collapsed over central lateral leads C3/4. Means and standard errors. Note that scale is inverted. $^*p < 0.05$

At midline leads (Cz/FCz), the 2 face type × 2 group × 2 attachment × 3 lead repeated measures ANOVA solely revealed a highly significant main effect for lead, $F_{(1,\,33)} = 12.12$, $p = 0.001$, $\eta_p^2 = 0.27$, with Nc amplitude responses being more negative at FCz ($M = -6.84$, $SE = 0.65$) than Cz ($M = -5.33$, $SE = 0.68$).

There also was a significant interaction effect between foster care status and face type, $F_{(1,\,33)} = 5.37$, $p = 0.03$, $\eta_p^2 = 0.14$, as well as attachment and face type, $F_{(1,\,33)} = 5.27$, $p = 0.03$, $\eta_p^2 = 0.14$. Regarding the interaction between foster care status and face type, pairwise comparisons showed that the difference between Nc amplitudes to mother as compared to stranger faces was only significant in the foster group with stranger faces ($M = -7.63$, $SE = 1.18$) eliciting larger amplitudes than mother faces ($M = -5.22$, $SE = 1.04$), $p = 0.01$. There was no difference in Nc amplitude responses to mother and stranger faces in the control group ($M_{mother} = -5.70$, $SE = 0.74$; $M_{stranger} = -5.55$, $SE = 0.84$). This resembles the interaction effect found at the central lead pair. For the significant interaction between attachment and face type, pairwise comparisons showed that Nc amplitude responses to mother faces varied as a function of attachment security (see **Figure 5**). More precisely, securely attached children elicited smaller Nc amplitudes to their mother's face ($M = -3.80$, $SE = 0.96$) than insecurely attached children ($M = -7.12$, $SE = 0.84$), $p = 0.014$. Regarding Nc amplitude responses to stranger faces the difference between insecurely and securely attached children did not reach significance ($M_{insecure} = -6.98$, $SE_{insecure} = 0.96$; $M_{secure} = -6.19$, $SE_{secure} = 1.09$). Also, pairwise comparisons between mother and stranger faces by attachment status showed that only in securely but not insecurely attached children the difference in Nc amplitude responses to mothers vs. stranger faces was significant, $p = 0.007$.

## Three-Way Interactions between Foster Care Status, Attachment and Face Type

In an exploratory manner we investigated whether differences in amplitude responses to faces varied as a function of the interaction between foster care status and attachment being aware that this analysis is based on very small cell sizes.

The three-way interaction between attachment, foster care status and face type, did not reach significance neither for P1 nor for N170 amplitude responses to faces. Regarding the Nc, the effect was not significant at the central lateral lead pair. However, at fronto-central midline leads, we found the interaction between attachment, face type and foster care status, $F_{(1,\,33)} = 6.43$, $p = 0.02$, $\eta_p^2 = 0.16$, to be significant, and thus, qualifying the above described interaction effects between attachment and face type, as well as foster care status and face type at the midline leads. More precisely, pairwise comparisons suggested that the effect of attachment security on mother face processing was especially prominent in the foster group, $p = 0.037$, while it did not reach significance in the control group. As **Table 2** shows, for the foster group Nc amplitudes to mother faces were more negative in insecurely than in securely attached children. Still, results should only be treated cautiously.

# DISCUSSION

In this study, we asked how early caregiving experiences affect neural correlates of facial familiarity processing, which has been shown to be an important biological marker of children's social-emotional development. The group of foster children included in this study showed the same level of attachment security 1 year

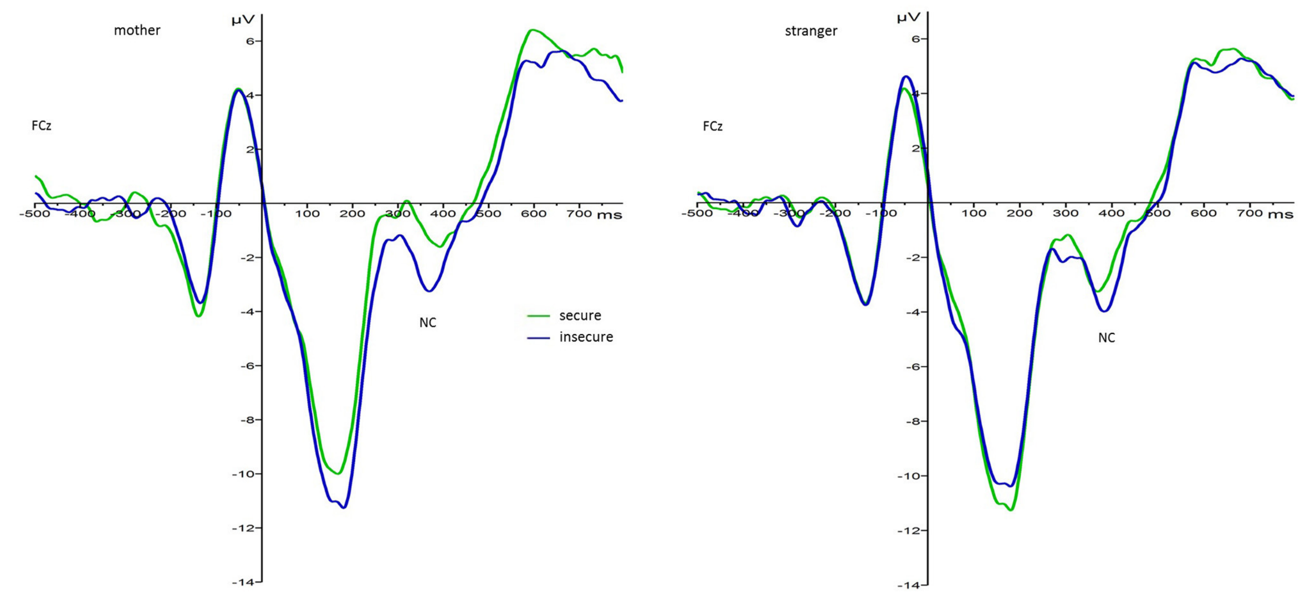

**FIGURE 5 |** Grand average waveforms for Nc amplitude responses (microvolts) in securely (green) and insecurely (blue) attached children collapsed over electrodes Cz/FCz and groups by face type.

after placement as the control group resembling previous studies with the same (Lang, 2014) as well as other samples of children placed in foster or adoptive care (see Van den Dries et al., 2009).

In accordance with empirical evidence on the time course of facial familiarity processing we found effects of facial familiarity to occur at occipito-temporal electrode sites as early as the N170 time window, as well as at fronto-central sites during the later Nc time window, but not the P1 component. As the P1 is known to be based on "low-level visual information" (Rossion and Jacques, 2012, p. 127) this finding confirms that (foster) mother and stranger faces did not substantially differ in terms of basic visual cues like, for instance, luminance or contrast, which further validates the use of the stimuli.

**TABLE 2 |** Nc amplitude responses at midline leads in the control group and the foster group by face type and attachment. Means and standard errors.

| Face | Attachment security | Group | |
|---|---|---|---|
| | | **Control group Mean *(SE)*** | **Foster group Mean *(SE)*** |
| Mother | Insecure | −6.78 (1.10) | **−7.47 (1.29)** |
| | Secure | −4.63 (1.01) | **−2.98 (1.63)** |
| Stranger | Insecure | −6.75 (1.24) | −7.21 (1.46) |
| | Secure | −4.34 (1.14) | −8.05 (1.85) |

*Values that significantly differ on a $p = 0.05$ level when compared pairwise are shown in bold.*

## Neural Responses to Faces with Regard to Foster Care Status, Attachment Security and Facial Familiarity

### P1 Amplitude Responses

In the current study, foster children and control children did not differ regarding P1 amplitude responses. Previous studies with children with a history of institutionalization, however, have found dampened P1 amplitude responses to faces, which has been interpreted as a sign of cortical hypo-arousal due to experiences of early deprivation (Moulson et al., 2009; Mesquita et al., 2015). There may be several explanations for these diverse findings. First, foster children's previous experiences may not be comparable to those of institutionalized children, most of whom have been affected by social deprivation from early on. This does not mean that neglect within a family environment is considered less severe; however, the heterogeneity of previous experiences in our foster sample may have obscured the effect of early deprivation on the P1 amplitude response. Second, findings from one study suggest that even within a group of institutionalized children only a subgroup showed dampened P1 amplitudes which was associated with atypical social behavior (Mesquita et al., 2015). Thus, different mechanisms underlying children's heterogeneous behavioral organization may have obscured effects in our sample. Third, the time living within the foster home may have been sufficient for a catch-up. This explanation is supported by findings from Moulson et al. (2009) who found the P1 (and other component's) amplitude responses in an intervention group to fall in between institutionalized and control children. Future research including larger sample sizes are needed to further reveal conditions under which subgroups are affected by what has been interpreted as cortical hypo-arousal.

In the same line, we did not find attachment security to affect face processing as early as the P1 time window. In concordance with the above non-findings of effects of foster care status at this early stage, it is suggested that children in our sample may have had experienced a "good enough" environment to develop such basic visual processing abilities (see Winnicott, 1973).

## N170 Amplitude Responses

As expected we found both groups to differentially process faces as early as the N170 time window. Interestingly, in our sample, N170 amplitude responses were clearly dampened for foster children as compared to control children, suggesting an effect of possible hypo-arousal, yet, at a later processing stage. The N170 amplitude was affected by facial familiarity and attachment security with amplitudes being smaller, or less negative, in the stranger face condition than in the mother face condition, and, in insecurely attached as compared to securely attached children.

### *Differences between foster and control children*

We found distinct group differences in facial processing regardless of face type. In our study, foster children as compared to control children elicited smaller amplitudes to both types of faces. Indeed, foster children's N170 amplitude responses did not fall below the zero level. Previous studies have shown smaller amplitudes in a series of face-sensitive components when comparing early socially deprived children with control children (Moulson et al., 2009) as well as when comparing currently institutionalized children that show atypical vs. typical social behavior (Mesquita et al., 2015). In our study, however, only the N170, but not the P1, was affected. Thus, the extent to which early facial processing stages are impaired may depend on specific sample characteristics. Consequently, in most foster children the early home environment or recent experiences within the foster home may have provided sufficient sensory input to acquire basic perceptual skills for a normal P1 function. In contrast, the N170, based on more elaborate processing, may more depend on early contingent face to face interactions, which may be restricted in foster children's early experiences. Thus, foster children's experiences may have led to a less matured neural network that in turn respond to social cues with relative hypoactivation within the N170, but not the P1, time window.

Interestingly, studies with the Bucharest sample have shown that in institutionalized children basic perceptional skills like facial emotion and facial familiarity processing have evolved despite severe early deprivation (Moulson et al., 2009). Thus, it is possible, that brain activation is generally affected by early adverse experiences in terms of cortical hypoarousal as the neural system did not receive the expected overall social input, while the input, on the other hand, may still be enough to develop basic perceptual skills.

Importantly, cortical hypoactivation has shown to be related to atypical social behavior like social disinhibition in studies on global measures of brain activity (Tarullo et al., 2011) as well as in studies suggesting hypoactivation in face-sensitive brain regions (Mesquita et al., 2015). Integrating findings from the behavioral part of our analyses that show enhanced social disinhibition in foster children (Kungl, 2016) provides supporting evidence for this relationship.

### *Effects of facial familiarity*

The familiarity effect is in line with our expectations as well as with other studies who found the N170 to be sensitive to facial familiarity and also to the salience of faces in children and adults (e.g., Caharel et al., 2002, 2006; Dawson et al., 2002; Todd et al., 2008; Wild-Wall et al., 2008; Moulson et al., 2009; Mesquita et al., 2015). Research suggests that facial familiarity affects early visually evoked potentials as it implies the activation of mental representations, which, by nature are stronger in familiar, and thus well-known, than in unfamiliar faces (Herzmann et al., 2004; Leibenluft et al., 2004; Wild-Wall et al., 2008; Taylor et al., 2009).

In our study familiar faces elicited larger N170 amplitude responses than unfamiliar faces in both groups, which is in line with previous findings (Caharel et al., 2006, 2011; Wild-Wall et al., 2008; Dai et al., 2014, but see Todd et al., 2008). Additional testing N170 latencies in our sample revealed the N170 amplitude response to be significantly faster in the mother face than in the stranger face condition (Kungl, 2016), which suggests a facilitated visual coding of (foster) mother faces possible due to the "extensive visual experience" children have with this stimulus (Rossion and Jacques, 2012, p. 113).

In contrast to our expectations but consistent with previous findings (e.g., Moulson et al., 2009), there was no modulation of the familiarity effect by foster care status, and thus, individual experiences (e.g., the amount time children have spent with their (foster) mother).

This finding may be explained referring to priming or repetition studies suggesting the facial familiarity effect to require relatively short familiarization with the stimulus (Jemel et al., 2003; Caharel et al., 2011; but see Schweinberger et al., 2002). Thus, it is indicated that recent long-term exposure (during the time in the foster home) rather than lifelong experiences with the foster mother's face was sufficient to elicit a familiarity effect. Future research on mother-stranger face processing should include personally irrelevant but familiarized faces to detangle effects of personal salience and priming on the N170 amplitude.

### *Effects of attachment security*

As expected, the N170 amplitude response clearly differed between securely attached and insecurely attached children. More precisely, securely attached children showed higher N170 amplitude responses than insecurely attached children regardless of foster care status. However, as foster children have shown to elicit smaller N170 amplitude than control children the effect added up in insecurely attached foster children showing the smallest deflections during this elaborated stage of facial processing. In conclusion, we again found children's socio-emotional experiences to have a strong effect on face processing in general, however, not facial familiarity processing in particular.

Interpreting this finding in line with the above, it is suggested that contingent social interactions within an adequately stimulating social environment may result in the formation of robust mental representations associated with an elaborated neural network that forms in an adaptive experience-dependent process (e.g., Nelson, 2001; Herzmann et al., 2004). When being exposed to social stimuli (here: faces) an elaborated neural network gets activated which may reflect in increased N170 amplitudes. If this assumption is true, it could be said that securely attached children show an expertise in the processing of social stimuli. Future research should address this question by, for example, additionally conducting a facial recognition task. Furthermore, it would be interesting whether the effect is face-specific. To address this question, future research should include ERPs to faces as well as objects.

The current data does not allow to make any assumptions on the causality of the effect. Indeed, it is possible that children with less processing activity in response to social cues were less likely to develop secure attachments to their (foster) mother. In this sense, this group of children could also be viewed as less responsive to changes in the social environment in terms of susceptibility (Ellis et al., 2011), which in turn may have hindered socio-emotional development. However, this interpretation clearly needs further empirical support, and, to detangle cause and effect, longitudinal assessments would be necessary.

### Nc Amplitude Responses

#### *Effects of foster care status and familiarity*

The Nc component has repeatedly been associated with enhanced attentional processing (e.g., Reynolds and Richards, 2005) and its response to stranger faces has been shown to be influenced by different aspects of the mother–child relationship (e.g., Carver et al., 2003; Swingler et al., 2010). As expected, the interaction between group and face was significant. More precisely, only foster children elicited larger amplitudes to the stranger face as compared to the mother's face. Regarding foster children's heightened attention toward strangers on the behavioral level this clearly makes sense. Indeed, not only did we find foster children including the same sample to be described as showing more disinhibited behavior (e.g., Zimmermann, 2015) but also to show increased proximity seeking to the foster mother and elevated levels of looking behavior and verbal initiations directed to an approaching stranger during a behavioral assessment (described in Kungl, 2016). Thus, our neurophysiological findings on increased Nc amplitude responses (implying enhanced attention) to stranger faces in foster children may be a neural correlate of high vigilance around strangers. To further validate this assumption we ran additional analyses including children's looking behavior directed to an approaching stranger (see above) and found that the more children were looking at the stranger throughout the interaction the faster they responded to a stranger face in the ERP experiment in terms of shorter Nc latencies (Kungl, 2016). We suggest that our increased Nc amplitudes in foster children may reflect a neural correlate of aberrant social behavior in children from adverse rearing backgrounds. However, this assumption needs to be verified and the causality of the effect should be addressed in further studies.

#### *Effects of attachment security*

At midline leads we found that in response to mother faces Nc amplitudes were significantly decreased in securely attached children irregardless of foster care status. As the Nc amplitude reflects attentional processing of salient stimuli (e.g., Todd et al., 2008), this finding suggests, that securely attached children allocate less attentional resources when "faced" with their mother, probably because her face is associated with an internalized secure base in these children (Bowlby, 1982). Also, as internal working models of attachment are indicative of the child's appraisal of their social partners (Bretherton et al., 1990) in insecurely attached children, the mother's face may represent a more ambiguous stimulus and increased Nc amplitudes may be reflective of an increased effort in the evaluation of the mother's face's meaning. The effect may then be indicative of the activation of a certain neural circuit underlying the insecure status in the sense of contradicting cognitive and emotional responses. In concordance with our finding, Carver et al. (2003) found Nc responses to the mother face to vary in conjunction with proposed changes in children's social and emotional development. They argued that it is only after the establishment of the attachment relationship with the mother as the primary caregiver, that children devote less attentional resources to her face. In this line, our results add to this argument by suggesting that individual differences in attachment security moderate the effect described by Carver et al. (2003) and further confirms that experiences with the attachment figure are associated with different regulatory strategies that reflect on a psychophysiological level (Spangler and Grossmann, 1993). Future research may even be able to further reveal differences in mother's face processing when differentiating between ambivalent and insecure-avoidant attached children.

In addition to this two-way interaction between attachment security and face type there was a triple interaction between attachment, face type and group at midline leads. It suggested that the effect between attachment and face type was especially prominent in foster children. Looking at the means it is also obvious that large Nc amplitude responses to stranger faces were especially robust regarding effects of attachment security in foster children. This makes sense, as behavioral studies in children from adverse rearing environments have shown, stranger sociability to be rather independent from attachment security (e.g., Chisholm, 1998; Smyke et al., 2002; Zimmermann, 2015). Importantly, due to small cell sizes, it is unclear, if the 3-way interaction really qualifies the interaction between attachment and face type described above. Thus, this effect should only be interpreted cautiously and clearly needs replication including a larger sample of foster children. This would optimally provide the possibility of analyzing differences in Nc amplitude responses to stranger faces with regard to marked signs of atypical social behavior. Indeed, an ERP study comparing institutionalized children with atypical behavior to those with typical behavior, suggests that not all children's neural processing is affected by early experiences of pathogenic care in the same way (Mesquita et al., 2015).

## Limitations

There are several limitations to the study. First, we included 37 children, but the number of foster children was relatively small ($n = 13$). This uneven distribution was due to a relatively high drop out in the foster care sample. In a drop-out analysis, however, we showed that the remaining sample of foster children did not differ from the original sample, neither in age, nor in any of the central study variables, nor in mental health status. Future studies need to include a larger sample of foster children.

Furthermore, it should be considered that in foster children, attachment security was assessed about 13 months after placement while the ERP assessment took place at an average of 21 months within the foster home. Still, we did not assume changes in foster children's attachment security during this time window for two reasons. First, longitudinal data with the same sample indicated that the attachment relationship between foster mother and child formed within the first months of placement. More precisely, attachment security increased during the first 6 months in the foster home and then remained relatively stable (Lang, 2014). And second, previous studies suggest a general stability of attachment security during childhood (Main et al., 1985; Wartner et al., 1994).

The next limitation concerns the age range of our sample. Notably, neural structures develop rapidly during the early years and 3–6 years may be too wide to capture important developmental aspects of facial familiarity processing. As it was shown by Carver et al. (2003), the neural processing of the mother's and a stranger's face underlies significant changes over the preschool years. In the current study, however, we focused on group differences in two age-matched samples and thus, we assume our results to be due to different relational experiences rather than age effects.

Furthermore, it has to be noted, that foster children are not a homogeneous sample in terms of their prior experiences, and, they have also different (sub-) clinical symptoms (Zimmermann, 2015). For example, it may be crucial to differentiate between disinhibited and inhibited as well as typical and atypical social behavior (see Mesquita et al., 2015). Again, heterogeneity in our sample may have obscured specific processing patterns that are crucial to our understanding of different pathways leading to distinct behavioral outcomes. In line with this argument, it could be very informative to include a categorical measure of attachment that distinguishes between insecure-avoidant and insecure-ambivalent attached children. Especially, with regard to attentional processing of familiar faces it could be assumed, that in insecure ambivalent—as compared to insecure avoidant—the use of hyperactivating strategies may be evident even on a neural level. Still, with regard to our study aims and sample characteristics (e.g., age range, sample size) using a dimensional measure was the better choice.

Also, it has to be noted, that our results are correlational and that we cannot make any statement about the direction of effects. In the particular case of foster children, effects of intervention are of major interest. It has been shown that improvements in the caregiving environment have positive effects on a behavioral (e.g., Gabler et al., 2014; Lang, 2014) as well as on a neurophysiological level (Moulson et al., 2009). Thus, future studies may include more than one measuring point assessing ERPs in relation to aspects of the attachment relationship, first, at time of placement, and second, after a certain amount of time spent within the foster home. Also, future studies may benefit from including mother variables like sensitivity, that are directly related to improvements in attachment in foster children (Gabler et al., 2014).

An important methodological limitation refers to the design of the ERP experiment. As noted earlier, there seemed to be a visually evoked potential, probably due to the presentation of the fixation cross at −300 ms (see **Figure 2**), which may have affected subsequent components. Considering this limitation the baseline correction was applied to activity prior to the fixation cross. Still, it is unclear if decreased N170 amplitudes are due to differences in the processing of face stimuli *per se*. However, as the face-sensitive P1 component, which precedes the N170, did not show between subject effects we did not expect N170 effects to be due to prior processing differences. Nevertheless, results should be interpreted cautiously.

A final methodological limitation refers to the fact that we have only included female faces. In the current study caregivers were all female, however, with regard to reticence toward strangers and the processing of stranger faces, including male caregiver faces and male stranger faces may provide a more precise picture of the child's inner organization with regard to its actual social environment.

## Summary

Applying a neurophysiological approach by comparing high and low risk samples, the current investigation could show that facial processing—that is fundamental to adequate psycho-social functioning—is particularly sensitive to early caregiving experiences. It was indicated that adverse rearing backgrounds affect the growing organism on multiple levels possibly compromising the child's flexible psycho-social adjustment in later stages of development. Integrating results regarding ERP responses to faces at different stages during the time course of facial familiarity processing, we found that recognizing a familiar face elicits an increased neural response as early as the N170 time window suggesting a strong mental representation. Furthermore, at this stage, foster children as well as insecurely attached children showed dampened amplitudes, suggesting that children in more benign caregiving environments have developed increased expertise in face processing possibly due to having experienced more frequent face to face interaction. Finally, it was not until the Nc time window, reflecting advanced cortical processing, that foster children and control children differed with regard to facial familiarity. Here, we found foster children to show enhanced attentional processing in response to stranger faces, which may be a correlate of their aberrant social behavior toward strangers. Our neurophysiological and behavioral findings (see Kungl, 2016) provide further evidence that individual behavioral responses occurring during mother-stranger interaction are related to facial familiarity processing in normative development as well as in children at risk. Such investigations are important as alterations in social information processing may have cascading effects on children's development (Cicchetti, 2002). Longitudinal studies are needed to test the assumption that changes in neural correlates of psycho-social functioning would go along with changes in social behavior.

Here, effects of attachment based interventions within the foster home could be a major focus.

## ETHICS STATEMENT

The original study was approved by the Ethics Commission of the German Psychological Association (GS07200, 9/12/2009). For the EEG assessment foster mothers (foster group) and mothers (control group) were informed about the study's aims and methods. In addition, they were informed that their participation is voluntary and that they can withdraw from it any time without stating reasons, and that the data were treated according to the data protection law, saved anonymously and was to be deleted at any point if requested. Also they were informed about the EEG assessment. No invasive methods were used. Foster mothers and mothers signed the informed consent form before participation.

## AUTHOR CONTRIBUTIONS

MK: concept, design, recruitment of participants, supervision, acquisition and analyses of neurophysiological data, statistical analyses, interpretation of results, drafting, critical review. IB: overall study design, recruitment of participants, supervision, reliability training for coders, acquisition and analyses of behavioral data. GS: overall study design, supervision and guidance during all stages of the research processes, statistical analyses and interpretation of results, critical review.

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# Attachment Security in Infancy: A Preliminary Study of Prospective Links to Brain Morphometry in Late Childhood

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A large body of longitudinal research provides compelling evidence for the critical role of early attachment relationships in children's social, emotional, and cognitive development. It is expected that parent–child attachment relationships may also impact children's brain development, however, studies linking normative caregiving experiences and brain structure are scarce. To our knowledge, no study has yet examined the associations between the quality of parent–infant attachment relationships and brain morphology during childhood. The aim of this preliminary study was to investigate the prospective links between mother–infant attachment security and whole-brain gray matter (GM) volume and thickness in late childhood. Attachment security toward the mother was assessed in 33 children when they were 15 months old. These children were then invited to undergo structural magnetic resonance imaging at 10–11 years of age. Results indicated that children more securely attached to their mother in infancy had larger GM volumes in the superior temporal sulcus and gyrus, temporo-parietal junction, and precentral gyrus in late childhood. No associations between attachment security and cortical thickness were found. If replicated, these results would suggest that a secure attachment relationship and its main features (e.g., adequate dyadic emotion regulation, competent exploration) may influence GM volume in brain regions involved in social, cognitive, and emotional functioning through experience-dependent processes.

**Keywords: mother–child attachment, infancy, childhood, brain development, social brain, gray matter, volumetrics, cortical thickness**

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## INTRODUCTION

Seminal work by Harlow and Harlow (1962) suggested that the primate tendency to attach to a caregiver is innate and does not merely reflect physiological needs. Human children attach to a caregiver who is physically present, even if the caregiver does not fulfill a primary physical need, such as feeding, and even if the caregiver adopts abusive behaviors (Bowlby, 1956; Ainsworth, 1967; Cyr et al., 2010). Attachment is a specific, preferential, and enduring emotional tie between an infant and a caregiver, promoting survival and allowing children to feel safe and protected (Bowlby, 1969/1982). Infant attachment is expressed by behaviors such as separation distress, greeting reactions upon reunion, and the tendency to turn to a specific caregiver for reassurance when distressed (Sroufe, 1979; Cassidy, 2016). These innate, universal behavioral tendencies are driven by a biologically based attachment system (Cassidy, 2016). Importantly, however, they are subsequently gradually modulated by caregiver responses, progressively leading to the development of individual differences in the expression and organization of infant attachment behavior (Ainsworth et al., 1978; Fearon and Belsky, 2016). These individual differences are considered to index the "quality" or "security" of attachment relationships. Specifically, a critical tenet of attachment theory is that securely attached children have confident expectations of themselves as being able to solicit the caregiver's proximity, and of the caregiver as being responsive and available when needed (Bowlby, 1973, 1988). In contrast, infants develop insecure attachments over the course of interactions with caregivers who have difficulty responding adequately to their emotional needs (see meta-analysis by De Wolff and Van IJzendoorn, 1997). Hence, virtually all children become attached to a caregiver, but not all develop secure attachment relationships (Cassidy, 2016).

Decades of longitudinal research have supported the notion that individual differences in infant and child attachment security to primary caregivers are of critical importance for child social, emotional, and cognitive development. Several meta-analyses suggest that variations in attachment security are associated with individual differences in a range of child outcomes: higher attachment security (as compared to insecurity) is associated with better social competence (Groh et al., 2014, 2017a), emotion understanding (Cooke et al., 2016), quality of peer relationships (Pallini et al., 2014), language competence (Van IJzendoorn et al., 1995), as well as fewer internalizing (Groh et al., 2012, 2017a; Madigan et al., 2013) and externalizing behavior problems (Fearon et al., 2010; Groh et al., 2017a).

Such associations between attachment security and child social, emotional, and cognitive development are sometimes interpreted as suggesting that attachment experiences influence the development of children's brain structures underlying socio-emotional and cognitive functioning (Gunnar et al., 2006; Belsky and de Haan, 2011; Tottenham, 2014). Indeed, although many brain development processes, such as neuronal differentiation, synaptogenesis, and pruning, are guided largely by biological factors (Rakic, 1988), caregiving experiences can also shape brain development in two ways. *Experience-expectant* processes refer to development that occurs in response to experiences that are typically shared by all members of a species (Greenough et al., 1987). Caregiver presence is expected in humans, and indeed caregiver deprivation is associated with alterations of brain structure and function (Eisenberger and Cole, 2012; Tottenham, 2012). Closer to our purposes, *experience-dependent* processes refer to brain development that varies from one person to another as a result of specific individual experiences (Greenough et al., 1987). For example, animal studies indicate that variations in the quality of caregiving have long-term consequences for brain development, notably in brain areas that support stress regulation, social behaviors, and reward processing (Meaney, 2001; Yu et al., 2013; Peña et al., 2014). Accordingly, it is plausible that the security of parent–child attachment, as an important indicator of the quality of the early caregiving environment, may contribute to shaping the developing brain.

This hypothesis is sensible when considering that a core feature of a secure attachment relationship is that the caregiver acts as a secure base from which the child can confidently explore, and seek proximity when distressed (Ainsworth, 1985). During exploration, securely attached children can freely play an active, purposeful role in exploring the surrounding social and physical world, which provides rich stimulation for the developing brain. When, however, they encounter a distressing event during exploration (e.g., hurting oneself while playing), the very nature of their secure attachment relationship allows these children to return to their caregiver for help and soothing (Ainsworth, 1985), which gradually fosters the development of emotion regulation (Calkins, 2004; Cole et al., 2004). Overall, secure attachment relationships are believed to favor both confident exploration and effective emotion regulation in children, which are likely to influence structural development in brain regions involved in a range of social, emotional, and cognitive functions. In fact, it has been proposed that the quality of the attachment bond between children and their caregivers is especially likely to be associated with brain structures underpinning social functioning (Rilling and Young, 2014; Tottenham, 2014), known as the "social brain" and including the superior temporal sulcus, medial prefrontal and anterior cingulate cortices, inferior frontal gyrus, anterior insula, as well as the amygdala (Blakemore, 2008; Adolphs, 2009).

Yet, in contrast to the abundance of research linking attachment security to behavioral outcomes, the links between brain structure and child attachment are still poorly understood (Coan, 2016). Indirect evidence comes from studies of children exposed to maltreatment, which suggest that severely adverse caregiving experiences can lead to morphological alterations in brain regions underpinning social, emotional, and cognitive functions later in life (Teicher and Samson, 2016). Children and adults exposed to childhood maltreatment present abnormal brain volumes and thickness compared to non-exposed individuals in several brain regions (see Lim et al., 2014; Riem et al., 2015, for meta-analyses; Kelly et al., 2013; Whittle et al., 2013; Teicher and Samson, 2016). Nonetheless, these findings should be considered alongside the numerous confounding factors that characterize maltreating families (e.g., poor mental and physical health, poverty, poor quality of sleep, prenatal drug and alcohol use; Edwards et al., 2003; Hussey et al., 2006; Smith et al., 2007; Cuddihy et al., 2013). Given that these factors also influence brain development (Jednoróg et al., 2012; Goodkind et al., 2015; Urrila et al., 2017), the poor quality of parent–child relationships may or may not be the cause of the structural abnormalities observed in the brains of maltreated children (Belsky and de Haan, 2011). Studies in the general population are required to fully understand the association between caregiving experiences and brain morphology.

In contrast to the relatively large body of research on maltreatment, empirical evidence for links between normative variations in parent–child relationship quality and brain development in typically developing children is scarce, and almost all relevant studies have examined parental behavior rather than parent–child relationship quality *per se*. Overall, these studies suggest that normative variations in different dimensions of parental behavior are associated with differences in gray matter (GM) volume and thickness in several brain regions, although directionality varies. Specifically, higher maternal sensitivity has been found to relate to larger subcortical GM volume in infants (Sethna et al., 2017), but also to smaller hippocampal volumes and to (marginally) smaller amygdalar volume in infants (Rifkin-Graboi et al., 2015). Kok et al.'s (2015, 2017) longitudinal studies suggested that parental sensitivity in infancy was not associated with hippocampal and amygdalar volumes in school-aged children, but was associated with larger total GM volume as well as thicker cortex in the bilateral middle frontal gyri, precentral gyri, and left postcentral gyrus. Greater maternal support during the preschool years is associated with larger hippocampal volumes in school-aged children (Luby et al., 2012, 2013, 2016), while self-reported parental praise is related to larger left insula in children aged 5–18 years (Matsudaira et al., 2016). The presence of more positive maternal behavior has been linked to decreased volumetric development in the right amygdala as well as accelerated cortical thinning in the right anterior cingulate and bilateral prefrontal cortices in adolescence (Whittle et al., 2014). On the other hand, negative aspects of parental behavior (e.g., self-reported hostility and observed aggressive behavior) are related to smaller total GM volume (Lévesque et al., 2015) and attenuated cortical thinning in the right superior frontal, superior parietal, and supramarginal gyri, as well as a reduced volumetric development in the left nucleus accumbens in adolescence (Whittle et al., 2016). These brain structures are crucial for children's social, emotional, and cognitive development, given that they underpin social cognition, emotion regulation, threat detection, attention monitoring, stress regulation and reward processing (Meaney, 2001; Dölen and Malenka, 2014; Frank et al., 2014; Kalisch and Gerlicher, 2014; Deen et al., 2015).

In light of the growing literature pertaining to specific dimensions of parental behavior and brain morphology, it is surprising that almost no research has focused directly on the quality of the parent–child dyadic relationship, of which attachment security is perhaps the best documented and most widely recognized indicator. Given that the quality of parenting behavior is moderately associated with parent–child attachment security (De Wolff and Van IJzendoorn, 1997), the body of literature presented above suggests that parent–child attachment security may relate to children's brain morphology. Yet, to our knowledge, only two studies have examined the relations between brain structure and the quality of parent–child attachment relationships, and both focused on subcortical volumes (amygdala, hippocampus, caudate nucleus, thalamus) once participants reached adulthood. These studies suggest that poorer attachment quality to mother in infancy (assessed with the Strange Situation Procedure; SSP, Ainsworth et al., 1978) relates to larger volume of the amygdalae in adulthood (Moutsiana et al., 2015; Lyons-Ruth et al., 2016). These two longitudinal studies highlight the potentially long-lasting link between early parent–child attachment and subcortical brain structure. However, it is not known whether the longitudinal links are already apparent during childhood, whether the direction of association is stable, and whether attachment may also relate to other brain regions. These are important questions in light of increasing evidence that developmental considerations play a crucial role in the links between caregiving experiences and regional brain development, including directionality of such links (Tottenham and Sheridan, 2009; Teicher et al., 2016). For example, higher-quality parenting is associated with smaller hippocampal volumes in infants and children [Luby et al., 2012, 2013, 2016; Rifkin-Graboi et al., 2015; but see Sethna et al.'s (2017) results indicating larger subcortical GM volume]; however, higher-quality parenting is associated with larger hippocampal volume in adolescence (albeit in a sample of children exposed to cocaine during gestation; Rao et al., 2010).

Building on previous studies (Moutsiana et al., 2015; Lyons-Ruth et al., 2016), the current report examines the longitudinal associations between mother–infant attachment security and whole-brain GM volume and thickness in late childhood. Previous studies have used an *a priori* regions-of-interests approach to investigate the links between parent–child relationship quality and brain structure, which may limit the scope of the conclusions that can be drawn; a whole-brain approach was therefore used here. We assessed early mother–child attachment security with the Attachment Behavior Q-Sort (AQS; Waters and Deane, 1985), which yields a continuous score for attachment security rather than assignment to a particular attachment category. This approach maximizes statistical power by affording excellent detection of fine individual differences, and may be especially appropriate in the context of small sample sizes (Groh et al., 2017b). Psychometric work also suggests that a dimensional approach is coherent with the underlying structure of individual differences in attachment (Fraley and Spieker, 2003). Given the scarcity of literature on attachment security and brain morphology in typically developing children, and the fact that a large number of brain regions have been variously linked to caregiving experiences, the statistical analyses were exploratory and no *a priori* hypotheses were formulated with regards to the location of putative associations or the direction of associations, considering also that some aspects of brain development trajectories follow an inverted U-shape (Shaw et al., 2008; Giedd et al., 2015).

## MATERIALS AND METHODS

### Participants

Participants included in the present study ($n = 33$) were followed annually as part of a larger longitudinal research project that documents the prospective associations between the early caregiving environment and several facets of child development (see Bélanger et al., 2015). In the present study, we report on attachment security assessed at 15 months of age (T1; $M = 15.65$, $SD = 0.97$, range = 14.50 – 18.00) and structural magnetic resonance imaging (MRI) data collected when children were 10–11 years of age (T2, $M = 10.59$, $SD = 0.46$, range = 10.0 – 11.67 years). The study was approved by the local research ethics committee of aging-neuroimaging of the CIUSSS du Centre-Sud-de-l'île-de-Montréal and all families provided written informed consent for participation.

Families were recruited from random birth lists of a large Canadian metropolitan area, provided by the Ministry of Health and Social Services. Inclusion criteria for participation were full-term pregnancy (i.e., at least 37 weeks of gestation) and the absence of any known physical or mental disability, severe developmental delay in the infant, acquired brain injury, and standard MRI counter-indications. For the current analyses, 64 families were invited to participate in structural MRI when children reached 10 years of age; among them, 35 (54.69%) agreed to participate. Families who agreed to participate ($n = 35$) did not differ from those who refused ($n = 29$) in terms of family income, parental age, education, and ethnicity, as well as child attachment security to mother in infancy (all *p*s > 0.21, see **Table 1**). Of the 35 families who agreed to take part in the MRI protocol, one child was excluded from the analyses because of excessive head motion (translation > 2.5 mm or rotation > 2.5 degrees) and one because of suspected neuropathology. Consequently, data from 33 children [20 girls and 13 boys; $\chi^2(1) = 1.46$, $p = 0.23$] were used in the analyses. Group comparisons between families included in the analyses ($n = 33$) and those who declined the MRI protocol ($n = 29$) were not significant.

## Attachment Security Assessment

Mother–infant attachment security was assessed at T1 using the Attachment Behavior Q-Sort (AQS; Waters and Deane, 1985). The observer-version of the AQS is considered one of the gold-standard measures of attachment (Van IJzendoorn et al., 2004) as it shows excellent construct validity, converging with attachment security assessed with the SSP, with child socio-emotional adaptation, and with maternal sensitivity (see Van IJzendoorn et al., 2004; Cadman et al., 2017 for meta-analytic evidence), while also demonstrating discriminant validity with respect to child temperament (Cadman et al., 2017). In fact, meta-analytic data suggest that the AQS is more closely related to child outcomes than the SSP (Fearon et al., 2010), which makes it an instrument of choice to study putative associations between early attachment and brain morphology.

In this study, trained research assistants observed infant behaviors throughout a 70- to 90-min home visit modeled after the work of Pederson and Moran (1995). This visit was purposely designed to create a situation during which maternal attention was solicited by both infant demands and research-related tasks (e.g., mothers had to fill in questionnaires while infants were not cared for by the research assistant). This aimed at challenging mothers' capacity to divide their attention between competing demands, thus reproducing the natural conditions of daily life when caring for an infant. Restricting maternal availability to infant demands is a classic trigger of the attachment system in infancy (Ainsworth et al., 1978). The research assistants completed the AQS immediately after the visit. In order to maximize the reliability of the observations performed during these home visits, which was central to this study, we followed Pederson and Moran's (1995) recommendations for training our home visitors. Research assistants first attended a 2-day training workshop on techniques of home visiting and structured observation of mother–infant interactions. They reviewed several videotapes to practice coding the AQS. The assistants then performed their first few home visits with a more experienced colleague, and the two completed the AQS together. When the junior home visitors were deemed ready to lead home visits independently, the next two or three visits were followed by a debriefing session with an experienced graduate student, to review the salient elements of the visit before scoring the AQS. Inter-rater reliability testing (described below) took place only after assistants had successfully completed this training.

The AQS consists of 90 items measuring the quality of the child's attachment behaviors toward a specific figure (the mother in this case). Each item of the AQS describes a potential child behavior. Based on observations performed

**TABLE 1 |** Sociodemographic information and attachment security scores for families who accepted vs. declined participation in the magnetic resonance imaging (MRI) protocol.

| | Accepted MRI $n = 35$ | Declined MRI $n = 29$ | Group comparisons |
|---|---|---|---|
| **Parental age at recruitment** | | | |
| Mothers | 31.63 ± 5.05 | 32.02 ± 3.50 | $t(62) = -0.36$; $p = 0.73$ |
| Fathers | 33.40 ± 5.29 | 34.07 ± 4.86 | $t(62) = -0.52$; $p = 0.60$ |
| **Parental years of education** | | | |
| Mothers | 15.40 ± 2.23 | 15.26 ± 2.32 | $t(62) = 0.24$; $p = 0.81$ |
| Fathers | 15.60 ± 1.94 | 14.97 ± 2.10 | $t(62) = 1.30$; $p = 0.21$ |
| **Ethnicity** | | | |
| Mothers | 80.00 | 86.21 | $\chi^2(1) = 0.43$; $p = 0.51$ |
| Fathers | 74.30 | 75.90 | $\chi^2(1) = 0.02$; $p = 0.89$ |
| Family income | 74.29 | 79.31 | $\chi^2(1) = 0.22$; $p = 0.64$ |
| Language at home | 80.00 | 82.76 | $\chi^2(1) = 0.08$; $p = 0.78$ |
| Attachment security | 0.48 ± 0.26 | 0.50 ± 0.20 | $t(62) = -0.42$; $p = 0.67$ |

*For ethnicity, family income, and language, values represent percentages of families with a Caucasian mother/father, an income above $60,000, and French as the main language. For parental age, parental education, and attachment security, values represent mean ± standard deviation. Two children who underwent MRI were excluded from main statistical analyses (n = 33): excluding them from the group comparisons did not change the results.*

during the entire home visit, research assistants sorted those behaviors into nine clusters of 10 items each, ranging from "very similar" to "very unlike" the observed child's behaviors. The global score for attachment security consists of the correlation between the observer's sort of the 90 items and a criterion sort for the prototypically secure infant (Waters and Deane, 1985). Attachment security scores can thus range from −1.0 (highly insecure) to 1.0 (highly secure). Prototypical security represents a fluid balance between exploration of the environment and appropriate reliance on the caregiver for support when needed. To examine inter-rater reliability, 23.1% of the home visits were conducted by two research assistants, who then completed the AQS independently. Agreement between the two raters' sorts was satisfactory, intra-class correlation (ICC) = 0.71.

## Pubertal Status

A parent-report version of the rating scale for pubertal development (Carskadon and Acebo, 1993) was completed at the time of the MRI (T2). Parents evaluated their child's pubertal development using a scale ranging from 1 = "not yet started" to 4 = "seems completed." Children's pubertal status was derived from three items for both boys (body hair growth, voice change, facial hair growth) and girls (body hair growth, breast development, menarche), as described by Carskadon and Acebo (1993).

## Structural Magnetic Resonance Imaging

### Acquisition

Neuroimaging data were collected at T2 using a 32-channel head coil on a Siemens 3 Tesla scanner (MAGNETOM Trio, Siemens, Erlangen, Germany). Structural data were acquired using a three-dimensional T1-weighted 4-echo magnetization-prepared rapid gradient-echo sequence [3D-T1-4echo-MPRAGE sagittal; repetition time (TR): 2530 ms; first echo time (TE): 1.64 ms; echo spacing ΔTE: 1.86 ms; flip angle: 7°; 176 slices; slice thickness: 1 mm; no gap; matrix: 256 × 256; field of view (FoV): 256 mm; in-plane resolution: 1 mm× 1 mm; duration: 363 s].

### Pre-processing

Pre-processing for the voxel-based morphometry (VBM) and the surface-based morphometry (SBM) analyses were performed using the SPM12 package (Statistical Parametric Mapping, Institute of Neurology, London, United Kingdom) and the CAT12 Toolbox[1] running on MATLAB version R2016a (MathWorks, Inc., Natick, MA, United States). For VBM, T1-weighted images were segmented into GM, white matter (WM), and cerebrospinal fluid (CSF) using age-appropriate stereotaxic tissue probability maps (NIHPD 7.5-13.5 asymmetric[2]; Fonov et al., 2011). Pediatric templates were used to minimize the potential confounds introduced by developmental differences in cortical morphometry (Yoon et al., 2009). Next, the segments were spatially normalized to the Montreal Neurological Institute (MNI) space with a voxel size of 1.5 mm × 1.5 mm × 1.5 mm. Finally, the resulting GM maps were modulated and smoothed with 8-mm full-width-at-half-maximum (FWHM) smoothing kernels. For SBM, T1-weighted images were segmented and spatially normalized as for VBM. The cortical surface was reconstructed from volumetric data using the projection-based thickness method. The cortical thickness maps were resampled onto the cortical surface and smoothed with a standard 15-mm FWHM smoothing kernel.

### Statistical Analyses

The threshold-free cluster enhancement (TFCE) method implemented in CAT12 was used to identify statistically significant clusters. TFCE is a cluster-based thresholding method that overcomes the problem of choosing an arbitrary cluster-forming threshold, while keeping the sensitivity advantage of cluster-based thresholding (Smith and Nichols, 2009). TFCE uses a permutation approach that maximizes statistical power in small sample studies (Pernet et al., 2015). Using 5,000 permutations and non-parametric testing, a voxel-wise *p*-value map is produced. An explicit GM mask based on the mean normalized GM images of all participants was used to ensure that the analyses were restricted to GM. Resulting statistical maps were thresholded at $p < 0.05$ corrected for multiple comparisons by false discovery rate (FDR; Chumbley et al., 2010).

## Main Analyses

The main analyses focused on GM volume and thickness. A multiple regression analysis was performed using CAT12 to predict GM volumes in late childhood from attachment security in infancy, after accounting for confounding variables (described below). Similar analyses were performed to predict cortical thickness, and right and left hemispheres were analyzed separately. In order to account for differences in overall brain size, total intracranial volume (ICV) was controlled for in the VBM analyses (Barnes et al., 2010; Malone et al., 2015). As ICV is not related to cortical thickness (Toro et al., 2008; Winkler et al., 2010), it was not controlled for in the SBM analyses. Child age and sex, pubertal status, as well as maternal education are associated with cortical volume and thickness (Barnes et al., 2010; Blakemore et al., 2010; Jednoróg et al., 2012), and were therefore included as covariates in both the VBM and SBM analyses.

The AQS score was missing for one child. In line with recommendations for best practices for handling missing data, multiple imputation was employed to estimate the missing value (Enders, 2010) using the Markov Chain Monte Carlo procedure (Geyer, 1992) in SPSS software version 24.0 (IBM Corp., Armonk, NY, United States). Ten imputations were used and then averaged to maximize the precision of imputed data (Graham, 2009; Enders, 2010). To reach maximal accuracy, the imputations were performed based on the original 64 families using child sex and age at T1, as well as parental age and education at the time of recruitment as predictors in the imputation equation.

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[1] www.neuro.uni-jena.de/cat/

[2] www.bic.mni.mcgill.ca/ServicesAtlases/NIHPD-obj1

# RESULTS

## Descriptive Statistics

At the time of initial recruitment (when children were 7 months old; $n = 33$), mothers and fathers were, respectively, on average 31.73 ($SD = 5.10$) and 33.27 ($SD = 5.00$) years old and had on average 15.36 ($SD = 2.28$; range 10–18) and 15.58 ($SD = 2.00$; range 11–17) years of education. The families' average income fell in the \$60,000 to \$79,000 bracket. The majority of mothers (78.80%) and fathers (75.80%) were Caucasian. Most families had French as their first language (78.80%). Attachment security scores at T1 varied from −0.28 to 0.75 ($M = 0.49$, $SD = 0.26$).

At T2, almost half of the children (45%) were pre-pubertal, two were early pubertal (6%), 15 were mid-pubertal (45%), and one was post-pubertal (3%). Average brain volumetric data were: 1529.34 $cm^3$ ($SD = 106.58$, range = 1317.63–1854.37) for total ICV; 833.27 $cm^3$ ($SD = 53.40$, range = 725.37–987.76) for total GM volume; 442.40 $cm^3$ ($SD = 44.44$, range = 367.07–552.58) for total WM volume; and 253.67 $cm^3$ ($SD = 23.68$, range = 205.73–314.04) for total CSF. **Table 2** displays the bivariate correlations among attachment security, child age and sex, pubertal status, maternal education, and volumetric data (total ICV, total GM volume, total WM volume, and total CSF). No outliers were identified on any of the attachment or anatomical measures.

## Voxel-Based Morphometry

Multiple regression analysis indicated that after accounting for child age, sex, pubertal status, maternal education, and total ICV, children who were more securely attached to their mother in infancy had larger GM volumes in the right hemisphere covering the superior temporal sulcus and gyrus, extending to the middle temporal gyrus, and into the temporo-parietal junction. Increased GM volume in the left superior temporal sulcus and in the bilateral precentral gyri was also related to higher attachment quality (see **Figure 1** and **Table 3**). No significant supra-threshold voxels were found for negative contrasts.

## Surface-Based Morphometry

Multiple regression analysis indicated that attachment security in infancy was not significantly related to cortical thickness in late childhood, neither positively nor negatively, over and above child age, sex, pubertal status, and maternal education ($p > 0.001$, uncorrected).

# DISCUSSION

To our knowledge, this is the first study to examine the prospective associations between attachment security in infancy and whole-brain GM volume and thickness in childhood. The main findings indicate that children who were more securely attached to their mother in infancy (15 months) had larger GM volume in the bilateral superior temporal sulci, right superior temporal gyrus, right temporo-parietal junction, and the bilateral precentral gyri in late childhood (10–11 years). These results survived a multiple comparisons correction after controlling for several potentially confounding variables. No significant association was found between attachment security and cortical thickness. Consistent with animal studies indicating that enriched caregiving is associated with optimal brain development (Greenough et al., 1987; Van Praag et al., 2000; Meaney, 2001), the current study provides rare data in humans consistent with the idea that attachment relationships may affect children's brain development, as reflected by larger GM volume in the frontal and temporal lobes. Moreover, these results contribute to the emerging literature indicating that variations in the quality of caregiving experiences within the normative range are associated with child brain morphology (Luby et al., 2012, 2016; Whittle et al., 2014, 2016; Kok et al., 2015, 2017).

Specifically, better quality mother–child relationships in infancy were found to be predictive of larger GM volume in the superior and middle temporal gyri, superior temporal sulci, temporo-parietal junction, and precentral gyri in late childhood. This appears to be the first evidence of a relation between a direct observational measure of caregiving quality (whether parenting or attachment) and GM volume in these specific brain regions. The lack of prior comparable findings may be partly expected, given that no previous studies have investigated the association between parent–child relationship quality or parental behaviors and *whole-brain* GM volume in a pediatric community sample. However, the current findings are broadly consistent with studies

**TABLE 2 |** Correlations between attachment security, average brain volumetric data, and covariates.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| (1) Attachment security | | | | | | | | | |
| (2) Total ICV | −0.09 | | | | | | | | |
| (3) Total GMV | 0.05 | $0.94^{**}$ | | | | | | | |
| (4) Total WMV | −0.30 | $0.92^{**}$ | $0.80^{**}$ | | | | | | |
| (5) Total CSF | 0.04 | $0.66^{**}$ | $0.46^{**}$ | $0.48^{**}$ | | | | | |
| (6) Child sex[a] | 0.04 | $-0.53^{**}$ | $-0.53^{**}$ | $-0.51^{**}$ | −0.25 | | | | |
| (7) Child age | −0.26 | 0.03 | 0.00 | 0.15 | −0.12 | −0.23 | | | |
| (8) Maternal education | 0.21 | −0.31 | −0.27 | −0.25 | −0.31 | 0.21 | −0.10 | | |
| (9) Pubertal status[b] | 0.13 | $-0.38^{*}$ | $-0.39^{*}$ | $-0.33^{t}$ | −0.21 | −0.16 | $0.69^{***}$ | 0.11 | |

[a]*Child sex was coded 1 = boy; 2 = girl.* [b]*Pubertal status was coded 1 = prepubertal; 2 = early pubertal; 3 = mid pubertal; 4 = late pubertal. ICV, intracranial volume; GMV, gray matter volume; WMV, white matter volume; CSF, cerebrospinal fluid.* $^{t}p < 0.10$, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

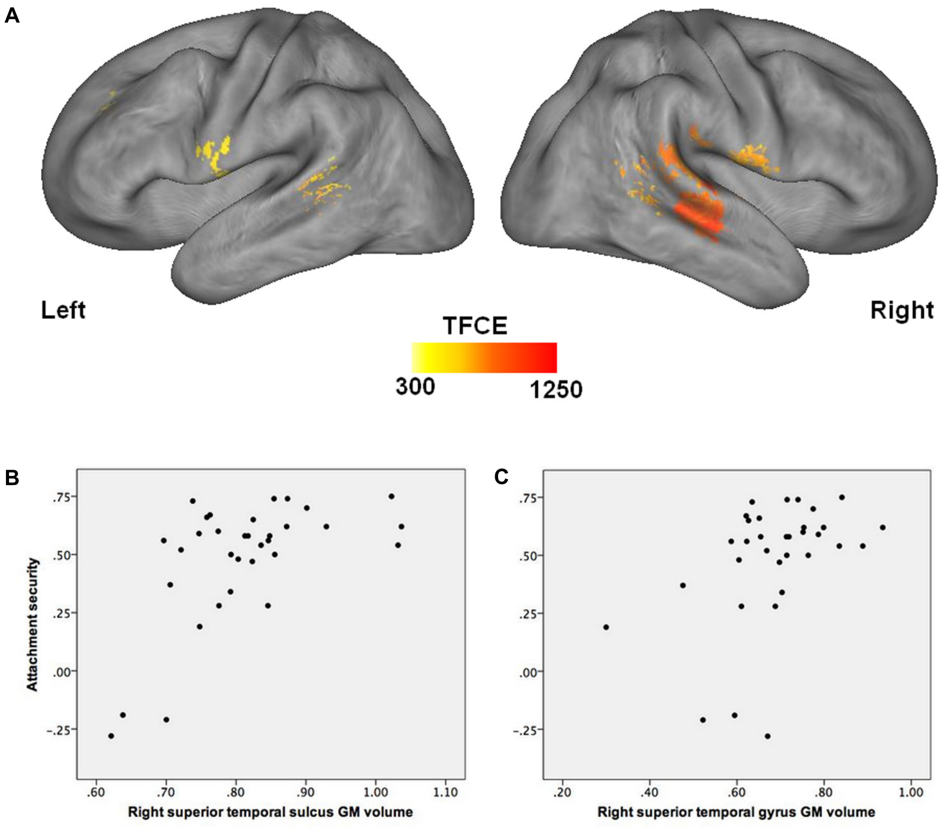

**FIGURE 1 |** Association between attachment security in infancy and GM volume in late childhood. **(A)** Higher attachment security in infancy is associated with greater GM volume in the right superior temporal sulcus and gyrus, temporo-parietal junction, and precentral gyrus, as well as in the left superior temporal sulcus and precentral gyrus (FDR corrected, $p < 0.05$), after accounting for child age, sex, pubertal status, maternal education, and total intracranial volume. **(B)** Correlation between attachment security in infancy and GM volume in the right superior temporal sulcus in late childhood [$x = 45$; $y = -21$; $z = -4$]. **(C)** Correlation between attachment security in infancy and GM volume in the right superior temporal gyrus in late childhood [$x = 68$; $y = -33$; $z = 20$]. GM, gray matter.

**TABLE 3 |** Regional volumes significantly associated with attachment security in infancy ($p < 0.05$, False Discovery Rate correction).

| Regions | BA | *k* | MNI coordinates (*x*, *y*, *z*) | *TFCE* |
|---|---|---|---|---|
| **Right** | | | | |
| Superior temporal sulcus[a] | 48/21 | 601 | 45, −21, −4 | 1122.72* |
| | | | 57, −24, −3 | 1120.15* |
| Superior temporal gyrus | 48 | 150 | 68, −33, 20 | 816.95 |
| Temporo-parietal junction | 21 | 34 | 60, −39, 2 | 744.62 |
| | | | 60, −48, 9 | 735.12 |
| Precentral gyrus | 48 | 43 | 63, −3, 9 | 649.53 |
| **Left** | | | | |
| Superior temporal sulcus | 22 | 22 | −58, −40, 8 | 660.78 |
| Precentral gyrus | 48 | 51 | −52, −3, 15 | 450.97 |

**Results hold at $p < 0.05$, Family Wise Error correction. [a]Cluster peak was in the superior temporal sulcus, but the cluster also covered the superior and middle temporal gyrus. BA, Brodmann area; k, number of voxels; TFCE, threshold free cluster enhancement statistic.*

reporting smaller GM volume or surface in the superior and middle temporal gyri of maltreated children (Hanson et al., 2010; De Brito et al., 2013; Kelly et al., 2013, 2015; Lim et al., 2014). These areas are critical for processing emotional stimuli (Allison et al., 2000), a function that is impaired in maltreated children, as indicated by event-related potential and functional MRI studies (see da Silva Ferreira et al., 2014 for a systematic review; Pollak et al., 2001). Importantly, the preliminary results presented here suggest that even normative variations in relationship quality may have a long-lasting impact on the development of these brain regions. This is a promising first step, but independent replication is necessary.

In contrast to previous studies reporting an association between parental behavior and cortical thickness in typically developing children (Whittle et al., 2014, 2016; Kok et al., 2015), no significant association was found in this sample between attachment security in infancy and cortical thickness in late childhood. Methodological differences, such as the modest sample size and related limited statistical power in the current study, may account for this discrepancy. Developmental considerations may also be at play. Brain volume and thickness follow an inverted U-shape developmental trajectory characterized by an increase during childhood, a region-specific peak in late childhood and early adolescence, and a subsequent decrease (Shaw et al., 2008; Giedd et al., 2015). Results reported here are age-specific (10–11 years); in a younger or older sample, results may be different. Previous work by Kok et al. (2015) indicates that maternal sensitivity in early childhood is associated with brain volume and thickness in 8-year-old children. Moreover, as Teicher and Samson (2016) underscore, caregiving experiences may not relate to brain structures at one specific period of development, but rather, they may be associated with the trajectory of brain development over time (see also Whittle et al., 2014). Thus, one intriguing possibility that could be investigated in future work is that attachment security may not relate to cortical thickness at specific ages, but rather to the rhythm of cortical thickening and then thinning over time. Alternatively, the findings may be theoretically meaningful, indicating for instance that, although related to an extent, parenting behavior and parent–child attachment may have a different impact on brain development. Of note, we did not find links between attachment and amygdalar volume as observed by Moutsiana et al. (2015) and Lyons-Ruth et al. (2016). In addition to the different composition of the samples studied and the different attachment measure used, developmental considerations may again underlie discrepant findings, given that the previous studies found links between early attachment and amygdalar volume in adulthood. Longitudinal designs including repeated MRI would be useful to more accurately depict the developmental aspects of the brain-attachment associations.

## Attachment and the Developing Brain: Proposed Mechanisms

Children more securely attached to their primary caregivers are exposed to a variety of experiences that differ from those characterizing insecurely attached children. These experiences may influence children's brain development in regions involved in social, cognitive, and emotional functioning. A central way in which the experience of securely attached infants differs from that of their insecurely attached counterparts is with regards to the quality of the emotion regulation provided by the caregiver. Indeed, one of the hallmarks of a secure attachment relationship is the caregiver's capacity to provide adequate external regulation when the infant encounters an affectively challenging situation during exploration (e.g., frustration when faced with a complex toy, fear of a large dog in the park). As a result, securely attached children are exposed to repeated experiences of successful regulation in emotionally taxing situations, which provides a strong basis for the gradual development of self-regulation (Calkins, 2004; Cole et al., 2004). The superior and middle temporal gyri are activated when subjects need to down-regulate their negative affect (Ochsner et al., 2004; Frank et al., 2014), and extensive evidence from human and non-human primates points to a crucial role for the superior temporal gyrus and sulcus for processing emotional faces stimuli (Britton et al., 2006; Pagliaccio et al., 2013). If replicated, the current findings would suggest that the repeated experiences of successful emotion regulation that characterize secure attachment relationships may promote optimal development in brain regions that subsume socio-emotional regulation, such as the superior and middle temporal gyri, through experience-dependent processes.

An alternative hypothesis for the observed relation between attachment and brain structure pertains to one of the central notions of attachment theory, that of "internal working models" (Bowlby, 1969/1982, 1973, 1980, 1988). These models consist of mental representations of self and others, which are thought to be shaped by daily interactions with primary caregivers. The repeated experiences of responsive care that characterize secure attachment are believed to promote the development of positive internal working models of self and others (Bretherton and Munholland, 2016). It is theorized that these models are progressively internalized, becoming an integral part of the child's personality, and are increasingly generalized to new relationships, guiding behavior and interpretation in new social situations and helping children correctly anticipate future social interactions (Bretherton and Munholland, 2016). Empirical evidence indeed shows that securely attached infants develop positive expectations about social interactions (Johnson et al., 2010; Biro et al., 2015). Importantly, the superior and middle temporal gyri, temporo-parietal junction, and precentral gyrus are involved in the representation and elaboration of past and future events (Kelley et al., 2002; Addis et al., 2007; Spreng et al., 2009; Holland et al., 2011; Jacques et al., 2011) and representation of self and others (Ruby and Decety, 2001; Ochsner et al., 2004). The positive expectations about social relationships characterizing secure attachment working models may lead securely attached children to engage more confidently in social interactions. Thus, these children are likely to be more frequently engaged in stimulating social interactions which may result in recurrent activation of brain regions involved in the representation of self and others in social contexts. As such, secure attachment could promote the optimal structural development of the superior and middle temporal gyri, temporo-parietal junction, and precentral gyrus.

Lastly, social perception and social cognition may play a role in the attachment-brain structure links uncovered here. Social perception is an important basis for the development of attachment relationships. In order to effectively attain a caregiver's proximity, children have to adapt their attachment behaviors toward their caregivers according to the context, caregiver location, and the specific characteristics of the caregiver with whom they are interacting (Cassidy, 2016; Sroufe, 2016). Recognizing the caregiver's face and affective state as well as following his or her eye gaze and movements support the contextual adaptation of infant attachment behavior for proximity seeking. As such, empirical evidence indicates that higher levels of attachment security in infancy are associated with better emotion recognition skills up to 10 years later (Steele et al., 2008). Assuming that future research replicates the current results, the association between attachment security and GM volume in the superior and middle temporal gyri may therefore be related to the importance of these brain regions for social perception, such as the detection of faces, eye gaze, and biological motion (Puce et al., 1998; Allison et al., 2000; Haxby et al., 2000; Engell and Haxby, 2007; Saygin, 2007). It is possible that securely attached children are more successful in adapting their attachment behaviors to the context by recruiting temporal regions involved in social perception, which in turn promotes the development of these regions. The value of attachment security for complex social cognitive processes and social functioning is also well established (Thompson, 2016), and numerous studies have underscored the role of the superior temporal sulcus and gyrus, middle temporal gyrus, and the temporo-parietal junction in theory of mind, moral reasoning, and empathy (see Bzdok et al., 2012, for a meta-analysis). Larger GM volumes in the superior and middle temporal gyri have been related to more optimal social skills, such as better emotion recognition (Shdo et al., 2017) and better ability to predict others' behavior based on mental states (Powell et al., 2014). Conversely, reduced GM thickness or volume in the superior and middle temporal gyri has been associated with lack of empathy and compassion and severity of conduct disorder symptomatology (Huebner et al., 2008; Fahim et al., 2011; Wallace et al., 2014). Overall, these studies suggest that GM volume and functional activity in the superior temporal sulcus and gyrus, middle temporal gyrus, and temporo-parietal junction are closely linked with social cognition and social functioning, of which attachment security is a well-known predictor (Thompson, 2016). Social cognitive experiences embedded in secure attachment relationships provide children with a more sophisticated understanding of the psychological dimensions of social interactions (Thompson, 2016) and may therefore contribute to shaping the structural development of regions involved in social cognition, such as the superior temporal sulcus and gyrus, the middle temporal gyrus, and the temporo-parietal junction.

## Limitations

The results presented here must be interpreted in the context of some limitations. First, the longitudinal but non-experimental design precludes causal inference and determination of directionality. The possibility that larger GM volumes in the superior and middle temporal gyri, the superior temporal sulci, the temporo-parietal junction, and the precentral gyri were already present in these children in infancy, and may have predisposed them to develop secure attachment to their mothers, cannot be excluded. In fact, given that developmental processes are transactional by nature (Sameroff, 2009), it is reasonable to expect that any caregiving-brain associations are probably bidirectional, reflecting the action of mutual reciprocal influences between parent and child (Serbin et al., 2015). The non-experimental design also leaves open some third-variable explanations, notably the possibility that shared genes between mother and child may be partly responsible for the links observed. This is unlikely to have played a major role in the current results though, given that several genetically informed studies show that the variance in mother–child attachment security (O'Connor and Croft, 2001; Bokhorst et al., 2003; Roisman and Fraley, 2008) and the variance in maternal caregiving behavior (Roisman and Fraley, 2008) are almost entirely attributable to environmental influences, with small to negligible genetic contributions. Other third-variable explanations are possible though, one of which being that caregiving experiences (e.g., exposure to higher parental sensitivity) could influence both the quality of attachment relationships and the development of corresponding brain regions. Second, the small sample size and the use of several covariates reduced statistical power, potentially leading to underestimation of the links between attachment and brain volumes and thickness. Clearly, replication in larger independent samples is necessary to confirm the links reported here, especially for clusters in the right temporo-parietal junction and precentral gyrus, as well as in the left precentral gyrus and superior temporal sulcus, due to the small number of voxels contained in these clusters. Third, the attachment measure used in the current study does not allow the assessment of attachment disorganization (the most extreme form of attachment insecurity, assessed exclusively through the SSP), which one study found to be related to amygdalar volume (Lyons-Ruth et al., 2016). Disorganized attachment relationships are associated with the development of psychopathology, poor emotion regulation skills, and poor relationships with peers and adults (Lyons-Ruth and Jacobvitz, 2016), which could be reflected in children's brain morphology, especially in brain regions known to be involved in socio-emotional functioning (limbic system, social brain). Fourth, we did not assess father–child attachment security, which may differentially influence brain development given that fathers have unique contributions to children's social and cognitive development (see Cabrera and Tamis-LeMonda, 2013). However, Kok et al. (2015) reported that the associations between parental sensitivity and brain morphology were similar for mothers and fathers in their sample.

# CONCLUSION

This 9-year longitudinal study suggests that better mother–child attachment quality in infancy is related to greater GM volume in the superior temporal sulcus and gyrus, the temporo-parietal junction, and precentral gyrus in late childhood, whereas no associations with measures of cortical thickness were found. This appears to be the first study to investigate the link between infant-caregiver attachment quality and brain morphometry in childhood. The use of a gold-standard observational measure of attachment security in the ecological context of the family home, along with whole-brain analyses using a pediatric template, enabled the identification of novel associations between attachment and brain regions involved in social, cognitive, and emotional functioning, and these associations were robust to several important covariates. Although preliminary and in need of replication, the present results provide further evidence that infant quality of attachment toward a primary caregiver is important not only for children's social, emotional, and cognitive functioning, but may also be involved in their brain development. As in previous studies focusing on maltreatment (e.g., da Silva Ferreira et al., 2014; Puetz et al., 2017), future research in normative samples could test, using other methodologies (e.g., diffusion tensor imaging, functional connectivity, event-related potentials), the breadth of the links between attachment security in infancy and brain morphology and functions.

## ETHICS STATEMENT

The research ethics committee of aging-neuroimaging of the CIUSSS du Centre-Sud-de-l'île-de-Montréal approved the study. The goal of the study was explained to children and their parents, who signed a detailed inform consent form. We report how we determined our sample size, all manipulations, and all measures in the study.

## AUTHOR CONTRIBUTIONS

ÉL participated in data collection, performed statistical analyses, and drafted the initial manuscript. AB designed the study, wrote parts of the manuscript and revised it for intellectual content. MB contributed to designing the study, edited and revised the manuscript for intellectual content. FD contributed to data analyses and interpretation, wrote parts of the manuscript and revised it for intellectual content. VD participated in data collection and methodological choices, and revised the manuscript for intellectual content. All authors gave their final approval of the manuscript to be published and agreed to be accountable for all aspects of the work.

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# Inhibitory Control Mediates the Association between Perceived Stress and Secure Relationship Quality

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Past research has demonstrated negative associations between exposure to stressors and quality of interpersonal relationships among children and adolescents. Nevertheless, underlying mechanisms of this association remain unclear. Chronic stress has been shown to disrupt prefrontal functioning in the brain, including inhibitory control abilities, and evidence is accumulating that inhibitory control may play an important role in secure interpersonal relationship quality, including peer problems and social competence. In this prospective longitudinal study, we examine whether changes in inhibitory control, measured at both behavioral and neural levels, mediate the association between stress and changes in secure relationship quality with parents and peers. The sample included 167 adolescents (53% males) who were first recruited at age 13 or 14 years and assessed annually three times. Adolescents' inhibitory control was measured by their behavioral performance and brain activities, and adolescents self-reported perceived stress levels and relationship quality with mothers, fathers, and peers. Results suggest that behavioral inhibitory control mediates the association between perceived stress and adolescent's secure relationship quality with their mothers and fathers, but not their peers. In contrast, given that stress was not significantly correlated with neural inhibitory control, we did not further test the mediation path. Our results highlight the role of inhibitory control as a process through which stressful life experiences are related to impaired secure relationship quality between adolescents and their mothers and fathers.

**Keywords: adolescence, inhibitory control, perceived stress, relationship quality, functional magnetic resonance imaging**

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## INTRODUCTION

Though adolescence can be a difficult transitional period in which risks to both physical and mental health, including depression, substance abuse, and suicide increase (Dahl, 2004), adolescents who have secure relationships with both their parents and peers may be able to navigate this period more successfully (Nickerson and Nagle, 2005). However, chronic stress has been implicated as a risk factor for interpersonal challenges. Past research has demonstrated negative associations between exposure to stressors and quality of interpersonal relationships, including parent–child relationships and peer relationships, among children and adolescents (Bonn, 1995; Mohr, 2006; Brown and Fite, 2016; Platt et al., 2016). Nevertheless, underlying mechanisms of this association remain unclear. Based on the neuroscience literature illustrating stress effects on prefrontal functioning and the developmental psychology literature indicating important roles of self-regulation in social development, we examined inhibitory control as a potential mediator in the association between stress and secure relationship quality.

Extant research has shown that children and adolescents with stressful life experiences tend to have negative relational experiences—with peers as well as parents. With respect to peer relationships, children who have been rejected by their peers are more likely than non-rejected children to have been exposed to multiple chronic stressors, including financial strain, living with a single parent, violence in the home, parental divorce, and family illness (Bonn, 1995; Baldry, 2003; Mohr, 2006). Furthermore, these stressors seem to create cumulative risk for adverse peer relations, suggesting that these difficulties are visible to children's peer groups and predictive of adjustment difficulties within that peer group (Bonn, 1995). With respect to parent–child relationships, in one available study conducted to assess potential mechanisms in the association between stressful life events and child anxiety, a dysfunctional parent–child relationship emerged as a significant mediator, demonstrating a link whereby stressful life events may increase a parent's self-reported dissatisfaction with their parent–child relationship (Platt et al., 2016). Another study demonstrated that the activation of stress hormones, including cortisol, predicted adolescents' perception of problems within the family unit (Marceau et al., 2012). Finally, studies examining stressful life events on attachment outcomes indicate that caregiver stressful life events (e.g., abuse, neglect, divorce, caregiver death, and caregiver substance use) are associated with changes in attachment style over time (Waters et al., 2000; Weinfield et al., 2000).

To date, how stressful life experiences may be related to interpersonal relationships is not clearly understood. Mohr (2006) posits that the association between stress and interpersonal relationship quality may be due to the behavior exhibited by the children and youth experiencing these high degrees of family adversity. Often times, these individuals have difficulties modulating their own behavior and affect in interpersonal relationships. Unregulated, impulsive, and even perhaps aggressive behavior as a result may provoke negative interpersonal relationships. Similarly, research has suggested that the association between stressful life events and relationship quality may develop through social functioning deficits through an inappropriate pattern of relating to others and an inability to self-regulate (Brown and Fite, 2016).

Within the neuroscience literature, previous research has demonstrated that stress is associated with impaired structure and function of the prefrontal cortex (PFC), a brain region that contributes to self-regulation capabilities (see Hermans et al., 2014 for a review). Given that adolescence is a prolonged period of brain development, the immaturity and plasticity associated with this continued development, while adaptive in nature, leaves the brain vulnerable to potentially detrimental effects of enduring stress (Tottenham and Galván, 2016). While stress has deleterious effects on many brain regions (i.e., hippocampus, amygdala, see McEwen, 2007 for a review), given the present study's focus on inhibitory control using the multi-source interference task (MSIT), we chose to restrict our review of the detrimental effects of stress on the brain to the PFC. Literature has shown the PFC to be the primary brain region related to self-regulation abilities, including cognitive inhibitory control and performance on the MSIT (Bush et al., 2003; Koechlin et al., 2003; Hermans et al., 2014). In rodent studies, chronic stress has been shown to alter the neuronal networks in the PFC by reducing dendritic length, branching, and spinal density (Arnsten, 2009). In a study designed to assess comparable changes in human adults experiencing stress, functional imaging data revealed that executive functions engage the PFC network and that the disruption of the integrity and connectivity of the PFC network results in impaired executive function abilities (Liston et al., 2009). Though caution must be taken in generalizing these results from rodents to humans, the disruption of the frontoparietal attention network in this study seems consistent with the demonstration in rodent studies of significant alterations to dendrites that not only impair connections within the PFC but also with surrounding areas (Liston et al., 2009). As a result, these structural changes may have important implications for the functioning of the PFC as a top-down regulatory system as well as the functional coupling between structures in these networks. Furthermore, the effects of stress on the PFC may be particularly harmful for developing brains. Indeed, in a study examining stress effects on cognitive control performance and related prefrontal functioning, although both adolescents and adults showed impaired inhibitory control performance, adolescents exhibited less recruitment of the dorsolateral prefrontal cortex (DLPFC) during inhibition under high stress versus low stress, whereas adults showed the opposite activation pattern in the DLPFC (Rahdar and Galván, 2014). In sum, current literature suggests that brain regions associated with the development of cognitive control in childhood and adolescence are generally affected by stress (see Arnsten, 2009 for a review). Particularly, in adolescents, stress-related dopamine release might flood an already saturated dopaminergic system to risk and reward. Excess dopamine receptor binding in the adolescent PFC then could lead to compromised PFC function, further subverting maturing regulatory functions (Uy and Galván, 2017).

Recent research is beginning to clarify the effects of these structural changes due to stress, suggesting impairments in executive functions, including in inhibitory control, attention, and memory. For example, children exposed to chronic stress via poverty display multiple self-regulatory deficits. In a behavioral study, children who experienced chronic poverty were rated by both parents and teachers as weaker in inhibitory control and delaying gratification (Evans and Kim, 2012). Similarly, in a functional magnetic resonance imaging study, adolescents who had experienced early life stress displayed impaired inhibitory control, as demonstrated by both poorer behavioral performance and greater activation in brain regions associated with inhibitory control (Mueller et al., 2010). Such results are consistent with findings using an adult sample demonstrating that those experiencing chronic stress exhibited cognitive deficits on a number of tasks requiring executive functions, including inhibitory control (Arnsten, 2009). Although correlational, taken together, previous findings suggest that there may be neurocognitive consequences of exposure to chronic stress.

Such consequences may manifest themselves within the quality of interpersonal relationships. For instance, Farley and Kim-Spoon (2014) emphasized the impact of self-regulation on interpersonal relationships during adolescence with individuals who were better able to self-control demonstrating higher quality relationships with parents and peers. Indeed, the literature demonstrates a robust link between inhibitory control and interpersonal relationship quality, suggesting that inhibitory control is necessary for successful interpersonal relationships. In early childhood, children who exhibit poorer inhibitory control at age 3 were more likely to have negative relations with peers at age 4 than those with better inhibitory control (Balaraman, 2003). Another study demonstrated that inhibitory control contributes to later social competence among preschoolers (Nigg et al., 1999). Further, in a recent longitudinal study spanning from early childhood to middle adolescence, poorer executive function abilities (including inhibitory control, working memory, and attention) increased the likelihood of peer problems later on (Holmes et al., 2016). These studies directly support the assertion that inhibitory control is related to peer relationship quality. Though no prior studies have explicitly tested the association between adolescent inhibitory control and parent–adolescent relationship quality, we draw on reviews suggesting that inhibitory control abilities are critical for developing positive relationships in general, encompassing parent–child, peer, friend, and romantic partner relationships (Farley and Kim-Spoon, 2014), and expect that adolescents with poor inhibitory control may experience difficulties in their relationships with mothers and fathers.

In the current longitudinal study, we aimed to investigate whether inhibitory control may be an explanatory process of the detrimental effects of stress on interpersonal relationships. Specifically, we hypothesized that earlier perceived stress is related to later secure interpersonal relationship quality over time via inhibitory control abilities (after controlling for baseline levels of the mediator and outcome). Past research thus far has primarily focused on objective indicators of stress (e.g., financial difficulties, familial violence; Bonn, 1995; Baldry, 2003; Mohr, 2006), thus limiting our understanding of the role of an individual's subjective interpretation of stressors. According to the theoretical model proposed by Lazarus (1990), the experience of a stressor depends, at least in part, on the individual's perception of how well they can control and manage it. Given that adolescence is a period in which stress tends to increase due to puberty, autonomy and identity formation, and relationship reorganization (Arnett, 1999; Tottenham and Galván, 2016), it is important to examine adolescents' perceived stress as a risk factor related to the changing nature of their interpersonal relationships with parents and peers. The present study extends the literature in several significant ways. First, it focuses on individual perceptions of stress rather than objectively stressful events. Second, it examines the roles of both behavioral and neural indicators of adolescent inhibitory control as an explanatory mechanism in the association between perceived stress and secure relationship quality. Third, it examines potentially differential effects of stressful experiences on relationships with mothers, fathers, and peers. Finally, given sex differences in the brain, including volumetric differences in areas related to executive functions (including inhibitory control) and in interpersonal relationships that suggest that females are more sensitive to interpersonal cues (e.g., Rose and Rudolph, 2006; Gur and Gur, 2016), we also explored differences in the patterns of the associations among perceived stress, inhibitory control, and secure relationship quality between males and females.

## MATERIALS AND METHODS

### Participants

The current community sample included 167 adolescents (53% males, 47% females) from southwestern Virginia, the United States of America. Adolescents were 13 or 14 years of age at Time 1 ($M = 14.13$, $SD = 0.54$), 14 or 15 years of age at Time 2 ($M = 15.05$, $SD = 0.54$), and 15 or 16 years of age at Time 3 ($M = 16.07$, $SD = 0.56$; data were collected between January 2014 and January 2017). Adolescents primarily identified as 80% Caucasian, 13% African–American, and 7% other. Mean family income was $25,000–$34,999 per year at Time 1 and Time 2 and $35,000–$49,999 per year at Time 3. At Time 1, 157 families participated. At Time 2, 10 families were added for a final sample of 167 parent–adolescent dyads. However, 24 families did not participate at all possible time points for reasons including: ineligibility for tasks ($n = 2$), declined participation ($n = 17$), and lost contact ($n = 5$) during the follow-up assessments. We performed attrition analyses using general linear model (GLM) univariate procedure to determine whether there were systematic predictors of missing data. Results indicated that rate of participation (indexed by proportion of years participated to years invited to participate) was not significantly predicted by demographic variables ($p = 0.86$ for age, $p = 0.49$ for income, $p = 0.05$ for sex, $p = 0.20$ for race, contrasted as White vs. non-White) or study variables at Time 1 ($p = 0.40$ for perceived stress, $p = 0.49$ for inhibitory control, $p = 0.62$ for mother relationship quality, $p = 0.60$ for father relationship quality, $p = 0.87$ for peer relationship quality).

### Procedures

Adolescent participants and their parents were recruited as part of a longitudinal study via email announcements, flyers, notice on the internet, or snowball sampling (word-of-mouth). The current study used data from Time 1, Time 2, and Time 3; each assessment was approximately 1 year apart from the previous one. Data collection took place at the university's offices where adolescents and their primary caregivers were interviewed by trained research assistants. Both parents and adolescents received monetary compensation for their time. All procedures were approved by the institutional review board of the university with written informed consent and assent from all participants.

## Measures

### Perceived Stress

Perceived stress was assessed using adolescent self-report at Time 1 using the 10-item perceived stress scale (PSS; Cohen and Williamson, 1988) that has been well validated to assess for perceptions of stress. Adolescents were asked to respond on a 5-point Likert scale from "0 = Never" to "4 = Very Often" about thoughts and feelings they've experienced within the past month. Sample items include, "In the last month, how often have you felt nervous and 'stressed'?" and "In the last month, how often have you felt that you were on top of things?" (reverse scored). Mean scores were calculated across the 10 items from participants at Time 1, such that higher scores were indicative of higher perceived stress ($\alpha = 0.83$).

### Secure Relationship Quality

The short version of the Inventory of Parent and Peer Attachment was utilized at Time 1 and Time 3 to determine the degree of adolescents' perceived security in their relationships with parents and peers (IPPA; Raja et al., 1992). Adolescents responded to three separate scales, each capturing a different relationship, including mother, father, and peers, using a 5-point Likert scale from "1 = Almost Never or Never True" to "5 = Almost Always or Always True." Means scores were calculated for each relationship across the three subscales (communication, trust, and alienation; four items each) to create an overall attachment score, such that higher scores indicate higher levels of perceived secure relationship quality. Sample items include "I tell my mother/father about my problems and troubles" for the parent scales and "My friends encourage me to talk about my difficulties" for the peer scale ($\alpha = 0.78$–$0.92$).

### Inhibitory Control

At Time 1 and Time 2, adolescents' inhibitory control was captured by the MSIT (Bush et al., 2003), using an in-house software application written in python using the VisionEgg (Straw, 2008) stimulus presentation library. In this task, participants were presented with sets of three numbers for duration of 1.75 s and asked to identify the number that differs from the other two. In the neutral condition, the distractor numbers were zeros, and the identity of the target was congruent with their position on the button box and screen. In the interference condition, the distractors were 1, 2, or 3 and the target's identity was incongruent with its position on the button box and screen. Adolescents performed this task while their blood-oxygen-level-dependent (BOLD) response was monitored using functional magnetic resonance imaging. Participants completed 4 blocks of 24 neutral trials interleaved by 4 blocks of 24 interference trials for a total of 96 neutral trials and 96 interference trials. As with prior literature, we found a significant MSIT interference effect (i.e., main effect of congruency) in reaction time for correct responses, $t(153) = 69.58$, $p < 0.001$, as well as accuracy for correct responses, $t(153) = -15.47$, $p < 0.001$. These results showed that accuracy was lower and reaction time was higher (i.e., slower) for interference compared to neutral trials. A *behavioral* inhibitory control factor score was calculated using two indicators from this task: (1) the difference in accuracy of the neutral and interference trials (accuracy interference minus neutral) and (2) the intra-individual variability in reaction time or the intra-individual standard deviations across correct response latency trials in the interference condition. These two indicators were significantly correlated ($r = -0.52$, $p < 0.001$). Higher scores for the accuracy difference and lower scores for the intra-individual variability indicated better cognitive control. Confirmatory factor analysis (CFA) was performed to produce a factor score using standardized scores of these two indicators. At both waves, the models were fully saturated ($\chi^2 = 0$, $df = 0$, $p = 0$, CFI = 1.00) with significant loadings for the two indicators (Time 1: 0.72, $p < 0.001$; Time 2: 0.57, $p < 0.001$).

### Imaging Acquisition and Analysis

Functional neuroimaging data were acquired on a 3T Siemens Tim Trio MRI scanner with a standard 12-channel head matrix coil. Echo-planar images (EPIs) were collected using the following parameters: slice thickness = 4 mm, 34 axial slices, field of view (FoV) = 220 mm × 220 mm, repetition time (TR) = 2 s, echo time (TE) = 30 ms, flip angle = 90 degrees, voxel size = 3.4375 mm × 3.4375 mm × 4 mm (during analysis the images were resliced so that voxels were 3 mm × 3 mm × 3 mm), 64 × 64 grid, and slices were hyperangulated at 30 degrees from anterior–posterior commissure. The structural scan was acquired using a high-resolution magnetization prepared rapid acquisition gradient echo sequence with the following parameters: TR = 1200 ms, TE = 3.02 ms, FoV = 245 mm × 245 mm, and 192 slices with the spatial resolution of 1 mm × 1 mm × 1 mm.

Data were pre-processed and analyzed using SPM8 (Wellcome Department of Imaging Neuroscience, London, United Kingdom). Functional images were corrected for head motion using a six-parameter rigid-body transformation, realigned, and normalized to a Montreal Neurological Institute (MNI) template using parameters derived from a segmented anatomical image coregistered to the mean EPI. The resulting image was spatially smoothed using an 8 mm full-width at half-maximum Gaussian kernel. Each participant's preprocessed imaging data were whitened and analyzed using a GLM that included a boxcar regressor for each condition of interest, six motion-parameters as nuisance regressors, and a high-pass filter with cutoff at 128 s. Temporal autocorrelations were estimated using an autoregression AR(1). A subsequent second-level random effects analysis was conducted on individual interference minus neutral contrasts. Spherical regions-of-interest (ROI), 6 mm in radius and centered at peak voxels in the second-level analysis, were extracted using a family-wise corrected (FEW) threshold of $p < 0.001$.

Regions-of-interest values were considered based on (1) regions known to be engaged by inhibitory control related to interference and error processing (Koechlin et al., 2003; Roberts and Hall, 2008; Fitzgerald et al., 2010) and (2) regions significantly correlated with behavioral performance (i.e., absolute magnitude of correlation >0.2 with the behavioral performance factor score at each assessment). Seven ROIs in Time 1 (left posterior-medial frontal cortex, right inferior frontal gyrus, left and right inferior parietal lobules, right insula, right superior frontal gyrus, and left middle frontal gyrus) and three ROIs in Time 2 (left posterior-medial frontal cortex, left middle frontal gyrus, and left inferior frontal gyrus) met the criteria. Two of these ROIs emerged in both assessments (left posterior-medial frontal cortex, left middle frontal gyrus), and were chosen as manifest indicators of the *neural* inhibitory control factor scores created for Time 1 and Time 2. At each wave, CFA was performed to produce a factor score using standardized scores of two ROIs. At both waves, the models were fully saturated ($\chi^2 = 0$, $df = 0$, $p = 0$, CFI = 1.00) with significant loadings for two indicators (Time 1 factor loadings: 0.81, $p < 0.001$; Time 2 factor loadings: 0.77, $p < 0.001$).

## Plan of Analysis

For all study variables, descriptive statistics were examined to determine normality of distributions and outliers. Skewness and kurtosis were examined for all variable distributions and acceptable levels were skewness less than 3 and kurtosis less than 10 (Kline, 2011). Outliers were identified as values $\geq 3$ *SD* from the mean. In these cases ($n = 7$), values were winsorized to retain statistical power and attenuate bias resulting from elimination (Ghosh and Vogt, 2012). Multivariate GLM analyses exhibited that demographic variables (adolescent age, gender, race, and family income) at Time 1 were not significant predictors of mother, father, or peer relationship quality at Time 3 (all *p*s > 0.10). Thus, they were not included as covariates in the main analyses.

The hypothesized model was tested via structural equation modeling (SEM) in MPlus 7.4 (Muthén and Muthén, 2012). The analyses followed recommendations for testing mediation models by Hayes (2013). To begin, we calculated a residualized change score for inhibitory control by regressing inhibitory control at Time 2 on inhibitory control at Time 1. We also calculated residualized change scores for relationship qualities with parents and peers by regressing each relationship quality at Time 3 on corresponding relationship quality at Time 1. The residualized change scores represent the change across time, and compared to simple difference scores, have the advantage that they adjust for baseline differences (MacKinnon et al., 2013).

The mediation model included paths (a) from perceived stress at Time 1 to changes in inhibitory control from Time 1 to Time 2, (b) from changes in inhibitory control to secure relationship quality with mother, father, and peers from Time 1 to Time 3, and (c) from perceived stress at Time 1 to changes in secure relationship quality with mother, father, and peers. We also estimated correlations among the three secure relationship quality outcomes. Overall model fit indices were determined by $\chi^2$ goodness of fit test, root mean square error of approximation (RMSEA), and confirmatory fit index (CFI). RMSEA values of less than 0.05 were considered a close fit while values less than 0.08 were considered a reasonable fit (Browne and Cudeck, 1993), and CFI values of greater than 0.90 were considered an acceptable fit while values greater than 0.95 were considered an excellent fit (Bentler, 1990). We calculated bias-corrected bootstrap confidence intervals (CIs) for the indirect effects using 10,000 bootstrapping samples (MacKinnon et al., 2004). These CIs take non-normality of the estimates into account and are therefore not necessarily symmetric (Muthén and Muthén, 2012). Full information maximum likelihood (FIML) estimation procedure (Arbuckle, 1996) was used for missing data since FIML estimates are superior to those obtained with listwise deletion or other *ad hoc* methods (Schafer and Graham, 2002). In order to test whether the regression paths were moderated by sex, we additionally ran a multiple group model and tested whether imposing equality constraints on the regression parameters between males and females degraded model fit significantly using the Wald test.

# RESULTS

Correlations and descriptive statistics for all study variables can be found in **Table 1**. We first tested the effects of perceived stress at Time 1 on secure relationship quality for mothers, fathers, and peers at Time 3 after controlling for their respective relationship qualities at Time 1 (represented by residualized change scores) via *behavioral* inhibitory control at Time 2 after controlling for behavioral inhibitory control at Time 1 (represented by a residualized change score). The original model was a fully saturated model, with $\chi^2 = 0$, $df = 0$, $p = 0$, CFI = 1.00, RMSEA = 0. The direct effects from perceived stress at Time 1 to the secure mother relationship quality residualized change score ($b = 0.10$, $SE = 0.07$, $p = 0.136$) and secure father relationship quality residualized change score ($b = 0.05$, $SE = 0.09$, $p = 0.604$) were not significant. The effect from behavioral inhibitory control to the secure peer relationship quality residualized change score was also not significant ($b = 0.02$, $SE = 0.07$, $p = 0.826$). For model parsimony, we constrained these paths to zero.

The final model showed an excellent fit, $\chi^2 = 2.25$, $df = 3$, $p = 0.52$, CFI = 1.00, RMSEA = 0 (see **Figure 1** for standardized coefficients). Higher levels of perceived stress at Time 1 were associated with lower inhibitory control residualized change scores ($b = -0.25$, $SE = 0.08$, $p = 0.001$). In turn, lower inhibitory control residualized change scores were related to lower secure relationship quality residualized change scores for adolescents and their mothers ($b = 0.30$, $SE = 0.07$, $p < 0.001$) and fathers ($b = 0.32$, $SE = 0.09$, $p < 0.001$). The indirect effects of perceived stress at Time 1 on the secure mother relationship quality residualized change score ($b = -0.08$, $SE = 0.03$, 95% CI [$-0.160$, $-0.026$], $b^* = -0.09$) and the secure father relationship quality residualized change score ($b = -0.08$, $SE = 0.03$, 95% CI [$-0.159$, $-0.029$], $b^* = -0.08$), through the behavioral inhibitory control residualized change score, were significant. For secure peer relationship quality, higher levels of perceived stress at Time 1 directly predicted a lower secure peer relationship quality residualized change score ($b = -0.12$, $SE = 0.05$, $p = 0.03$). Given that the behavioral inhibitory control residualized change score was not significantly associated with the secure peer relationship quality residualized change score, the indirect effect of perceived stress on the secure peer relationship quality residualized change score through the behavioral inhibitory

**TABLE 1 |** Descriptive statistics and bivariate correlations among perceived stress, behavioral and neural inhibitory control, and secure relationship quality.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (1) Perceived stress T1 | | | | | | | | | | | | | | | | |
| (2) Behavioral IC T1 | 0.02 | | | | | | | | | | | | | | | |
| (3) Behavioral IC T2 | −0.20* | 0.53* | | | | | | | | | | | | | | |
| (4) Behavioral IC residualized change score (T2 on T1) | −0.27** | 0.00 | 0.85** | | | | | | | | | | | | | |
| (5) Neural IC T1 | 0.08 | −0.37** | −0.29** | −0.13 | | | | | | | | | | | | |
| (6) Neural IC T2 | 0.12 | −0.23* | −0.26** | −0.14 | 0.36** | | | | | | | | | | | |
| (7) Neural IC residual score at T2 on T1 | 0.11 | −0.15 | −0.18 | −0.12 | 0.00 | 0.93** | | | | | | | | | | |
| (8) Mother relationship quality T1 | −0.36** | −0.14 | 0.11 | 0.21* | 0.00 | −0.03 | −0.09 | | | | | | | | | |
| (9) Mother relationship quality T3 | −0.24** | 0.00 | 0.32** | 0.41** | −0.12 | −0.06 | −0.05 | 0.62** | | | | | | | | |
| (10) Mother relationship quality residualized change score (T3 on T1) | 0.03 | 0.07 | 0.31** | 0.34** | −0.12 | −0.04 | 0.00 | 0.00 | 0.78** | | | | | | | |
| (11) Father relationship quality T1 | −0.26** | −0.15 | 0.11 | 0.21* | 0.01 | −0.08 | −0.11 | 0.47** | 0.43** | 0.23** | | | | | | |
| (12) Father relationship quality T3 | −0.28** | −0.06 | 0.27** | 0.38** | −0.09 | 0.02 | 0.08 | 0.23* | 0.43** | 0.38** | 0.71** | | | | | |
| (13) Father relationship quality residualized change score (T3 on T1) | −0.04 | 0.06 | 0.29** | 0.31** | −0.06 | 0.10 | 0.19 | −0.10 | 0.18* | 0.32** | 0.00 | 0.71** | | | | |
| (14) Peer relationship quality T1 | −0.27** | −0.13 | 0.06 | 0.15 | −0.09 | −0.01 | 0.00 | 0.36** | 0.14 | −0.11 | 0.20* | 0.11 | −0.07 | | | |
| (15) Peer relationship quality T3 | −0.26** | −0.07 | 0.09 | 0.14 | −0.27** | −0.18 | −0.09 | 0.31** | 0.39** | 0.25** | 0.29** | 0.28** | 0.09 | 0.42** | | |
| (16) Peer relationship quality residualized change score (T3 on T1) | −0.14 | −0.02 | 0.06 | 0.07 | −0.22* | −0.16 | −0.09 | 0.18* | 0.36** | 0.32** | 0.22* | 0.25** | 0.14 | 0.00 | 0.91** | |
| *M* | 1.48 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 4.04 | 3.96 | 0.00 | 3.84 | 3.61 | 0.00 | 3.99 | 4.10 | 0.00 |
| *SD* | 0.66 | 0.83 | 0.71 | 0.61 | 0.87 | 0.80 | 0.76 | 0.61 | 0.67 | 0.54 | 0.67 | 0.88 | 0.63 | 0.56 | 0.47 | 0.43 |

*T1 = Time 1; T2 = Time 2; T3 = Time 3. *p < 0.05, **p < 0.01, ***p < 0.001.*

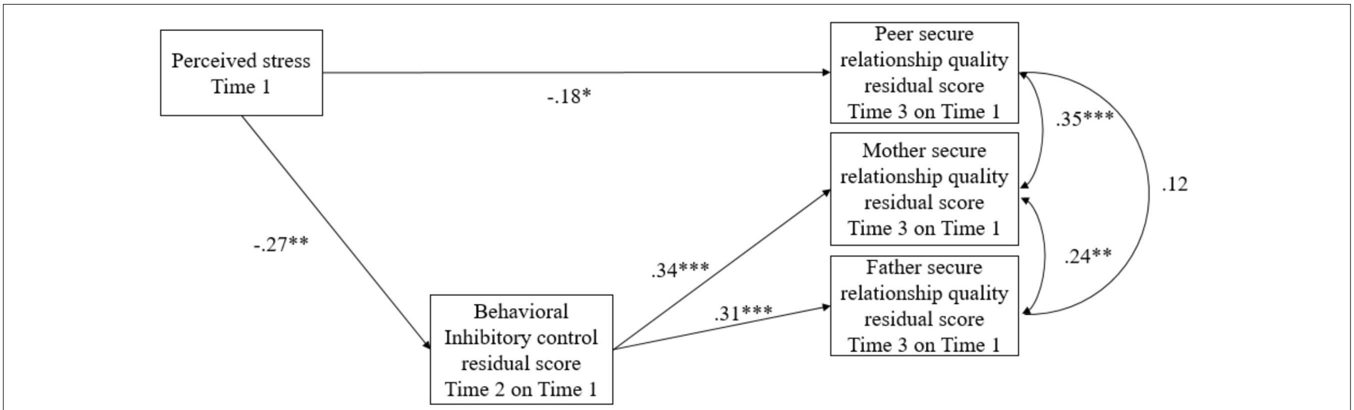

**FIGURE 1 |** Standardized parameter estimates for the associations among perceived stress, the behavioral inhibitory control residualized change score, and secure relationship quality residualized change scores. $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

control residualized change score was not estimated. In addition, the secure mother relationship quality residualized change score significantly correlated with that of the secure father relationship quality residualized change score ($b = 0.07$, $SE = 0.03$, $p = 0.009$) and the secure peer relationship quality residualized change score ($b = 0.08$, $SE = 0.02$, $p < 0.001$). However, the correlation between the secure father relationship quality residualized change score and the secure peer relationship quality residualized change score was not significant ($b = 0.03$, $SE = 0.02$, $p = 0.174$).

We then tested the effects of perceived stress at Time 1 on the secure relationship quality for mothers, fathers, and peers at Time 3 after controlling for their respective levels at Time 1 (represented by residualized change scores) via *neural* inhibitory control at Time 2 after controlling for neural inhibitory control at Time 1 (represented by a residualized change score). The original model was a fully saturated model, with $\chi^2 = 0$, $df = 0$, $p = 0$, CFI = 1.00, RMSEA = 0. Perceived stress at Time 1 did not predict the neural inhibitory control residualized change score ($b = 0.16$, $SE = 0.11$, $p = 0.145$, $b^* = 0.14$) or the three secure relationship quality residualized change scores (mother: $b = 0.03$, $SE = 0.07$, $p = 0.691$, $b^* = 0.04$; father: $b = -0.08$, $SE = 0.09$, $p = 0.390$, $b^* = -0.08$; peer: $b = -0.08$, $SE = 0.06$, $p = 0.16$, $b^* = -0.13$). The predictive effects of the neural inhibitory control residualized change score was only significant for the secure father relationship quality residualized change score ($b = 0.19$, $SE = 0.08$, $p = 0.025$, $b^* = 0.23$), but not for the secure mother relationship quality residualized change score ($b = 0.003$, $SE = 0.08$, $p = 0.973$, $b^* = 0.004$) or the secure peer relationship quality residualized change score ($b = -0.06$, $SE = 0.06$, $p = 0.272$, $b^* = -0.11$). Given that perceived stress at Time 1 was not related to the neural inhibitory control residualized change score, we did not further test the indirect effects of perceived stress at Time 1 on the three secure relationship quality residualized change scores via the neural inhibitory control residualized change score. In this model, the secure mother relationship quality residualized change score significantly correlated with that of the secure father relationship quality residualized change score ($b = 0.11$, $SE = 0.03$, $p = 0.001$, $b^* = 0.32$) and the secure peer relationship quality residualized change score ($b = 0.08$, $SE = 0.02$, $p < 0.001$, $b^* = 0.33$). However, the residual covariance between the secure father relationship quality residualized change score and the secure peer relationship quality residualized change score was not significant ($b = 0.04$, $SE = 0.02$, $p = 0.105$, $b^* = 0.15$).

To test whether the associations among perceived stress, inhibitory control, and secure relationship quality may vary by sex, we performed an omnibus multiple groups Wald test for behavioral inhibitory control model and neural inhibitory control model, respectively. The Wald test compared all regression paths between males and females in the original saturated model. In both tests, multiple groups analyses did not reveal any significant sex differences: Wald $\chi^2(10) = 9.31$, $p = 0.503$ for behavioral inhibitory control model and Wald $\chi^2(10) = 7.50$, $p = 0.677$ for neural inhibitory control model. Therefore, results suggested that the associations among perceived stress, behavioral/neural inhibitory control, and secure relationship quality were comparable between males and females.

## Supplemental Analyses

We reran the models with level scores (instead of residualized change scores) and tested the effects of Time 1 perceived stress on Time 3 secure relationship quality with mother, father, and peers via Time 2 behavioral/neural inhibitory control. Overall, the results on the level of these variables are highly similar to our original results using residualized change scores, confirming that the results of the residualized change score model are robust. Detailed results for behavioral/neural inhibitory control follow.

For *behavioral* inhibitory control, the original model was a fully saturated model, with $\chi^2 = 0$, $df = 0$, $p = 0$, CFI = 1.00, RMSEA = 0. The effect from behavioral inhibitory control to secure peer relationship quality was not significant ($b = 0.03$, $SE = 0.06$, $p = 0.637$, $b^* = 0.04$). For model parsimony, we constrained this path to zero. The final model showed an excellent fit, with $\chi^2 = 0.22$, $df = 1$, $p = 0.64$, CFI = 1.00, RMSEA = 0. Higher levels of perceived stress at Time 1 were associated with lower inhibitory control at Time 2 ($b = -0.21$, $SE = 0.01$, $p = 0.016$, $b^* = -0.20$). In turn, lower inhibitory control was related to lower secure relationship quality for adolescents and their mothers

($b = 0.27$, $SE = 0.07$, $p < 0.001$, $b^* = 0.28$) and fathers ($b = 0.25$, $SE = 0.10$, $p = 0.012$, $b^* = 0.20$) at Time 3. The indirect effects of perceived stress on secure mother relationship quality ($b = -0.06$, $SE = 0.03$, 95% CI [−0.144, −0.007], $b^* = -0.06$) and secure father relationship quality ($b = -0.05$, $SE = 0.03$, 95% CI [−0.134, −0.007], $b^* = -0.04$), through behavioral inhibitory control, were significant. For secure peer relationship quality, higher levels of perceived stress at Time 1 directly predicted lower secure peer relationship quality ($b = -0.18$, $SE = 0.06$, $p = 0.002$, $b^* = -0.25$). Given that behavioral inhibitory control was not significantly associated with secure peer relationship quality, the indirect effect of perceived stress at Time 1 on secure peer relationship quality at Time 3 through behavioral inhibitory control at Time 2 was not estimated.

We then tested the effects of perceived stress at Time 1 on secure relationship quality for mothers, fathers, and peers at Time 3 via *neural* inhibitory control at Time 2. The original model was a fully saturated model, with $\chi^2 = 0$, $df = 0$, $p = 0$, CFI = 1.00, RMSEA = 0. Perceived stress at Time 1 did not predict neural inhibitory control ($b = 0.04$, $SE = 0.03$, $p = 0.194$, $b^* = 0.19$), however, it predicted significant lower secure relationship quality with mothers ($b = -0.24$, $SE = 0.085$, $p = 0.005$, $b^* = -0.23$), fathers ($b = -0.37$, $SE = 0.115$, $p = 0.001$, $b^* = -0.28$), and peers ($b = -0.17$, $SE = 0.059$, $p = 0.005$, $b^* = -0.23$). The predictive effects of neural inhibitory control were not significant for secure mother relationship quality ($b = -0.008$, $SE = 0.32$, $p = 0.979$, $b^* = -0.003$), secure father relationship quality ($b = 0.29$, $SE = 0.39$, $p = 0.455$, $b^* = 0.071$), or secure peer relationship quality ($b = -0.36$, $SE = 0.20$, $p = 0.067$, $b^* = -0.17$). Given that perceived stress at Time 1 was not related to neural inhibitory control at Time 2, we did not further test the indirect effects of perceived stress at Time 1 on secure relationship quality at Time 3 via the neural inhibitory control at Time 2.

## DISCUSSION

The present study sought to elucidate the underlying role of inhibitory control in explaining the association between stress and secure interpersonal relationship quality in adolesence. Results demonstrated indirect paths via adolescent behavioral inhibitory control such that perceived stress was related to lower inhibitory control which in turn was related to lower secure relationship quality between adolecents and their mothers and fathers. These findings were obtained despite controlling for baseline levels of inhibitory control and secure relationship quality. Our data suggested a direct link between adolescents' perceived stress and their secure relationship quality with peers, such that higher perceived stress predicted poorer secure relationship quality with peers; however, the effects of stress on secure peer relationship quality was not mediated by behavioral inhibitory control. In contrast to the findings of behavioral inhibitory control, stress was not significantly correlated with neural inhibitory control. Thus, we did not test the indirect effects of perceived stress on secure relationship quality via neural inhibitory control. Finally, the pattern of findings was not moderated by sex, indicating that the associations among stress, behavioral and neural inhibitory control, and secure relationship quality were comparable between males and females.

The indirect effect of perceived stress on adolecent's secure mother and father relationship quality via behavioral inhibitory control supported our hypothesis. In line with previous research in adults indicating an association between stress and impaired executive functioning related to self-regulation capabilities (Scholz et al., 2009; Hermans et al., 2014), our data indicated that adolescents who reported high levels of stress at an earlier time exhibited poor inhibitory control performance over time. In contrast to prior work using acute, experimentally manipulated stress, our measure of perceived stress assessed subjective evaluations of naturally occurring stress—which are thought to be more severe and ecologically valid than laboratory induced stress (Starcke and Brand, 2012). Our findings also expand prior findings by demonstrating the effects of stress on longitudinal changes in inhibitory control. Further, our results were supportive of prior work proposing that individuals with better self-regulation abilities have higher interpersonal relationship quality during adolescence (Farley and Kim-Spoon, 2014). Likely, adolescents with poorer inhibitory control display inappropriate, dysregulated behavior that leads to poorer interpersonal relationship quality (Brown and Fite, 2016).

Based on previous literature emphasizing the importance of self-regulation on interpersonal relationship quality (Farley and Kim-Spoon, 2014), we expected to find indirect paths from perceived stress to all three types of secure interpersonal relationships in adolescence (i.e., mother, father, and peer) through inhibitory control. However, differences in the nature of adolescent relationships with parents versus peers may explain why indirect effects through behavioral inhibitory control were significant for secure mother and father relationship quality but not for secure peer relationship quality. Although it is often thought that adolescents' reliance on their parents for support decreases during this period, the literature has shown this is not necessarily the case. While peer relationships become more prominent in adolescence, parents have been and continue to be a source of support for many adolescents, indicating the continual primary attachment relationship during this period (Lieberman et al., 1999; Nickerson and Nagle, 2005). That is, parents do serve as important attachment figures throughout childhood and adolescence. The distinct differences in adolescents' relationships with their parents versus their peers may suggest that inhibitory control, a within-person characteristic that is stable across time and context (Nigg, 2017), matters more for parent–adolescent relationships that involve more stable and intense interactions with relative permanance, compared to peer relationships that are everchanging, intentional, and relatively transient (Brown and Larson, 2009), partly due to the fact that adolescents often choose peers who like and accept them based on similarity (Veenstra and Dijkstra, 2011).

Our results demonstrating that inhibitory control was not directly associated with secure peer relationship qualilty appear to be inconsistent with previous research showing significant links between executive functions (including inhibitory control) and peer problems in early childhood through middle adolesence (Holmes et al., 2016). However, it is important to note that the predictive path between executive functions and peer problems decreased from 4.5 to 15 years of age in that study, indicating that executive functions became less important or less predictive of peer problems in adolescence as opposed to childhood (Holmes et al., 2016). One plausible explanation for this trend is the change in the nature of peer relationships from childhood to adolescence (Rubin et al., 1998). Adolescent peer relationships tend to increasingly value communication and disclosure which inhibitory control may not be as relevant to and therefore may not be the best predictor of secure peer relationship quality in adolescence (Holmes et al., 2016). A second explanation for the discrepency between our results and the findings by Holmes et al. (2016) may be the difference in the peer construct. The present study focused on secure relationship quality as indicated by perceived support and closeness, whereas the study by Holmes et al. (2016) focused on peer problems as indicated by peer rejection and victimization. Taken together, these findings suggest that poor inhibitory control may play an important role in predicting more extreme forms of difficulties in peer relationships, such as victimization rather than security of the relationship. Nonetheless, this result was not anticipated and thus requires further examination.

We found a significant direct link between perceived stress and secure relationship quality with peers. While no prior research to our knowledge has focused on perceived stress, objective stressful life events have been documented in the literature as a risk factor for negative peer relationships (Bonn, 1995; Baldry, 2003; Mohr, 2006). Thus, our results add to the extant literature as evidence for the link between perceived stress and secure peer relationship quality. Though future studies would benefit from testing additional mediators (e.g., emotion regulation, Kim and Cicchetti, 2010) that may explain the effects of perceived stress on peer relationship quality.

Our data suggested that, given the lack of significant association between stress and neural inhibitory control, the neural correlates of inhibitory control would not mediate the association between perceived stress and security in adolescent interpersonal relationships. The weak association between perceived stress and neural inhibitory control appears to be inconsistent with the neurosceince literature documenting the negative effects of stress on prefrontal functioning (Liston et al., 2009; Mueller et al., 2010). However, the nature of the stressful experience may be critical to understanding its relation to nerual processes underlying inhibitory control. For example, the present study found *behavioral* inhibitory control to be more strongly related to general perceived stress than neural inhibitory control. Prior studies involving adopted or foster children and adolescents with early-life stress defined by neglectful and abusive care revealed that these children showed impairements in neural inhibitory control compared to those who did not experience such early adversity (Mueller et al., 2010; Bruce et al., 2013). How different types of stressful experiences (e.g., caregiving adversity versus socioeconomic adversity) may be differentially related to brain development during adolescence warrants further investigation.

The present findings should be interpreted in light of several limitations. The outcome variable was self-reported by a single informant. Future studies should consider using multiple informants and multiple methods to reduce possible bias due to using a single informant. Additionally, although we used longitudinal data, the nature of correlational data prevent us from inferring causality. Moreover, future longitudinal research is recommended to test potential bidirectional effects among perceived stress, inhibitory control, and secure interpersonal relationship quality. For example, secure attachment relationships may promote adaptive responses to stress (e.g., Pierrehumbert et al., 2009) and inhibitory control (e.g., Bernier et al., 2012). At the same time, stress has the ability to deterioriate relationships (Bonn, 1995; Baldry, 2003; Mohr, 2006; Marceau et al., 2012; Platt et al., 2016). Thus, further research examining potential bidirectional effects between stress and secure relationship quality as they relate to inhibitory control is needed. The current investigation focused on mediated relationships between stressful life events and secure relationship quality via inhibitory control. Fruitful extensions for future research may include testing the role of inhibitory conrol in the stress-buffering hypothesis, which posits that attachment relationships have the ability to dampen the negative effects of stress on well-being (e.g., Hanson and Chen, 2010; Miller et al., 2016) and considering internal working models of attachment as an additional possible mediator in this association between stress and secure relationship quality (e.g., Collins and Feeney, 2004).

Furthermore, it will be particularly important to consider the bidirectional nature of the brain and environmental contexts (such as stressful life events and secure interpersonal relationships) within adolesence, given that stress exposures during adolescence can have more potent effects on the brain than when those exposures occur in adulthood – due to rapid brain development and increased plasticity of developing systems relative to adulthood (Tottenham and Galván, 2016). From a methodological viewpoint, it may be that selective weakening and strengthening of functional connectivity within cognitive control circuits (e.g., Botvinick et al., 2001) are the mechanism by which behavioral inhibition is achieved, whereas behavioral inhibition is the goal that mechanism is intended to achieve. Then, the BOLD responses in specific ROIs may not be effectively capturing such a mechanism. For example, evidence from research using task-based functional connectivity revealed the beneficial contributions of increased activation coherence within the cognitive control system (i.e., functional connectivity between the ventromedial PFC and dorsolateral prefrontal and parietal cortices) to less impulsive decision making among adolescents (Christakou et al., 2011).

Past research has rarely investigated the link between inhibitory control and positive developmental outcomes such as secure interpersonal relationship quality. Our longitudinal analyses suggest that adolescents with poor behavioral inhibitory control are likely to show poor secure relationship quality with both mothers and fathers over time. This association may be expected given that flexible inhibitory control promotes social affective skills (Crone and Dahl, 2012), ultimately enhancing interpersonal interaction quality. Aside from the direct association between stress and interpersonal relationships as found in prior studies (e.g., Bonn, 1995; Baldry, 2003; Mohr, 2006; Platt et al., 2016), the current study clarifies that perceived stress has detrimental effects on the behavioral manifestion of inhibitory control, and in turn is related to poorer secure relationship quality with parents.

## CONCLUSION

The identification of inhibitory control as a mechanism in the stress-secure interpersonal relationship quality association is beneficial in how it may inform intervention work for children and adolescents who are especially prone to chronic stress. Interventions that teach and practice skills related to inhibitory control may help protect against negative parent–adolescent relationships later on.

## ETHICS STATEMENT

This study was carried out in accordance with the recommendations of Virginia Tech Institutional Review Board for the Protection of Human Subjects, Office of Research Compliance with written informed consent from all subjects. All subjects gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the Virginia Tech Institutional Review Board for the Protection of Human Subjects.

## AUTHOR CONTRIBUTIONS

TH conceived the study, participated in data collection, participated in statistical analyses and interpretation of the data, and drafted the manuscript. ML performed statistical analyses and interpretation of the data and drafted the manuscript. DM performed statistical analyses and interpretation of the data and critically revised the manuscript. JL participated in statistical analyses and interpretation of the data and helped to draft the manuscript. KD-D critically revised the manuscript. BK-C participated in the design of the study and statistical analyses. JK-S conceived the study, participated in its design and coordination, and drafted the manuscript. All authors read and approved the final manuscript.

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# The Development of Attentional Biases for Faces in Infancy: A Developmental Systems Perspective

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We present an integrative review of research and theory on major factors involved in the early development of attentional biases to faces. Research utilizing behavioral, eye-tracking, and neuroscience measures with infant participants as well as comparative research with animal subjects are reviewed. We begin with coverage of research demonstrating the presence of an attentional bias for faces shortly after birth, such as newborn infants' visual preference for face-like over non-face stimuli. The role of experience and the process of perceptual narrowing in face processing are examined as infants begin to demonstrate enhanced behavioral and neural responsiveness to mother over stranger, female over male, own- over other-race, and native over non-native faces. Next, we cover research on developmental change in infants' neural responsiveness to faces in multimodal contexts, such as audiovisual speech. We also explore the potential influence of arousal and attention on early perceptual preferences for faces. Lastly, the potential influence of the development of attention systems in the brain on social-cognitive processing is discussed. In conclusion, we interpret the findings under the framework of Developmental Systems Theory, emphasizing the combined and distributed influence of several factors, both internal (e.g., arousal, neural development) and external (e.g., early social experience) to the developing child, in the emergence of attentional biases that lead to enhanced responsiveness and processing of faces commonly encountered in the native environment.

**Keywords: infancy, social development, attentional biases, perceptual processing, event-related potentials**

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## INTRODUCTION

Developing the ability to process and respond appropriately to social stimuli is critically important for social, cognitive, and emotional development. Attentional biases refer to a readiness to orient toward and maintain attention on a particular class of stimuli over others. These biases can be driven by mechanisms associated with increased probability of rapid orienting to certain types of stimuli and/or mechanisms involved in a lower probability of disengaging attention from certain types of stimuli (e.g., Cohen, 1972; Posner et al., 1987; Pool et al., 2016). Research indicates that in certain contexts even newborn infants possess attentional biases to orient toward and maintain visual fixation on faces and face-like stimuli over non-face stimuli (e.g., Johnson and Morton, 1991b;

Morton and Johnson, 1991; Pascalis et al., 1995; Valenza et al., 1996). These biases likely facilitate social responsiveness and perceptual learning in the earliest stages of postnatal development.

Controversy has arisen in the field over potential mechanisms that may account for these early emerging attentional biases. Some have argued in support of domain-general mechanisms that are driven by a match between low-level stimulus characteristics of face-like stimuli and stimulus properties that attract orienting and visual fixation of the developing newborn visual system (e.g., Kleiner and Banks, 1987; Gauthier and Nelson, 2001; Macchi Cassia et al., 2001; Nelson, 2001; Simion et al., 2001; Turati, 2004). In contrast, others have argued in support of domain-specific mechanisms associated with evolved neural systems dedicated to face detection (e.g., Johnson and Morton, 1991b; Farroni et al., 2006; Pascalis and Kelly, 2009; Johnson et al., 2015). Understanding the origins of attentional biases is of the upmost importance as the distribution of selective attention plays of fundamental role in early perceptual learning that may have cascading effects on subsequent cognitive development (e.g., Reid and Striano, 2007; Bahrick and Lickliter, 2014; Amso and Scerif, 2015; Reynolds, 2015).

Developmental systems theorists have proposed that phenotypic outcomes are the product of reciprocal and bidirectional interactions of multiple factors both internal and external to the developing organism (e.g., Gottlieb, 1991, 2007; Thelen, 1992; Thelen and Smith, 1994; Lickliter, 1996, 2000; Oyama et al., 2001; Gottlieb et al., 2006; Lewkowicz, 2011). In this paper, we review research on the development of attentional biases for faces in infancy. Under the framework of developmental systems theory, we propose that multiple factors influence the development of attentional biases, and these biases subsequently guide infant selective attention and perceptual learning in social contexts. We begin by reviewing research on early emerging perceptual preferences for faces and face-like stimuli over non-social stimuli, and the potential role of prior experience on attentional biases for faces. We subsequently review research on the development of face processing in multimodal contexts, followed by a section on physiological and neural mechanisms that are likely associated with attentional biases in infancy. The purpose of this paper is not to present exhaustive reviews of the extant literature in each of these areas of research. Instead, we review relevant findings and developmental theory for the purpose of building a conceptual framework for understanding potential mechanisms involved in the early development of attentional biases for faces. We propose that the attentional biases newborns demonstrate for face-like stimuli, and the relatively rapid developmental changes that occur in face processing during infancy can be explained under the framework of developmental systems theory through application of the following domain-general developmental principles: *constraints by design* (Lickliter, 2000; Lickliter and Harshaw, 2010), *experiential canalization* (Kuo, 1976; Gottlieb, 1991; Lickliter and Harshaw, 2010), and *distributed control* (Lickliter, 2000; Lickliter and Honeycutt, 2003).

## ATTENTIONAL BIASES FOR FACES IN NEWBORNS

Research has shown that even newborn infants prefer faces and face-like stimuli over non-social stimuli (e.g., Johnson et al., 1991a; Pascalis et al., 1995; Macchi Cassia et al., 2001). Several factors specific to faces have been shown to influence newborn attentional biases. For example, when viewing faces, newborns demonstrate visual preferences for: open-eyes compared to closed-eyes (Batki et al., 2000), attractive faces compared to less attractive faces (Slater et al., 1998, 2000a,b), direct compared to averted eye gaze (Farroni et al., 2002), and mother's face compared to a stranger's face (Field et al., 1984; Pascalis et al., 1995). Newborn attentional biases generalize to face-like patterns, such as top-heavy inverse triangles (Valenza et al., 1996; Simion et al., 2002), but by 3 months of age, infants only demonstrate preferences for faces, and the preference for top-heavy geometric patterns no longer exists (Chien, 2011). Taken together, these findings indicate an early preference for visual patterns that structurally resemble the human face (the top-heavy or inverse triangle pattern), which then progresses to a more specific preference for human faces that is likely tied to extensive early social experience and exposure to human faces which we discuss in more detail in a later section

The presence of an attentional bias for faces and face-like geometric patterns in the newborn period has led to substantial controversy and debate in the literature on the development of face processing. This debate revolves around differing theoretical views on potential mechanisms that may account for the presence of this attentional bias in newborns who have had highly limited postnatal visual experience with faces. Several models have been proposed that attempt to explain the presence of newborn attentional biases for faces as well as the rapid development of face processing across infancy. The two-process theory of face processing proposed by Johnson and Morton (1991b), Morton and Johnson (1991), and recently modified by Johnson et al. (2015) is one of the most influential theoretical models to date. According to this model, there are two systems involved in face processing. Conspec is the first system, which is a subcortical system involved in orienting to faces of conspecifics. This system accounts for newborn attentional biases for faces and face-like stimuli. The second system, Conlern, represents an acquired system of cortical circuits involved in processing faces (i.e., face recognition, categorization, etc.) that is influenced by experience and learning. An important component of this model is that Conspec is an innate system which serves to bias infant visual orienting toward faces of conspecifics, thus insuring appropriate input for further development and specialization of neural systems associated with Conlern. Neuroanatomical structures associated with Conspec include areas involved in the retino-tectal visual pathway: the superior colliculus, pulvinar, and amygdala complex (Johnson et al., 2015). Neuroanatomical structures involved in Conlern include: the fusiform gyrus, superior temporal sulcus, medial prefrontal cortex, and orbitofrontal cortex. Support for the proposal that newborn attentional biases are driven by a subcortical circuit come from findings indicating that newborns only show preferences for face-like stimuli when the stimuli are presented in the temporal visual field (Simion et al., 1998), which feeds differentially into the subcortical visual pathway (Sylvester et al., 2007).

There are several influential alternative models to the two-process theory of face processing. Slater (1993), Slater et al. (2010) have proposed a model based on Valentine's (1991) concept of Face Space. Similar to the two-process theory, this model posits that an attentional bias exists at birth for infants to orient toward face-like stimuli, and that experience with faces shapes the face processing system as a prototypical face space is constructed based on dimensions (e.g., age, attractiveness, race, species) that serve to discriminate the types of faces commonly encountered in the native environment. In contrast to Conspec (Johnson and Morton, 1991b; Johnson et al., 2015), Slater et al. (2010) propose that the initial bias to orient toward faces in the newborn period is not innate, and many of the properties of faces that attract newborn attention are not specific to faces. Slater et al. (2010) further propose that newborns demonstrate more advanced face processing consistent with rapid development of face space than the basic orienting functions served by Conspec. Evidence in support of their position comes from the finding that newborns demonstrate visual preferences for attractive faces. This effect is driven by attention to internal facial features and only found when newborns view upright faces (Slater et al., 2000a,b). Inversion effects are related to configural processing and developing expertise in face processing that would not be expected to occur if face processing was exclusively under the control of a subcortical system (i.e., Conspec). Further support for the possibility that cortical structures are involved in early face processing comes from a study conducted by Nakano and Nakatani (2014) using S-cone isolating stimuli which are processed exclusively by the geniculo-cortico visual pathway. Two-month-old infants were found to show a preference for upright compared to inverted S-cone isolating face stimuli indicating relatively advanced cortical processing of face stimuli by the end of the newborn period. Quinn and Slater (2003), Slater et al. (2010) have proposed that newborn attentional biases for faces may be the product of general properties of the nervous system, gestational proprioceptive feedback, and face-specific biases.

The possibility that attentional biases in the newborn period are likely influenced by multiple factors, including general properties of the nervous system and prenatal sensory experience, is in line with developmental systems theory and the concept of *constraints by design* (Lickliter, 2000; Lickliter and Harshaw, 2010; also see, Oyama, 1993). According to this concept, both the buffered nature of the prenatal environment as well as the relatively immature sensory capacities of the developing organism provide constraints that limit early sensory experience. Neonatal sensory limitations also serve as a source of perceptual organization in early development under this framework (Turkewitz and Kenny, 1982; Lewkowicz, 2000). The structure provided by these external and internal factors provides an orderly and consistent context for development and can serve as a source of stability in species-typical perceptual development (Lickliter, 1996, 2000). The concept of constraints by design is similar to the concept of global determinism, which is the notion that internal and external boundaries of developmental systems provide stability in outcomes that emerge in the process of development (Thelen, 1992).

In line with the concept of constraints by design, Simion et al. (2001) proposed that domain-general perceptual constraints on visual processing account for newborn attentional biases for faces and face-like patterns as opposed to a domain-specific innate facial representation. Studies providing support for this position have shown top heavy configural patterns can elicit a stronger visual preference in newborns than a schematic face (Easterbrook et al., 1999; Turati et al., 2002). Similarly, newborns' visual preferences have been found to be influenced by: the amplitude spectrum of the stimulus (Mondloch et al., 1999), contrast-polarity (Farroni et al., 2005), up-down asymmetry (Simion et al., 2002), and congruency between internal and boundary elements (Macchi Cassia et al., 2008). Taken together, these findings support the possibility that newborn attentional biases for faces are based on stimulus characteristics that are not unique to faces but do fall within an optimal range for visual processing given domain-general perceptual constraints of the immature visual system.

Wilkinson et al. (2014) proposed the binocular correlation model (BCM), which is arguably the most well-formulated model of newborn face preferences proposed to date. The model is based on an extension of the linear systems model (Banks and Salapatek, 1981; Banks and Ginsburg, 1985). The linear systems model has been used to model the filtering properties of the immature visual system based on factors such as the resolution of rods and cones, and the average contrast sensitivity function in order to quantify the visibility of stimuli for the newborn infant. Infant visual preferences are proposed to be proportionately related to the visibility of the stimuli being tested. The BCM extends the linear systems model from a monocular to a binocular visual system. The model also includes the addition of a factor of facial embodiment, such that the spacing of the eyes (i.e., inter-pupillary distance) is mapped to the lateral geniculate nucleus, thus providing structural information regarding faces to the visual system. The model predicts that infants will prefer to look at stimuli that result in stronger correlations between corresponding points in the visual arrays of both eyes, and that faces and face-like patterns will result in high levels of binocular correlation because of the match between inter-pupillary distance on the infant's face and salient areas of face stimuli that are likely fixation points (e.g., the eyes on the fixated face). One of the greatest strengths of this model is that it can be tested, and the authors (Wilkinson et al., 2014) did so by utilizing computational modeling in tandem with a humanoid robot. Through a series of simulations, the robot's looking to face-like patterns used in previous research on newborn face preferences was tested. Results from the modeling demonstrated consistency with newborn attentional biases found in previous studies and provided support for the BCM. A major advantage of the BCM is that, unlike the two-process theory of infant face processing, it does not rely on the existence of an innate representation of face information. Another strength of this model is the extension of linear systems model to binocular vision characteristic of the human visual system. A limitation of the current model is that it fails to replicate inversion effects often seen in newborns. However, Wilkinson et al. (2014) acknowledged that newborn facial processing is likely affected by more than just binocular correlation, and the addition of a bias for upper visual field salience (e.g., Easterbrook et al., 1999; Turati et al., 2002) would likely increase the accuracy of the model.

In addition to structural characteristics of the face and visual capacities of the newborn, it is possible that prenatal experience biases newborn infants to attend to certain types of social stimuli. In support of this possibility, findings from both comparative and human research have shown that recently hatched Bobwhite Quail chicks (e.g., Lickliter et al., 2002) and human newborns (DeCasper and Fifer, 1980; DeCasper and Spence, 1986; Fifer and Moon, 1989) demonstrate familiarity preferences for specific auditory stimuli they were exposed to during the late stages of prenatal development. Furthermore, human newborns prefer their mother's native language (i.e., maternal language) over non-maternal language (Spence and DeCasper, 1987; Moon et al., 1993), and newborns show evidence of detecting changes in affect in speech conveyed in their maternal language but do not show such evidence of affect discrimination in non-maternal language (Mastropieri and Turkewitz, 1999). These findings demonstrate effects of prenatal auditory experience on postnatal perceptual responsiveness resulting in increased sensitivity to stimuli encountered in the prenatal period. Lickliter (1994), Markham et al. (2008) have also shown that prenatal sensory stimulation in one sensory modality (e.g., visual) can influence subsequent postnatal perceptual responsiveness in another sensory modality (e.g., auditory).

It is possible that prenatal auditory stimulation could have similar effects on postnatal visual responsiveness and attentional biases in human development. For example, frequent exposure to the mother's voice during prenatal development followed by exposure to the mother's voice paired with her face shortly after birth could contribute to rapid development of visual preferences for human faces. These biases may then serve to facilitate selective attention to faces and voices in the newborn period. Although this possibility is speculative and remains untested, a series of studies conducted by Sai (2005) demonstrated the influence of maternal speech on newborn attentional biases for faces. Newborn infants who were exposed to their mother's speech between birth and testing preferred their mother's face over a stranger's face. In contrast, newborns who had no postnatal exposure to their mother's speech prior to testing showed no visual preference for their mother's face over a stranger's face. Although carrying out a systematic empirical investigation on the effects of prenatal sensory experience on postnatal visual responsiveness seems impractical at best, computational modeling could potentially be utilized to test the feasibility of the impact of prenatal sensory experience on visual responsiveness in the postnatal period. For example, Bednar and Miikkulainen (2006) utilized computational modeling to demonstrate that newborn face biases could be influenced by internally generated input patterns provided by ponto-geniculo-occipital waves that occur during REM sleep in the prenatal period. The authors proposed that the combined influence of prenatal learning and internal patterns could contribute to the development of neural circuitry involved in face processing.

In a recent exploratory study, Reid et al. (2017) utilized 4-D ultrasound technology to image fetal movements while projecting an upright or inverted triangle pattern composed of three lights through the mother's abdomen. The ultrasound was used to identify the location of the fetus, and the triangular pattern of lights was either projected inverted (i.e., top-heavy) or upright (bottom-heavy) relative to the fetal position. Fetal movements following the presentation of the light pattern were measured as an index of orienting, and more fetal movements were found during presentations of the inverted (face-like) triangle pattern of lights. The authors interpreted this as indicating postnatal experience is not necessary for explaining newborn preference for face-like patterns. This study represents an important step toward developing techniques for prenatal testing with human fetuses. However, given the highly exploratory nature of this study, validation and replication are needed before making strong conclusions based on these results.

The utilization of computational modeling (Bednar and Miikkulainen, 2006; Wilkinson et al., 2014) has provided some insight into potential mechanisms involved in newborn attentional biases for faces. In our opinion, the BCM (Wilkinson et al., 2014) provides the strongest model proposed to date for explaining attentional biases for face-like stimuli shortly after birth. This model provides an excellent example of the developmental concept of constraints by design. Newborn visual preferences are proposed to be largely determined based on perceptual constraints associated with the immature visual system as well as binocular correlations that occur based on the structured relations between the spacing and location of the newborn's eyes and general characteristics of faces and face-like patterns. Future research in the area should continue to utilize computational modeling simulations to test the feasibility of additional factors that may influence newborn attentional biases. We now turn our focus to the development of face processing across the infancy period.

## DEVELOPMENT OF FACE PROCESSING IN INFANCY

A large body of work has been carried out on the development of face processing in infancy. We propose that findings from the extant literature demonstrate the important role of *experiential canalization* (Kuo, 1976; Gottlieb, 1991; Lickliter and Harshaw, 2010) in the development of face processing. Experiential canalization refers to the concept that development is a cumulative process. As development proceeds, the range of behavioral potentials or plasticity narrows. This decrease in plasticity is driven by experience and the developmental history of the organism. Several lines of research provide examples of experiential canalization by demonstrating the effects of regular postnatal exposure to certain types of faces on the development of face processing across the infancy period.

Research indicates that minimal exposure is required for newborn infants to develop a preference for their mother's face (Pascalis et al., 1995; Sai, 2005). For example, Field et al. (1984) found that 45-hour-old infants showed a preference for their mother's face over a stranger's face with an average of just four discontinuous hours of interaction with their mothers for feedings before testing. Somewhat surprisingly, the authors found that newborns habituated to their mother's face with repeated exposure and showed novelty preferences for a stranger's face on later testing trials. Similarly, Barrera and Maurer (1981) found that 3-month-olds show an initial preference for the mother's face over a stranger's face followed by a shift to a novelty preference for the stranger's face on subsequent testing trials. These findings indicate that experience is a driving force behind these early face preferences. Although only an average of 4 h of exposure to their mother's face was needed for infants to demonstrate visual preferences for their mother's face (Field et al., 1984), further exposure within the testing context led to a shift to looking longer to the stranger's face. Farroni et al. (2013) utilized functional near infrared spectroscopy (fNIRS) to measure the cortical hemodynamic response of 1- to 5-day-old newborns in response to dynamic faces, arms, and moving objects. The results indicated face specific activation of bilateral posterior temporal cortex that was positively correlated with age in hours. Thus, at both the behavioral and neural levels, even very young infants' responses to faces are highly malleable and can change with very limited experience.

A large body of research has shown that infants show a preference for female faces in early development that is most likely due to heavy exposure to their mother or a female caregiver. A study of 3- to 4-month-old infants familiarized with both female and male faces found that infants consistently displayed a preference for female faces (Quinn et al., 2002). However, infants primarily raised by males demonstrate preferences for male faces over female faces (Quinn et al., 2002), indicating that gender preference is based on extensive experience with the infant's primary caregiver. In a subsequent study, Quinn et al. (2008) tested 3-month-old Caucasian infants and found they preferred female Caucasian faces over male faces, but did not prefer female over male faces when the faces were Asian. Thus, infant preference for female faces is specific to the race of the mother and is not present when the female face is of another race. Additionally, when testing newborn Caucasian infants, the participants did *not* show a preference for female Caucasian faces, further supporting the theory that it is repeated experience with their mother that biases infants' facial preference.

There has been a significant amount of research conducted on development of the other-race effect (ORE) in infancy. This effect refers to a disadvantage for processing and recognizing individual exemplars of other-race faces in comparison to own-race faces (Hugenberg et al., 2010). Sangrigoli and de Schonen (2004) found that 3-month-olds demonstrate evidence of the ORE that can be eliminated with very brief exposure to other-race faces. Kelly et al. (2007, 2009) found that the ORE increases from 3 to 9 months of age. However, the ORE is not found for infants: raised in environments in which they experience regular exposure to other-race faces (Bar-Haim et al., 2006), regularly shown picture books with other-race faces (Heron-Delaney et al., 2011), or given brief daily exposure to dynamic other-race faces (Anzures et al., 2012). Research utilizing eye-tracking indicates that across 4–9 months of age, infants develop differential scanning patterns for own- vs. other-race faces that coincides with decreased recognition memory ability for other-race faces (Liu et al., 2011; Wheeler et al., 2011; Xiao et al., 2013).

The effects of repeated exposure to certain types of faces has been studied more broadly in research on perceptual narrowing examining infant perception of "native" vs. "non-native" faces. Perceptual narrowing is a developmental process that occurs as infants gain extensive experience with stimuli specific to their native environment (Pascalis et al., 2002; Scott et al., 2007; Lewkowicz and Ghazanfar, 2009; Maurer and Werker, 2014). As the narrowing process unfolds infants transition from having perceptual sensitivities that are broadly tuned to a wide range of stimuli to being more narrowly focused on the stimuli encountered regularly in the native environment. Thus, perceptual narrowing can be viewed as a form of experiential canalization. The other-species effect (OSE) is an example of perceptual narrowing in face processing. The body of behavioral research on this effect suggests across the 6–9 months age range, there is maintenance of perceptual sensitivity for own-species faces and a decrease in perceptual sensitivity for other-species faces (e.g., Pascalis et al., 2002; Simpson et al., 2011). Simpson et al. (2011) proposed a learned attention model of face processing that states that with age and increased experience, infants learn to focus their attention on facial dimensions useful for identification of own-species faces encountered in their everyday experience. The proposal that learned attention drives perceptual narrowing in face processing is consistent with research showing that infants trained with picture books of individually labeled monkey faces between 6 and 9 months of age maintain the ability to individuate other-species faces at 9 months of age (Pascalis et al., 2005; Scott and Monesson, 2009, 2010). In contrast, control infants who receive no supplemental exposure to monkey faces, or infants that receive training with picture books without individually labeled monkey faces do not demonstrate the ability to individuate monkey faces at 9 months of age. Thus, the verbal pairing of individual labels with faces seems to have a significant influence on the maintenance of infants' sensitivity to own-species faces, again indicating the multimodal stimulation is an important aspect of early cognitive development and perceptual learning.

## NEURAL CORRELATES OF INFANT FACE PROCESSING

In addition to behavioral research, there has been extensive developmental cognitive neuroscience research done on face processing and perceptual narrowing in infancy. The event-related potential (ERP) has been widely used in research on face processing in both infants and adults. The N290 and P400 are two ERP components that have been shown to be associated with face processing in infancy (de Haan et al., 2003; de Haan, 2007).

The N290 is commonly identified at posterior electrodes between 290 and 350 ms after stimulus onset (Halit et al., 2003), and is greater in amplitude to faces than noise by 3 months of age (Halit et al., 2004). The P400 is also commonly found at posterior electrodes between 390 and 450 ms after stimulus onset. The P400 has a shorter latency to peak in response to faces than objects by 6 months of age (de Haan and Nelson, 1999), and a shorter latency to upright vs. inverted human faces (Halit et al., 2003) by 12 months of age. Stimulus inversion is used in face processing research to examine the development of configural processing in faces. Configural processing represents more advanced processing of faces in comparison to featural processing (Maurer et al., 2002). An impairment in processing inverted faces compared to upright faces is used as a marker for configural processing of face stimuli (Yovel and Kanwisher, 2005; Rossion and Curran, 2010). Thus, these findings indicate a trend across infancy toward configural processing of own-species faces.

Although 9-month-old infants do not typically show inversion effects in ERP responding to monkey faces (Scott et al., 2006), Scott and Monesson (2010) found that 9-month-olds given 3 months of training with pictures of monkey faces labeled at the individual level demonstrate both N290 and P400 inversion effects for inverted compared to upright monkey faces. This finding, coupled with the finding that 9-month-old infants given similar training can demonstrate behavioral evidence of discriminating monkey faces at the individual level shows the positive effects of pairing faces with verbal labels on the maintenance of infants' sensitivity to other-species faces (Pascalis et al., 2005; Scott and Monesson, 2009). Thus, augmented experience through extensive training has a positive impact on infants' ability to maintain sensitivity to other-species faces.

Research from our lab (Dixon et al., 2017), has shown that although infants demonstrate poor performance at individuating monkey faces based on perceptual narrowing, they do seem to be efficient at categorizing other-species faces at 9 months of age. In addition to analyzing face processing components, we analyzed the Negative central (Nc) ERP component associated with infant attentional engagement (Courchesne et al., 1981; de Haan and Nelson, 1997, 1999, Reynolds and Richards, 2005; Reynolds et al., 2010; Reynolds, 2015; Reynolds and Romano, 2016). We found that with a training phase that consisted of only 20 brief presentations of multiple exemplars of monkey faces from a specific monkey species (e.g., Capuchin monkeys), 9-month-olds were able to demonstrate strong evidence of subordinate-level categorization of other-species faces. Subordinate-level categorization is considered to be a marker for perceptual expertise (Quinn and Tanaka, 2007).

Results from our analysis of Nc are shown in **Figure 1**. Infants demonstrated greater Nc amplitude to monkey faces from a different species of those they were trained on (novel-species condition) compared to Nc amplitude for both novel monkey faces from the same species they were exposed to during training (novel-same) and the familiar faces seen during training (familiar). The amplitude of Nc during the training trials is also shown. This finding is indicative of increased attention to the novel-species monkey faces, and provides evidence of subordinate-level categorization for other-species. Although further studies are needed examining categorization of other-species faces across a broader age range, these findings provide some support for the possibility that selective attention may serve as a mechanism behind perceptual narrowing. By 9 months of age, infants may be distributing their selective attention during initial exposure to non-native stimuli in a manner effective for processing at the categorical level (i.e., "what is this?") as opposed to the individual level (i.e., "who is this?"). A visual intake strategy aimed at categorization as opposed to individuation would be the most efficient initial approach to perceptual processing of a novel species not encountered in the native environment.

The bulk of the extant literature thus indicates that experience plays a pivotal role in the process of developing attentional biases in early infancy. These biases subsequently affect the development of face processing expertise and social preferences in later infancy. Frequent exposure to the same types of stimuli, such as faces of the same gender and race as their primary caregiver in early development (Quinn et al., 2002, 2008) lead to basic familiarity preferences. Over time and with experience, these preferences translate to attentional biases that serve to facilitate processing of native stimuli at finer levels of discrimination (i.e., individuation) than non-native species (categorization). These findings demonstrate experiential canalization in the development of face processing and indicate that the effects of prior experience on developing face processing abilities may be mediated by differential distribution of selective attention for familiar compared to novel stimulus classes.

## THE DEVELOPMENT OF FACE PROCESSING IN MULTIMODAL CONTEXTS

Across studies reviewed above, infants were tested in unimodal visual conditions. However, social experience with faces is multimodal and often involves combined sensory input to the visual and auditory sensory modalities in the form of audiovisual speech. In the next section, we review research examining infant processing of faces in multimodal contexts that indicates characteristics of multimodal sensory stimulation play a critical role in directing infant attention and facilitating perceptual learning. We propose that in addition to highlighting the role of experiential canalization in early face processing, findings from this research provide an excellent example of the developmental concept of *distributed control* (Lickliter, 2000; Lickliter and Honeycutt, 2003). Distributed control indicates that the control of developmental outcomes is distributed across levels of the developmental system, and is determined by relations within and between organismic and contextual variables (Lickliter, 2000). Under this framework, no single factor is viewed as having causal priority in determining developmental outcomes. Instead, developmental outcomes are reciprocally determined based on the interdependent and mutually constraining influence of multiple factors (Oyama, 1985, 1993; Gottlieb, 1991, 1997; Lickliter, 2000; Lickliter and Honeycutt, 2003).

There is a large body of research demonstrating that multimodal stimulation is a highly salient source of information

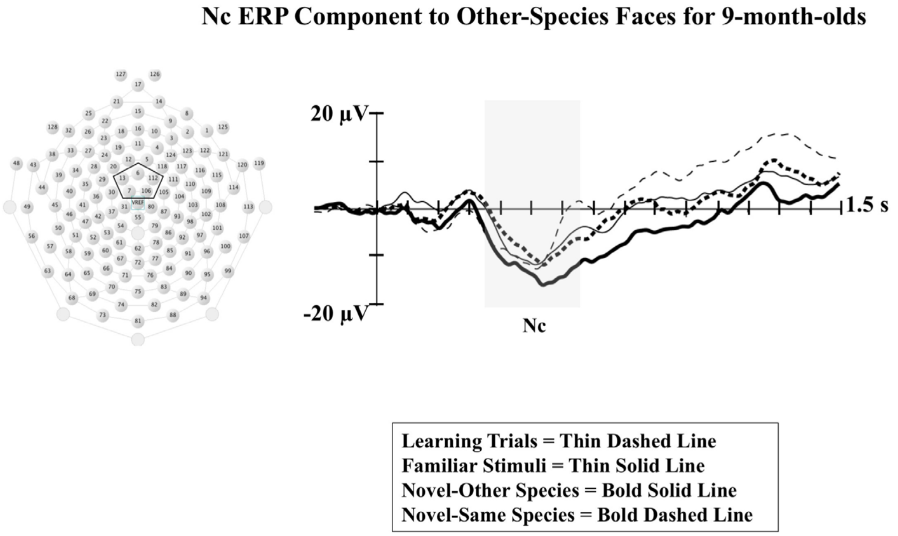

**FIGURE 1 |** The Nc component associated with infant visual attention is shown at midline central electrode clusters for 9-month-old infants in response to presentations of monkey faces that were either: familiar faces shown during an initial learning phase (first 20 trials), novel monkey faces from a different species than those seen in the learning phase (novel-other), or novel faces from the same species as those seen during the learning phase (novel-same). The midline central electrode cluster used in the analyses is indicated in the sensor net layout shown to the left. The shaded rectangle indicates the time window for the analysis of Nc. Time following stimulus onset is shown on the *X*-axis, and change in amplitude of the ERP (in microvolts) is shown on the *Y*-axis (Figure adapted from Dixon et al., 2017).

that serves to engage attention and facilitate perceptual processing and memory in human infants, human adults, and precocial avian species (Bahrick and Lickliter, 2000, 2002, 2012, 2014; Lewkowicz, 2000; Lickliter and Bahrick, 2000; Reynolds and Lickliter, 2004; Reynolds et al., 2013, 2014). Bahrick and Lickliter's (2000, 2002, 2014) intersensory redundancy hypothesis proposes that redundancy across two or more sensory systems directs selective attention to amodal properties of objects and social events that are perceived across multiple sense modalities. This focus of selective attention on the amodal properties of multimodal stimuli occurs at the expense of non-redundantly specified, modality-specific stimulus properties. Thus, in the context of face processing, intersensory redundancy would be expected to facilitate processing of amodal information provided by faces (e.g., affect, prosody; Flom and Bahrick, 2007), and interfere with processing modality-specific information provided by faces (e.g., distinctive facial features used for individuation and face recognition; Bahrick et al., 2013). The role of intersensory redundancy in directing selective attention and promoting perceptual learning of amodal information is proposed to be most important in early development when attentional resources and prior experience are both highly limited.

Flom and Bahrick (2007) conducted a series of habituation experiments examining the ability of infants to discriminate a change of affect conveyed through speech. Infants of 3, 4, 5, or 7 months of age were shown video clips a woman speaking with either a happy, sad, or angry affective expression. These video clips were presented in the following conditions: synchronous (redundant) audiovisual, asynchronous (non-redundant) audiovisual, unimodal auditory, or unimodal visual. Results showed that at 4 months of age, infants were only able to discriminate a change in affect in the synchronous audiovisual condition. By 5 months of age infants were able to detect the change in the unimodal auditory condition. Infants were only able to detect the change in affect in the unimodal visual condition at 7 months of age. Asynchronous audiovisual presentation was found to interfere with infants' detection of a change in affect. These findings provide an example of intersensory facilitation in that infants detected changes in affect in redundant audiovisual speech at an earlier age than in unimodal speech. Similarly, Coulon et al. (2013) found evidence of intersensory facilitation of neonatal imitation of mouth movements conveyed in audiovisual speech. Newborns imitated mouth movements produced by a model in an audiovisual congruent condition more quickly than in a unimodal visual condition. Furthermore, newborns failed to imitate mouth movements produced by a model in an audiovisual incongruent condition.

Face recognition relies on successful processing of facial features which are specific to the visual modality. If intersensory redundancy directs infant attention to amodal stimulus properties at the expense of modality-specific stimulus properties, then infants should show facilitation of face recognition under unimodal stimulus presentations in comparison to redundant multimodal stimulus presentations. In support of this prediction from the intersensory redundancy hypothesis, Bahrick et al. (2013) found infants were able to discriminate novel from familiar faces in a unimodal visual condition at 2 months of age; however, infants did not show evidence of discriminating novel from familiar faces in a synchronous audiovisual condition until 3 months of age. Consistent with the concept of distributed control, these findings indicate infant performance on measures of face processing is dependent on multiple factors; including (but not limited to): age, stimulus modality, and whether successful performance on the task relies on detection of amodal or modality-specific stimulus properties. Furthermore, the results of these studies imply that research on infant face processing that utilizes static visual stimuli may not generalize well to infant face processing of dynamic faces in multimodal contexts.

Bahrick et al. (2016) examined 2- to 8-month-old infants' attention to faces compared to objects under static and dynamic audiovisual and unimodal visual presentation conditions. Interestingly, they found no attentional bias for faces compared to objects for infants at 2 months of age. By 3 months of age, infants only attended more to faces compared to objects under dynamic presentation conditions, and from 4 months on, infants began to focus more on dynamic audiovisual faces compared to all other stimulus types. The authors concluded that enhanced selective attention to faces compared to non-social stimuli emerges gradually across infancy. Bahrick et al. (2013) have also proposed that infants are not innately attracted to faces over other sources of information in early infancy. In contrast, motion or action and intersensory redundancy are proposed to be higher on the salience hierarchy in early infancy in comparison to faces *per se*. Support for this hypothesis comes from research indicating that infants demonstrate poor face perception when faces are seen in naturalistic settings. For example, 5-month-olds shown videos of an actress engaged in a repetitive action (such as brushing her hair) show discrimination and evidence of long-term memory for the action, but they show no evidence of discrimination or memory for the actress unless the length of exposure is doubled or the repetitive action is eliminated (Bahrick et al., 2002; Bahrick and Newell, 2008). Thus, in dynamic, multimodal contexts, infants may be biased to focus selective attention on motion (or action) first, and then shift selective attention to stimulus properties lower on the salience hierarchy after each of the more salient properties is processed. Frank et al. (2009) utilized eye-tracking to examine the distribution of 3- to 9-month-old infants' selective attention while viewing animated films. They found that 3-month-olds' selective attention was driven by low-level stimulus salience, and infants gradually began to focus more on faces beyond 3 months of age. Taken together, these findings indicate that faces move to higher levels in the salience hierarchy compared to non-social stimuli from 4 months on (Frank et al., 2009; Bahrick et al., 2013).

Lewkowicz and Ghazanfar (2006), Lewkowicz and Hansen-Tift (2012), Lewkowicz (2014), and Minar and Lewkowicz (2017) have examined perceptual narrowing in audiovisual speech perception. For example, Lewkowicz and Hansen-Tift (2012) utilized infrared eye-tracking to investigate infant looking patterns across an age range of active language learning. Video clips of women speaking either English (native language) or Spanish (non-native language) were shown to 4 - to 12-month-old English-learning infants as well as monolingual English-speaking adults. Both adults and 4-month-olds looked mostly at the eyes of a talking face, but starting at 6 months of age, infants began to look more at the mouth of the speaker regardless of what language was being spoken. Around 10–12 months of age, infants listening to the English speaker began to shift the overall distribution of their selective attention such that relatively more looking was focused toward the mouth again, much like adults. But 10 and 12-month-olds listening to a woman speak in Spanish remained focused on the mouth to a greater extent.

These results indicate that in the youngest group at an earlier stage of language development, infants selectively attended to the mouth as a source of redundant information provided by the vocalizations and movements of the mouth. By 10–12 months of age, infants learning English have a more mature language foundation and may not need to rely on the mouth movements as heavily to process the audiovisual speech. However, the older infants listening to the non-native Spanish speaker may still require the redundant information presented by the mouth of the speaker. Interestingly, Kubicek et al. (2014) found that although 6-month-olds are capable of cross-modal matching of audio and video tracks of a woman speaking in both native and non-native speech, 12-month-olds are only able to do so with non-native speech. Although this finding seems counter-intuitive in the context of perceptual narrowing, the 12-month-olds' poor ability to match face and voice in the native speech condition may have been based on increased selective attention to the eyes relative to the mouth for native language speakers (Lewkowicz and Hansen-Tift, 2012). Thus, in the native speech condition, 12-month-olds may have not focused their selective attention on the redundant properties of speech provided by the mouth and this may have decreased their ability to engage in cross-modal matching.

In a recent study, Minar and Lewkowicz (2017) found that infants rely on multimodal cues for discriminating other-race faces. By 10–12 months of age, infants were only able to discriminate other-race faces when presented in a synchronous audiovisual condition. Furthermore, while they were able to discriminate own-race faces in a unimodal visual condition, they were unable to discriminate other-race faces in the unimodal visual condition. Taken together, these findings are in line with the most recent tenet of the intersensory redundancy hypothesis which proposes that older infants and children revert to relying on intersensory redundancy to facilitate perceptual processing and learning in more challenging contexts (Bahrick et al., 2010), and they demonstrate the effects of experience on intersensory perceptual narrowing.

## NEURAL CORRELATES OF INFANT MULTIMODAL PERCEPTUAL PROCESSING

In addition to behavioral measures, studies have also utilized neural measures to examine infant audiovisual processing. Hyde et al. (2010) conducted an ERP study examining unimodal and multimodal speech processing in 3-month-olds and adults. Participants were presented an actress saying "hi!" in infant-directed speech in unimodal auditory, unimodal visual, and bimodal audiovisual conditions. Results indicated that 3-month-olds demonstrate an enhanced N450 ERP component over fronto-temporal sites during bimodal audiovisual presentations.

The N450 ERP component is considered a precursor to the N2 component, which is associated with auditory processing in adulthood (Wunderlich and Cone-Wesson, 2006). This suggests that simultaneous visual stimulation facilitates auditory processing in early infancy continuing into adulthood and is consistent with findings of super additive multimodal effects on neural activity from comparative research (Jay and Sparks, 1984; Stein et al., 1994; Wallace et al., 1996; Wallace and Stein, 1997) and research with adults (e.g., Giard and Peronnet, 1999; Santangelo et al., 2008).

Several studies have examined the effects of audiovisual face-voice pairings on the Nc component associated with infant visual attention (Grossmann et al., 2006; Hyde et al., 2011; Vogel et al., 2012; Reynolds et al., 2014). In two initial studies, infants' audiovisual integration was tested by examining neural responsiveness to test stimuli presented that were either congruent or incongruent in affect with a preceding stimulus. Using this approach, Grossmann et al., (2006) found that infants demonstrate greater Nc amplitude to face-voice pairings conveying incongruent emotional information compared to face-voice pairings conveying congruent emotional information. Yet, Vogel et al., (2012) found that infants demonstrate greater amplitude Nc to face-voice pairings conveying congruent emotional information. These contrasting findings may have been due to procedural differences that could potentially alter the salience hierarchy of congruent vs. incongruent stimuli across studies. This would lead to differences in the directional effects of Nc as it is associated with depth of attentional engagement (Reynolds et al., 2010). Because the auditory and visual components of the stimuli used in these studies were not presented simultaneously, these studies did not provide insight into the neural underpinnings of the effects of intersensory redundancy on attention and perceptual processing in infancy.

Two studies have examined the effects of intersensory redundancy on neural correlates of infant attention and memory in response to audiovisual speech (Hyde et al., 2011; Reynolds et al., 2014). Both of these studies tested infants at 5 months of age, and analyzed Nc as an index of attentional engagement. The late slow wave (LSW) was examined as a neural correlate of infant recognition memory. Across studies, infants have been found to demonstrate reduced amplitude of the LSW with increased stimulus exposure (de Haan and Nelson, 1999; Snyder et al., 2002, 2010; Wiebe et al., 2006; Guy et al., 2013). Hyde et al. (2011) found greater amplitude of the LSW on synchronous audiovisual trials in comparison to asynchronous audiovisual trials, and interpreted this finding to indicate enhanced processing of synchronous audiovisual speech. In contrast, infants demonstrated greater amplitude Nc on asynchronous audiovisual trials in comparison to synchronous audiovisual trials. The authors interpreted this as increased infant attention to the novelty of speech presented asynchronously across the auditory and visual modalities.

Reynolds et al., (2014) conducted two ERP experiments examining 5-month-old infant visual attention and recognition memory for speech presented in unimodal visual, synchronous audiovisual, and asynchronous audiovisual conditions. The first experiment examined the effects of intersensory redundancy on attentional engagement. In contrast to Hyde et al. (2011) findings, infants were found to demonstrate greater amplitude Nc to synchronous audiovisual speech in comparison to asynchronous audiovisual or unimodal visual speech. Once again, these contrasting findings in the direction of Nc effects could be due to procedural differences. As the Nc reflects level of attentional engagement, variations in testing context would be expected to affect infant attention and relative amplitude of the Nc component (Richards, 2003). Importantly, both studies demonstrated LSW activity associated with enhanced perceptual processing on synchronous audiovisual trials. For example, Reynolds et al. (2014) utilized a block design in their second experiment to examine changes in LSW amplitude from early to late trials. Infants only demonstrated significant reductions in LSW amplitude from early to late trials in the synchronous audiovisual condition (see **Figure 2**). These findings indicate that the intersensory redundancy provided in the synchronous audiovisual condition led to enhanced infant attention (greater amplitude Nc) and enhanced perceptual processing resulting in recognition memory in the late block of trials (reduced amplitude LSW).

Taken together, the findings from a growing body of research utilizing both behavioral and neural measures indicate that infant selective attention and perceptual processing of amodal information is enhanced in multimodal testing conditions in comparison to unimodal testing conditions. However, consistent with the development of distributed control, the interaction of multiple factors (e.g., age, stimulus modality, previous experience) determines which stimulus properties an infant will focus selective attention on and ultimately process. After birth, infants are immersed in social environments. Sugden et al. (2014) utilized head mounted cameras on 1- and 3-month-old infants in their home environments, and found that 25% of the infants' waking time was spent exposed to faces. Research indicates that the distribution of selective attention to faces shows significant developmental change across infancy. This developmental change is likely tied to a number of factors, including (but not limited to) extensive experience with faces, individual differences, and early language development (e.g., Kushnerenko et al., 2013; Tomalski et al., 2013; Streri et al., 2016). In addition to the effects of prior experience on shaping attentional biases in early development, there are likely a number of neural and physiological mechanisms that influence attention to faces during infancy.

## NEURAL AND PHYSIOLOGICAL MECHANISMS INVOLVED IN ATTENTIONAL BIASES

Attention and arousal are tightly linked in early development. Comparative research (e.g., Radell and Gottlieb, 1992; Reynolds and Lickliter, 2004) and research with human infants (e.g., Gardner and Karmel, 1995; Geva et al., 1999) has shown that alterations in physiological arousal can modulate attention and either enhance or interfere with perceptual learning and

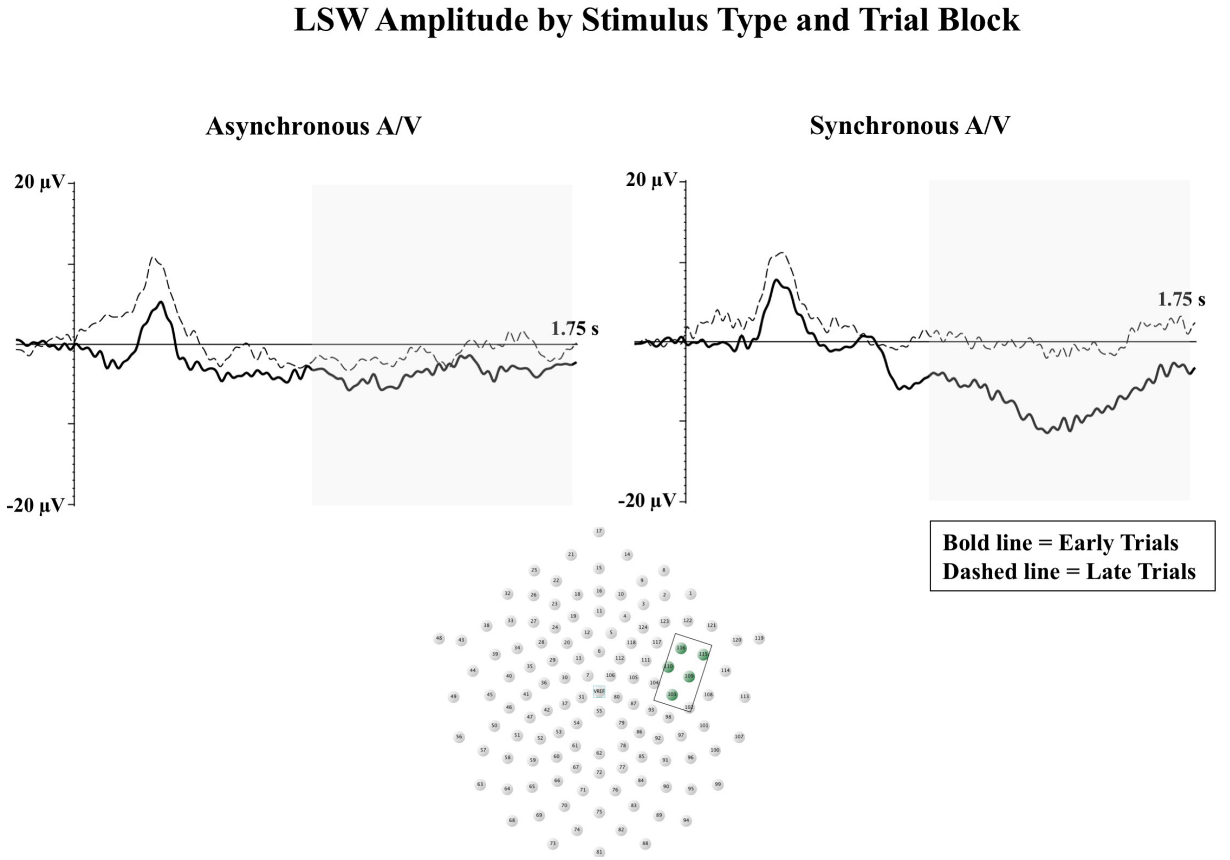

**FIGURE 2 |** The LSW is shown for early (bold line) and late (dashed line) blocks of trials at right anterior temporal electrodes. Waveforms from the synchronous audiovisual condition are shown in the right panel, and waveforms from the asynchronous audiovisual condition are shown in the left panel. The *Y*-axis represents the amplitude of the ERP in microvolts, and the *X*-axis represents time following stimulus onset. The time-window of the component analysis is shaded on the *X*-axis. The positioning of the electrodes included in the analysis are shown in the bottom panel (Figure adapted from Reynolds et al., 2014).

responsiveness in early development. For example, Gardner and Karmel (1995) found that both internally and externally induced arousal modulates infant selective attention such that newborn infants focus their attention on low frequency sine wave stimuli during high arousal states and they focus their attention on high frequency stimuli during low arousal states. Similarly, newborns' visual preferences in the paired-comparison task were found to shift from familiarity preferences when tested prior to feeding to novelty preferences after feeding (Geva et al., 1999). Blass and Camp (2001) tested 9- and 12-week-old infants for evidence of recognition of a research assistant. Initial exposure to the research assistant was either paired with delivery of a sucrose solution or not. The authors found that in subsequent testing, infants only demonstrated recognition of the research assistant when initial exposure was paired with the sweet taste of the sucrose solution. Additionally, only infants who were calm during testing demonstrated evidence of recognition memory.

Arousal-based effects on infant visual attention are strongest in the newborn period, and Gardner and Karmel (1995) have proposed they serve to maintain an optimal level of arousal for the child in the earliest stages of postnatal development. In comparative work with Bobwhite Quail embryos and chicks, Reynolds and Lickliter (2004) found that significant alterations in arousal associated with prenatal sensory stimulation have prolonged effects on arousal and perceptual processing that persist into early postnatal development. Several studies have demonstrated the importance of the primary caregiver for the regulation of arousal in young infants (e.g., Gable and Isabella, 1992; Calkins, 1994; Porter, 2003), indicating infants are dependent on caregivers for other-regulation during the early months of postnatal development. Gredebäck et al. (2012) utilized eye-tracking to examine fixation patterns and pupil dilation in a study on individual differences in face processing in infancy. They found that parental care influenced both gaze duration and pupil dilation for 14-month-olds viewing images of their parents or strangers. Specifically, infants who received similar levels of parental care from both their mother and father showed more broadly distributed gaze patterns than infants primarily cared for by their mother. Furthermore, infants showed larger pupil diameter when viewing images of their secondary caregiver displaying neutral affect. Thus, a promising direction for future research would be to examine arousal-based mechanisms that may be associated with the development of social orienting and face processing.

Arousal – attention relations are bidirectional. For example, attentional engagement leads to changes in arousal in infancy (for review, see Reynolds and Richards, 2008). Richards (2008), Reynolds et al. (2013), and Reynolds and Romano (2016) have proposed that there is a general arousal/attention system that accounts for the effects of attention on various aspects of arousal. Several areas of the brain contribute to this general arousal/attention system including, brainstem areas, thalamus, basal forebrain, and cardio-inhibitory centers in frontal cortex (Reynolds et al., 2013). The cholinergic system is also critically involved in sustained attention (Sarter et al., 2001). Activation of this system has a range of effects related to arousal, including: decreased heart rate, decreased motor activity, and release of acetylcholine (ACh) via corticopetal projections. These changes foster an optimal level of arousal for attention and perceptual processing. This arousal system shows considerable development across infancy and early childhood. Developmental changes associated with further development of the general arousal/attention system include: increased magnitude of the heart rate response associated with attention, longer durations of sustained attention, and decreases in distractibility across infancy and early childhood (Richards and Cronise, 2000; Reynolds and Richards, 2008). Guy et al. (2016) utilized heart rate, ERP, and cortical source analysis to examine face processing in 4.5- to 7.5-month-old infants. Their findings indicated that ERP components associated with infant face processing (i.e., N290, P400) were greater in amplitude on trials when heart rate was indicative changes in arousal associated with attention. Additionally, the results of the source analysis revealed occipital–temporal areas, such as the middle fusiform gyrus, as a potential source of the N290 ERP component.

Multiple brain networks show further development throughout infancy that have a significant influence on the characteristics of infant attention to both social and non-social stimuli. For example, at birth attention is primarily influenced by subcortical structures, including the superior colliculus. During the newborn period, visual fixations are believed to be primarily reflexive (Johnson et al., 1991c), and infant visual attention is reflexively drawn to areas of high-contrast in the visual field, motion, and stimuli that are larger in size. This subcortical reflexive system is consistent in many ways with Conspec (Johnson and Morton, 1991b); however, this system is domain-general as opposed to an innate system evolved for orienting to faces. It is not until about 2–3 months of age that areas of the brain involved in the voluntary control of visual fixation begin to reach functional onset, these include posterior parietal areas, the pulvinar nucleus of the thalamus, and frontal eye-fields (Posner and Petersen, 1990; Johnson et al., 1991c; Petersen and Posner, 2012). Finally, beyond 6 months of age, frontal areas (dorsolateral prefrontal cortex, orbitofrontal cortex, anterior cingulate) have a greater influence on attention. Further development of these frontal areas as well as increased frontal – parietal and frontal – temporal connectivity contribute to gains in the volitional control of attention, and increased inhibition to distracters. These developmental changes are likely tied to gains in social – cognitive processes, such as categorization of social agents and comprehension of the actions of social agents (Grossmann, 2015).

## LIMITATIONS AND FUTURE DIRECTIONS

Although a great deal of progress has been made in research on the development of face processing, controversy still remains regarding the mechanisms that account for both newborn face preferences and for the rapid development of relatively advanced face processing ability across the infancy period. The vast majority of research in the area has utilized cross-sectional designs. In order to gain insight into processes involved in the development of attentional biases for faces, more longitudinal studies need to be carried out across relatively broad age ranges. Additionally, scientists have been somewhat limited in neuroimaging tools that are available for use in research on early development given practical and ethical concerns related to the use of fMRI and PET with infant participants. To gain greater understanding of both neural processes and neural systems involved in early face processing, future studies should be aimed at capitalizing on: the excellent temporal resolution of ERP, the advanced spatial resolution of fNIRS, and the added level of insight provided by computational modeling.

## CONCLUSION

We propose that developmental systems theory provides an ideal framework for interpreting the development of attentional biases for faces in infancy. The extant findings from research on infant processing highlight the cumulative nature of development and are consistent with the concept of experiential canalization (Kuo, 1976) in that early experience serves to direct subsequent experience. It is our position that biases to attend to faces are not innately determined or set at birth, but instead are the product of domain-general developmental processes. The distribution of selective attention is determined by multiple influences; including previous experience, stimulus characteristics, arousal mechanisms, and the functional maturity of brain structures involved in attention. Consistent with the developmental concepts of constraints by design and distributed control (Lickliter, 2000), it is the interaction of these multiple factors that determines how selective attention is distributed at any given point in development. None of these factors are viewed as having causal priority in determining infant visual preferences; however, the relative influence of each factor will change across contexts and further development. For example, the influence of arousal on attention decreases beyond the newborn period (Gardner and Karmel, 1995), and the influence of experience and learning increases throughout early development as is demonstrated through the effects of perceptual narrowing. The process of learning through experience, combined with further development of neural systems involved in attention and cognitive processing, allows the infant greater efficiency and flexibility in social – cognitive processing from late infancy on.

## AUTHOR CONTRIBUTIONS

GR determined a general outline for the review paper and came up with the model presented in the paper regarding the development of attentional biases in infancy. After the authors discussed the general outline of the paper, KR wrote two initial drafts with feedback from GR. GR then wrote the submitted version of the paper utilizing portions of the initial drafts written by KR, as well as adding additional sections and adding the final model presented in the paper.

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REVIEW
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# Developmental Changes in Learning: Computational Mechanisms and Social Influences

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Our ability to learn from the outcomes of our actions and to adapt our decisions accordingly changes over the course of the human lifespan. In recent years, there has been an increasing interest in using computational models to understand developmental changes in learning and decision-making. Moreover, extensions of these models are currently applied to study socio-emotional influences on learning in different age groups, a topic that is of great relevance for applications in education and health psychology. In this article, we aim to provide an introduction to basic ideas underlying computational models of reinforcement learning and focus on parameters and model variants that might be of interest to developmental scientists. We then highlight recent attempts to use reinforcement learning models to study the influence of social information on learning across development. The aim of this review is to illustrate how computational models can be applied in developmental science, what they can add to our understanding of developmental mechanisms and how they can be used to bridge the gap between psychological and neurobiological theories of development.

**Keywords: reinforcement learning, cognitive modeling, decision-making, social cognition, lifespan, developmental neuroscience**

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In our daily lives, we constantly need to learn about the conditions of our environment to improve our future choices. Which ice cream will I enjoy most? What school should I send my children to? How much money should I save for retirement? While the kinds of choices we have to deal with change throughout the lifespan, so do the strategies with which we approach decisions in order to find an optimal solution. Understanding how learning and decision-making is affected by age is therefore crucial for adapting structures and processes in educational, occupational, or health contexts to different target groups.

Over the past few years, computational approaches such as reinforcement learning (RL) models (Sutton and Barto, 1998) have become increasingly popular in psychology and cognitive neuroscience. One big advantage of these models over descriptive (verbal) theories is that they allow us to explicitly formalize cognitive processes. That is, we can use these models to make explicit numerical predictions regarding the effects of experimental manipulations on outcome measures. This level of specificity is difficult to achieve with verbal theories alone. Moreover, computational models can be used to simulate behavior and thus also to simulate potential limitations of sub-processes that come with development, aging, or pathology (e.g., Nassar et al., 2016). Another important qualitative advantage of computational models is that they can provide access to latent cognitive processes. For example, many researchers are interested in the psychological processes underlying performance monitoring or in the question of how people handle conflicts between habitual and goal-directed response tendencies. Computational models allow us to formalize these latent processes and make them accessible for empirical approaches. Finally, one of the main reasons for the increasing popularity of these models in cognitive neuroscience is that they can be used to derive time varying variables of computational processes that can be correlated with neurophysiological data (e.g., O'Doherty et al., 2004; Gläscher et al., 2010). These so-called "model-based" analyses can provide insights into the neural dynamics underlying cognitive processes that are difficult to achieve with the standard approaches.

For researchers in lifespan developmental neuroscience, computational modeling techniques are particularly promising because they might provide new insights into developmental processes that lead to changes in learning and decision-making and how they relate to the development of neurobiological function (van den Bos et al., 2017). While most of the current research in the area of computational neuroscience has focused on individual learning and decision-making, there is an increasing interest in using computational methods to understand social influences on learning and choice behavior (Behrens et al., 2008, 2009; Diaconescu et al., 2014, 2017). This new emerging research trend seems particularly relevant for the developmental field because of the immense impact of social influences on developmental processes, especially during childhood and adolescence (Ainsworth, 1989; Herrmann et al., 2007; Blakemore, 2008; Somerville, 2013).

In this review, we will outline how developmental psychologists can make use of modeling approaches to study age-related changes in learning and decision-making. We will demonstrate how the basic computational algorithms of RL can be extended and modified to address questions about the developmental trajectories of learning and decision-making processes across one's lifespan. The first section will introduce and briefly summarize the fundamental principles of RL models. We will then discuss how the computational level is linked to psychological constructs and theories about human development by giving examples from the literature on the development of learning and decision-making in non-social settings. Finally, the employment of modeling techniques in the context of social decision-making will be reviewed, and we will show how existing models can be applied to developmental questions on social learning.

## BASIC REINFORCEMENT LEARNING MODELS

Many of our preferences (e.g., for one type of ice cream over another) are shaped by experience-driven learning mechanisms. That is, we sample our environment (our favorite ice cream parlor), and depending on our evaluation of the outcomes, we update the value representations of the different types of ice cream.

RL models provide a formalization of how a human (or non-human) agent learns from experience to maximize her reward in a given environment (Sutton and Barto, 1998). In many situations, RL can be understood in terms of a *Markov decision process (MDP)*. An MDP consists of distinct states an agent can find herself in (e.g., different sensory inputs), and each state provides the agent with a set of available actions. On performing one of these actions, the agent moves to a new state according to a transition function that defines the probability of arriving in this state given the previous state and the selected action. **Figure 1** illustrates how this structure applies to a simplified example (similar to a two-alternative forced choice task in a psychological experiment). Here, a person repeatedly chooses between two types of ice cream, where each choice is followed by either a pleasant taste (outcome value = 1) or a neutral taste (outcome value = 0). The outcome values are on an arbitrary scale and only become meaningful in relation to each other. Typically, positive values represent rewards and negative values losses or punishments. Importantly, whether a type of ice cream is experienced as pleasant or not can be different even after identical choices (maybe because there is variance in the product quality or because the taste also depends on factors that we do not account for, such as the person's mood). If the probability of experiencing a pleasant taste is higher after choosing one type of ice cream than after choosing the other, the person will eventually develop a preference for the most pleasant type of ice cream, thus maximizing the number of pleasant taste experiences in the long run.

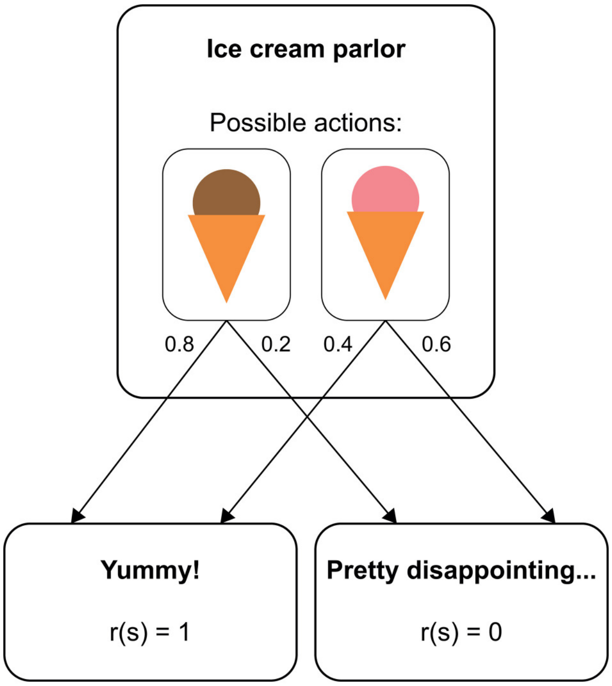

**FIGURE 1 |** Structure of a real-world decision as a Markov decision process. The state "ice cream 922 parlor" has two available actions, "chocolate ice cream" and "strawberry ice cream". With a certain probability (represented by numbers next to the arrows), each choice leads to either a reward state or a non-reward state.

In order to optimize behavior, the agent needs to iteratively update her reward expectation of different actions. In RL models, this is formalized as a state-action value *Q(s,a)* that represents the subjective expectation of reward from performing action *a* in state *s*. The example introduced above involves two state-action values, Q(ice cream parlor, chocolate) and Q(ice cream parlor, strawberry). If both state-action values are equal, the participant does not prefer either type of ice cream. With learning, the participant continuously updates her prediction about the value of the two flavors based on the perceived discrepancy between the expected and the actually experienced reward. This discrepancy is expressed by the *reward prediction error* δ that is computed after an agent has performed action *a* in state *s*:

$$\delta = \underbrace{r(s') + Q\left(s', a'\right)}_{\text{experienced reward}} - \underbrace{Q\left(s, a\right)}_{\text{expected reward}} \tag{1}$$

Here, $s'$ is the new state the agent has moved to, where she receives a reward with value $r(s')$ and is going to perform another action $a'$. Importantly, in this equation the experienced reward is the sum of the immediately obtained reward $r(s')$ and the prospective future reward represented by the state-action value for the action in the new state $Q(s', a')$.

To illustrate how the computation of a reward prediction error works, consider a person who expects chocolate ice cream to be moderately rewarding (Q(ice cream parlor, chocolate) = 0.6) and, having selected chocolate ice cream, experiences a pleasant taste ($r(s') = 1$). In this example task, the experienced reward is completely determined by the immediate reward because after tasting the ice cream, no further actions are available ($Q(s', a') = 0$). Then, the reward prediction error is computed as the difference between experienced and expected reward, which is $\delta = (1 + 0) - 0.6 = 0.4$. If the experienced reward is larger than the expected reward (better than expected outcome), the reward prediction error δ will take a positive value. Conversely, if the experienced reward is smaller than the expected reward (worse than expected outcome), δ will be negative.

The reward prediction error is then used to update the state-action value:

$$Q\left(s, a\right) \leftarrow Q\left(s, a\right) + \alpha\delta \tag{2}$$

The individual learning rate α indicates how strongly the most recent experience is weighted relative to previous experiences when updating the state-action value. If α = 0, the new experience is not at all taken into account (even if your current chocolate ice cream does not taste as predicted, you will not change your future expectation) and the state-action value remains unchanged. If α = 1, the new state-action value is completely updated by the new experience (your attitude toward a type of ice cream is determined only by the last time you tasted it). Intermediate values of α reflect a certain balance between the recent experience and previous ones. That is, you consider both your last cup of ice cream as well as other ice cream you have had in the past when making a decision. **Figure 2A** illustrates how a state-action value evolves given different learning rates.

## From Learning to Action Selection

So far, we have only considered the question of how value expectations are built and updated. However, for an agent it is also important how to translate value representations into actions. That is, how does our preference for one type of ice cream over the other makes us choose one of them? Most RL models assume that actions are selected probabilistically. The probability that an agent selects a particular action $a_i$ out of all available actions is usually modeled with a softmax function:

$$P\left(a_i|s\right) = \frac{\exp(\beta Q\left(s, a_i\right))}{\sum_k \exp(\beta Q\left(s, a_k\right))} \tag{3}$$

The inverse softmax temperature β controls the extent to which differences in state-action values affect action selection. If β = 0, differences in state-action values have no effect and all actions are selected with equal probability. With increasing values of β, it becomes more and more likely to select the action with the highest state-action value. The specific form of the softmax function guarantees that the probability of selecting an action is relative to the respective state-action value and that the probabilities of all available actions in one state add up to 1. **Figure 2B** exemplifies how β affects the mapping from state-action values to probabilities.

# LINKING MODEL PARAMETERS TO PSYCHOLOGICAL CONSTRUCTS

## Learning Rate

### Learning from Positive vs. Negative Prediction Errors

Until now, we have treated positive and negative prediction errors alike in terms of their effects on updating value representations. However, it is intuitively clear that a negative prediction error might have different implications for behavior than a positive prediction error. For example, your favorite ice cream might suddenly induce an allergic reaction (negative prediction error). Consequently, you will shift your preference and avoid this ice cream. In contrast, in most cases, positive prediction errors will reinforce existing behavior or preferences. Psychological theories assume that the ability to adapt behavior to negative consequence involves performance monitoring processes that rely on prefrontal structures such as the medial prefrontal and dorsolateral prefrontal cortex and the insula (Holroyd and Coles, 2002; Ullsperger and von Cramon, 2003; Ridderinkhof et al., 2004). In contrast, learning from positive outcomes has been suggested to involve dopaminergic projections to limbic and paralimbic areas such as the ventral striatum and ventromedial prefrontal cortex (vmPFC) (Schultz et al., 1997; Montague et al., 2004; D'Ardenne et al., 2008), although some subregions of the vmPFC may also be involved in error monitoring (Maier et al., 2015; Buzzell et al., 2017). Interestingly, these distinct neural systems have different developmental trajectories. Structural as well as functional magnetic resonance imaging (fMRI) revealed that prefrontal areas involved in learning from negative outcomes show a protracted development compared to limbic and paralimbic

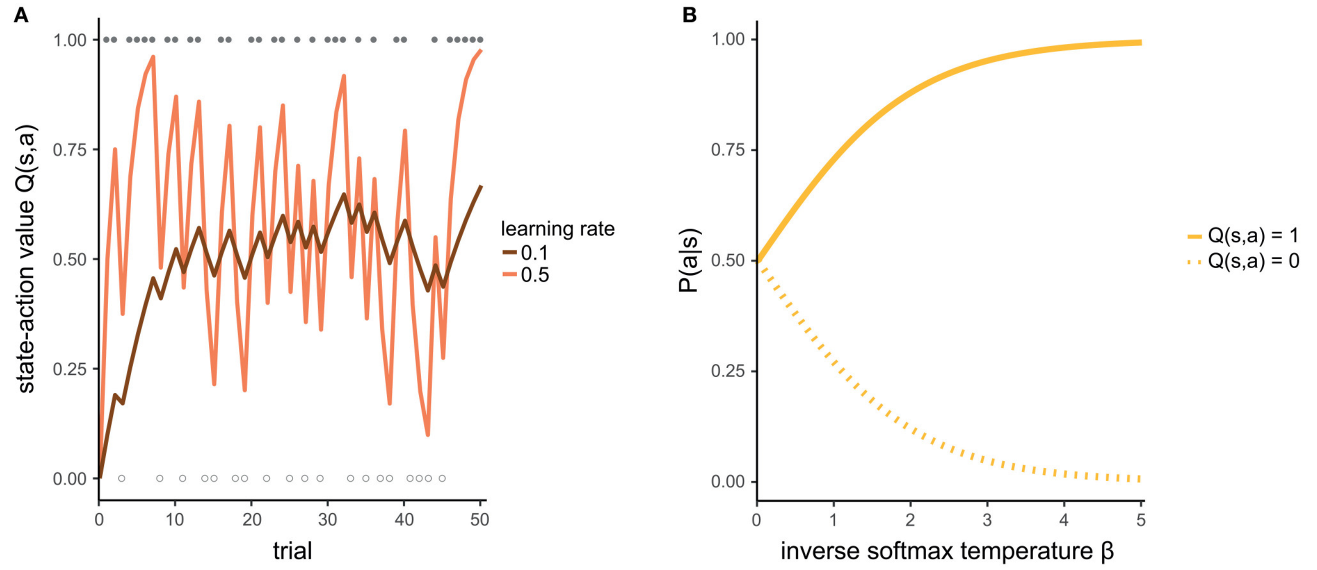

**FIGURE 2 | (A)** Development of a state-action value for two different learning rates. For the purpose of illustration, we assume that the agent makes identical choices across all trials. Filled and empty circles indicate trials in which the action was rewarded ($r = 1$) or not rewarded ($r = 0$), respectively. With a high learning rate (light line), the state-action value estimate fluctuates strongly, representing the rewards of the most recent trials. In contrast, with a low learning rate (dark line), the state-action value is more stable because it pools over more of the previous trials. **(B)** The higher the inverse softmax temperature, the more it is likely to prefer an action with a state-action value of 1 over another action with a state-action value of 0.

circuits involved in learning from reward (Sowell et al., 2003; Gogtay et al., 2004). Note however, that different subregions of the vmPFC show heterogeneous developmental trajectories (e.g., Shaw et al., 2008), which calls for a closer investigation of age-related effects in these areas. Moreover, a recent source localization EEG study (Buzzell et al., 2017) investigating error processing in 9–35 year old participants showed a linear association between age and error-related electrophysiological activity presumably originating from the insula or the inferior frontal gyrus. Both regions have been previously implicated in punishment-based learning (Palminteri et al., 2012) or the inhibition of maladaptive actions (Aron et al., 2004).

Consistent with the neuroimaging evidence for differential developmental trajectories in the brain systems involved in learning from positive and negative outcomes behavioral and electrophysiological studies indicate that children have problems in evaluating the informativeness of negative feedback during probabilistic learning (Crone et al., 2004; van Duijvenvoorde et al., 2008; Eppinger et al., 2009). What has been missing in many of the previous studies on learning from positive vs. negative outcomes is a clear characterization of the computational mechanisms underlying each of these different behavioral strategies.

Standard RL models assume one common updating mechanism for all kinds of outcomes regardless of their valence, which makes it difficult to capture diverging developmental trajectories for learning from gains vs. losses. To overcome this limitation, researchers have extended classical RL models by introducing two distinct learning rates, $\alpha_+$ and $\alpha_-$, instead of a single learning rate parameter. Thus, the specific learning rate can be applied depending on whether the reward prediction error signals a better than expected or a worse than expected outcome.

$$Q(s,a) \leftarrow \begin{cases} Q(s,a) + \alpha_+\delta \; if \; \delta \geq 0 \\ Q(s,a) + \alpha_-\delta \; if \; \delta < 0 \end{cases} \tag{4}$$

The only study that has investigated learning from gains and losses across development showed that the impact of negative reward prediction errors decreased with age (van den Bos et al., 2012). Studies in adolescents found an age-related enhancement in the sensitivity to worse than expected outcomes from adolescence to adulthood (Christakou et al., 2013; Hauser et al., 2015). Taken together, the few existing studies point to substantial changes in the impact of gains and losses across childhood development and adolescence. Clearly, more research is needed in this area, and future studies should adjust the tasks and procedures in a way that younger individuals (i.e., younger than 8 years of age) can be included.

## Adaptive Learning Rates

While distinct learning rates for positive and negative prediction errors allow for a somewhat more flexible responses to different situational demands, the impact of new information in these models remains constant over time. This is a questionable assumption, because most of our environments are changing dynamically and we have to flexibly adjust the degree of learning. For example, if you know that the quality of your favorite ice cream varies a lot between single scoops, it makes no sense to completely revise your value prediction just because the ice cream did not meet your expectations once. In contrast, if you learned that the ice cream manufacturer recently changed the recipe, even a single disappointing experience might make you buy a different type of ice cream next time.

The idea to adaptively adjust learning rates has also been implemented in RL models (Krugel et al., 2009). Here, the learning rate itself is updated in every trial depending on whether recent reward prediction errors increase (a change to the environment has occurred and the impact of new information should be high) or decrease (indicating stable environmental conditions). Recent work in adolescents shows no difference in learning rate adaptation between teenagers and adults in a reversal learning task (Javadi et al., 2014). However, so far, this is the only study in this domain, and childhood developmental differences have not (yet) been addressed. In addition, it should be noted that in current RL approaches the mechanisms that regulate the relationship between prediction error and learning rate are unclear. Recent work using Bayesian models of belief updating tried to address these shortcomings. For example, research by Nassar et al. (2016) on aging-related changes in learning rate adjustments showed that older adults have a specific deficit in uncertainty-driven learning that manifests as a problem in adjusting learning rates to small changes in prediction errors.

Future work should focus on developmental changes in the factors that regulate the degree of learning in dynamically changing environments. Furthermore, more research should be devoted to developmental differences in the interplay of medial prefrontal systems involved in the regulation of learning rates and their interaction with neuro-modulatory systems such as the norepinephrine and dopamine system. Finally, developmental disorders such as autism and attention deficit hyperactivity disorder are interesting research targets. For example, recent work suggests that adults with autism tend to overestimate the volatility of their environment, which makes them less sensitive to surprising environmental changes (Lawson et al., 2017). However, the ontogenetic development of these biases or their relationship to changes in neuro-modulatory systems remains to be determined.

## Softmax Temperature

We sometimes deviate from what would be the optimal behavior in a given situation. In the framework of RL, this means that an agent might pick an option that does not have the highest state-action value among all available actions. The degree to which state-action values guide action selection is regulated by the inverse softmax temperature, where lower values indicate a high level of behavioral stochasticity (i.e., choices are barely controlled by state-action values and are mainly due to chance) and action selection becomes more and more deterministic with increasing parameter values.

Two major psychological interpretations of the softmax temperature parameter have been offered: On the one hand, one can think of it as representing the individual sensitivity to differences in state-action values. From this perspective, deviations from the most rewarding options are considered as being due to random noise in the selection process or the lack of distinct value representations for alternative actions. Thus, theories that connect lifespan developmental differences in the dopaminergic system with transformations in the neural signal-to-noise ratio (Li et al., 2010; Li and Rieckmann, 2014) make the prediction that this parameter is likely to change across development.

Alternatively, choice stochasticity can be regarded as reflecting exploration of one's environment (as opposed to exploitation of familiar options). The inverse softmax temperature parameter then represents the degree of exploratory behavior (e.g., Daw et al., 2006). Enhanced exploratory behavior and risk-seeing is thought to be characteristic of adolescent behavior (Crone and Dahl, 2012; Crone and Steinbeis, 2017), which leads to the hypothesis that differences in the inverse softmax temperature parameter could also be accounted for by age-related shifts with respect to exploratory tendencies.

Indeed, developmental studies find that adolescents' behavior is best described by RL models with higher stochasticity as compared to younger adults. Javadi et al. (2014) used a reversal learning task with adolescents and younger adults and found that adolescents' choices were less controlled by differences in reward expectations than the choices of younger adults. Likewise, Christakou et al. (2013) report a lower inverse softmax temperature in adolescents than in adults for behavior in the Iowa Gambling Task. These age differences in choice stochasticity were associated with task performance and can be interpreted as reflecting increased exploratory behavior in adolescence.

It is beyond the scope of both conventional RL models and decision-making tasks to make a clear statement on whether observed choice stochasticity represents deliberately exploratory or merely random behavior. For future research, it would be desirable to better differentiate how these two processes develop across the human lifespan. In order to disentangle exploratory from random behavior, Wilson et al. (2014a) have put forward a decision-making task where they manipulate the amount of information an agent has about the outcomes of the available options before making choices. The authors argue that higher preferences for a less-known option signal that a decision-maker assigns value to collecting information about the environment, which is indicative of exploratory behavior. They also formalize this idea in a computational model of the action selection process. A recent study by Somerville et al. (2017) applied this paradigm and found that strategic exploratory behavior increased from adolescence to adulthood, while random behavior remained constant.

## Model-Based Learning

The RL models formalized above represent *model-free RL* approaches. That is, the learner is not assumed to have explicit knowledge about the task structure (i.e., a model of the environment). Model-free RL is neither computationally nor cognitively very demanding because at decision time, one just needs to retrieve and compare a limited set of state-action values (Daw et al., 2005). However, state-action values can be adapted only retrospectively after an outcome has been experienced, and thus model-free RL can be rather slow and inflexible in dynamic environments. For example, having eaten chocolate cakes ad nauseam every day of last week, one might have a temporarily reduced preference for everything that tastes like chocolate. Nevertheless, a model-free learner would not be able to consider this devaluation of chocolate ice cream beforehand but would need to experience the new dislike of chocolate ice cream multiple times, until the respective state-action values are sufficiently updated.

An alternative RL approach, *model-based learning*, might be more appropriate to describe human behavior in such situations. Here, the agent is aware of the principles of the environment, for example the rewards associated with each state and the probabilities for moving between states, and can use this knowledge for forward planning. In the example above, anticipating the taste of chocolate, the model-based learner can immediately reduce the reward expectation of going for chocolate ice cream. While this allows for more flexible behavior, it comes at the cost of greater computational or cognitive effort.

Current psychological theories assume that human behavior is best described as a mixture of model-free and model-based RL strategies (Gläscher et al., 2010; Daw et al., 2011). By using a hybrid model of model-free and model-based RL and estimating the relative weight of both processes, several studies have investigated how model-based control develops across the lifespan. From childhood to early adulthood, the ability to make use of model-based RL strategies in a prominent decision-making task increases progressively (Decker et al., 2016; Li and Eppinger, 2016; Potter et al., 2017), and this effect is mediated by an increasing ability in fluid reasoning (Potter et al., 2017). In older age, the use of model-based strategies declines (Eppinger et al., 2013b; Worthy et al., 2014), a process that does not seem to be fully explained by age-related impairment in working memory capacity (Eppinger et al., 2013b). Thus, the development of model-based decision-making across the human lifespan parallels age-related differences in cognitive control that show maturation until adulthood and a decline with aging (Braver and Barch, 2002; Luna et al., 2015).

While developmental studies so far have focused on differences in model-based control between individuals, there is also an increasing interest in the intraindividual adaptation of the model-based weight. Research with young adults has shown that humans adapt the balance between model-free and model-based RL according to situational demands such as current working memory load (Otto et al., 2013a), stress (Otto et al., 2013b; Radenbach et al., 2015), predictability of the environment (Daw et al., 2005; Lee et al., 2014; Eppinger et al., 2017), or incentive size (Kool et al., 2017). How exactly the brain determines which of the two systems is in charge at one point in time and how this arbitration process is affected by age is an interesting avenue for future research. Moreover, there are also other important questions with respect to model-based processes and how they change with age that have not yet been addressed: For example, it is currently unclear how models of the environment are represented in the brain and how these representations are updated. The few available studies suggest that fronto-parietal networks are involved in model-based learning (Gläscher et al., 2010) and that the orbitofrontal cortex may play a role in presenting latent (not directly observable) information about the structure of the world (Wilson et al., 2014b; Schuck et al., 2016). However, we are far away from a clear characterization of the underlying neural processes and how they change as a function of development.

## MODELING ANALYSES BEYOND PARAMETER ESTIMATION

### Model Selection

In the previous sections, we described how estimating the model parameters that best describe some behavior is an efficient way of specifying differences in learning and decision-making between age groups. However, the advantages of computational modeling are not limited to parameter estimation. Sometimes, there are multiple models available for explaining behavior in a task, each representing a different assumption about the involvement and interaction of specific cognitive processes. In this case, the direct comparison of competing computational models can reveal which out of a set of candidate models accounts best for behavior and can therefore be highly informative with respect to qualitative differences in cognitive processing between age groups.

For example, Palminteri et al. (2016) fitted RL models of increasing complexity to the behavior of adolescents and young adults in a probabilistic choice task. Specifically, these models differed with respect to whether they allowed for learning from counterfactual information (that is, information about the potential outcome of the option that was not chosen) and for the contextualization of outcomes relative to a reference point. They found that the simplest model explained adolescents' choices best while the most complex model accounted best for the decisions of the young adults. Thus, their findings suggest that learning strategies become more sophisticated with development. In a similar vein, Worthy et al. (2014) used model comparison to show differences in strategy use between younger and older adults in a decision-making task. Here, even though both age groups did not differ in overall task performance, older adults showed more evidence for a simple win-stay lose-shift heuristic compared to younger adults whose choices were best described by a weighted mixture of model-free and model-based RL.

### Model-Based fMRI

In the field of cognitive neuroscience, there is a strong interest in model-based fMRI analyses that focus on neural correlates of latent model variables, such as reward prediction errors or state-action values (O'Doherty et al., 2007). For instance, a central finding in studies combining RL models with fMRI is the observation that the blood oxygen level-dependent (BOLD) response in the ventral striatum reflects a reward prediction error signal (e.g., O'Doherty et al., 2004; Delgado et al., 2008). Developmental neuroscientists thus examined whether age-related differences in the strength of neural signals associated with these variables can offer a mechanistic explanation for differences in behavior. Indeed, in older adults, the neural correlates of reward prediction errors seem to be impaired (Chowdhury et al., 2013; Eppinger et al., 2013a; Samanez-Larkin et al., 2014) but can be partially restored by a pharmacological intervention that increases intracerebral dopamine, leading also to enhanced task performance (Chowdhury et al., 2013). Thus, RL models can provide access to mechanisms (e.g., integrity of reward prediction error signal) that link the neural level (dopamine) and the behavioral level (task performance).

In adolescents, the evidence for alterations of the reward prediction error signal is less clear. A study by Cohen et al. (2010) reported an increased BOLD response to positive reward prediction errors in the ventral striatum for adolescents compared to both children and young adults, suggesting a mechanism for greater reward sensitivity during this age. However, other studies (e.g., van den Bos et al., 2012; Christakou et al., 2013) could not replicate this effect, possibly due to differences in task design or the participants' age range.

In most of the previous research in younger adults, the BOLD response in the vmPFC is associated with changes in state-action values during learning (Gläscher et al., 2009). Yet, so far there are only a few studies that looked at age-related changes in this signal. Christakou et al. (2013) report the neural representation of state-action values to become stronger from adolescence to adulthood; however, they did not find this to be related to behavioral differences. In older adults, state-action value signals are reduced (Tobia et al., 2016; de Boer et al., 2017) and signal strength predicts performance in a probabilistic decision-making task (de Boer et al., 2017), suggesting that the age-related deterioration of value signals in the vmPFC may explain the behavioral deficits.

To summarize, computational modeling can identify developmental differences in learning and decision-making not only by capturing quantitative differences in parameters that represent psychological processes but also by comparing qualitatively different formalizations of cognitive mechanisms and by detecting age-related changes in the neurophysiological implementation of these processes.

## MODELING SOCIAL LEARNING MECHANISMS ACROSS THE LIFESPAN

So far, we have only considered how individuals learn from their own actions. However, humans are fundamentally social beings (Fiske, 2009). For decades, psychologists have observed that social context influences decision-making and behavioral adaptation is realized in accordance with our social environment (e.g., Lewin, 1952; Asch, 1956). Yet most computational studies on the development of learning and decision-making have left social factors aside. The RL models reviewed above can be extended to describe mechanisms of social learning and exchange. In the following, we outline how such extensions have been implemented. We stress their relevance for key questions that have been asked about the development of social cognition over the past decades. We first tap into a process that remains important throughout the course of the human lifespan, namely the ability to learn *from* others, by observation, by social feedback, or from instruction. A further key question of developmental psychology has always been the development of social cognition or Theory of Mind (ToM; Frith and Frith, 2003). Thus, in a second step we describe how computational formulations can help to elucidate how we learn *about* others, that is, update our ToM about others.

### Learning from Others

#### Observational Learning

Although the process of learning from the consequences of one's own behavior through direct experience, as reviewed above, is pivotal for survival, it is rather time-consuming and potentially dangerous. Thus, many species have developed the ability to learn from others via observational learning (e.g., Tomasello et al., 1987), which is also of great interest from a human ontogenetic perspective as it is suggested as an important factor for cognitive and social development (Nielsen and Tomaselli, 2010; Meltzoff, 2013; Waismeyer and Meltzoff, 2017).

In RL terms, learning from observations means to compute observational prediction errors, namely the deviance of the expected reward and the reward that the other person receives, depending on the state the other person is in and the action the other person has undertaken.

$$\delta_{obs} = \underbrace{r_{obs}(s')}_{\text{observed reward}} - \underbrace{Q(s,a)}_{\text{expected reward}} \tag{5}$$

$$Q(s,a) \leftarrow Q(s,a) + \alpha_{obs}\delta_{obs} \tag{6}$$

$\delta_{obs}$ is then multiplied by the observational learning rate $\alpha_{obs}$ which represents how fast participants learn from observed, not directly experienced outcomes. This update rule leads to an observationally-updated state-action value that individuals can use to make their own decisions. Observationally achieved state-action values can subsequently be updated using experienced prediction errors after taking an action and experiencing an outcome oneself.

Burke et al. (2010) applied such a computational account to a probabilistic, reward-based observational learning paradigm during fMRI in younger adults. They could show that observational outcome prediction errors correlated with activity in the vmPFC and the ventral striatum, similar to experienced outcome prediction errors (O'Doherty et al., 2004).

Learning from others' actions even in the absence of outcome information has been modeled using action prediction errors (Burke et al., 2010; Suzuki et al., 2012) that are computed as the probability that the observed choice $a_i$ would not have been selected by oneself:

$$\delta_{act} = 1 - \underbrace{P(a_i|s)}_{\text{expectation about action}} \tag{7}$$

Note that such action prediction errors are unsigned in nature, coding surprise about an observed action, rather than surprise and valence like in the case of a rewarding vs. punishing outcome. By means of this action prediction error, the choice probability is directly updated and the strength of this update is controlled by an imitation factor κ, in analogy to the learning rate in experiential learning (compare Equation 2).

$$P(a_i|s) \leftarrow P(a_i|s) + \kappa\,\delta_{act} \tag{8}$$

Action prediction errors have been shown to be associated with activity in the dorsolateral prefrontal cortex in young adults (Burke et al., 2010; Suzuki et al., 2012).

A recent EEG study (Rodriguez Buritica et al., 2016) investigated observational learning in school-aged children by manipulating the amount of social information as well as the social partner the children were learning from (comparing child to adult learning model). The results of these study show that children seem to have problems to rapidly assess the informational value of social feedback during learning and consequently up-regulate their response to observed and experienced negative feedback, as reflected in the amplitude of medial prefrontal event-related potential (ERP) components. Moreover, children tend to imitate behavior more when the observed player is a child, compared to an adult, indicating that social information does impact the degree to which information is integrated during learning (Rodriguez Buritica et al., 2016).

Rodriguez Buritica et al. (2016) did not use computational modeling in their study. However, the computational account of observational learning described above could be readily applied to these data. One advantage would be that learning could be captured in a trial-by-trial manner (behaviorally as well as neurally), which avoids the block-wise average approach the authors have used here as an approximation to learning. In this framework, it would be interesting to contrast electrophysiological correlates of experiential and observed outcome prediction errors as well as action prediction errors in a modeling-informed trial-by-trial ERP analysis. Such modeling-informed single-trial analyses of the feedback-related negativity (FRN) and different types of prediction errors have recently been demonstrated in young adults (Ullsperger et al., 2014; Reiter et al., 2016). Given the relatively late maturation of the ventrolateral and particularly the dorsolateral prefrontal cortex (Gogtay et al., 2004) and the involvement of these brain regions in observational learning in young adults (Burke et al., 2010), it is apparent that an interesting next step would be to study the development of these processes using model-based fMRI, ideally in a longitudinal fashion. Imitation plays a crucial role for the acquisition of behavior from early infancy on (for example during language acquisition). The modeling account introduced here might prove useful to study the building blocks of imitative behavior, namely observed action prediction errors in toddlers. In the absence of choice data in early childhood studies, computational models could be fit to eye tracking data like saccadic response speed or pupillometry (Vossel et al., 2014; Hepach and Westermann, 2016) or electrodermal activity (Li et al., 2011b), using response models for continuous data.

Interestingly, an fMRI study in young adults has recently looked at the involvement of model-based processes in observational learning (Dunne et al., 2016). In this study, model-based observational prediction errors that are used to update one's internal model about the environment were associated with activation in the fronto-parietal network. Because model-based learning abilities change markedly over the course of one's lifespan (see above) and recent findings show that social cognition might age differently than non-social cognition (Reiter et al., 2017b), it would be intriguing to study model-based social learning processes from a (lifespan) developmental perspective.

## Learning from Social Feedback

Humans are particularly prone to learning from social reinforcers, like a smile, praise, or a compliment and sensitive to learning from social punishment, like exclusion or rejection. From early childhood until later life, social feedback plays a crucial role during development and education in many areas, including language development or the development of social competences (Gros-Louis et al., 2006; Sebastian et al., 2010; Shinohara et al., 2012; Warlaumont et al., 2014). Translated to the RL modeling framework, this means that $r(s')$ for the computation of reward prediction errors (see Equation 1) can be social in nature. Indeed, neuroimaging studies have suggested a "common neural currency" for basic and social rewards (Behrens et al., 2008, 2009; Lin et al., 2011; Kishida and Montague, 2012) by demonstrating that social and monetary rewards elicit activation in overlapping brain regions.

In the developmental domain, one study (Jones et al., 2014) investigated learning from social feedback in children, adolescents and adults using a probabilistic learning task in combination with RL modeling and fMRI. In this study, different social cues were associated with different social reward probabilities. Social reward consisted of receiving a note from the co-player indicating interest in the participant. Surprisingly, the authors found a quadratic effect on learning rates for positive social feedback: Adolescents showed lower learning rates for positive feedback than children or adults. As discussed by the authors, this is in contrast to the common notion of higher sensitivity toward social reward in adolescents (Somerville, 2013; Foulkes and Blakemore, 2016). The authors argue that adolescents differentiate less between the cues that are associated with different amounts of positive social feedback.

Future studies interested in developmental differences regarding sensitivity to social feedback might more explicitly contrast learning from social reinforcers with learning from other (e.g., monetary) reinforcers across the lifespan. Computationally, fitting $r(s')$ as a free parameter (i.e., as a measure of reinforcement sensitivity; Gold et al., 2012), allows to compare sensitivity toward different types of reinforcers (e.g., social vs. monetary) between age groups. Recent modeling accounts have also captured subjective relevance in a Pavlovian conditioning approach (Katthagen, 2017). These computational approaches could be particularly suitable to re-assess the postulated higher relevance of social feedback in adolescence (Blakemore, 2008; Foulkes and Blakemore, 2016) using a modeling approach.

## Learning from Others' Instructions

A human-specific ability pivotal for development and education is the ability to learn from others' instructions. For example, we do not need to burn our hands to learn not to touch a hot stove; a verbal warning from others is usually sufficient.

In RL modeling terms, instructions prior to one's own experience can be operationalized by changing the initial state-action value (i.e., in an experimental setting the state-action value of the first trial of an experiment) according to an instruction received before one's own experiences with this stimulus are gained. In the example above, this might mean that someone has actually told you how exceptionally tasty the chocolate ice cream from a certain ice cream parlor is. Instead of starting the ice cream tasting from scratch (i.e., in computational terms, with equal initial state-action values for all ice creams of 0, respectively), you might be biased toward white chocolate ice cream now (which might have a higher state-action value of, e.g., 0.8) before you have actually tasted it. To also model an ongoing effect of instructed knowledge *during* learning, an additional parameter can be introduced to the equation for updating state-action values which amplifies gains and reduces losses following the choice of the instructed stimulus (Doll et al., 2009).

$$Q\left(s, a_{instructed}\right) \leftarrow \begin{cases} Q\left(s, a_{instructed}\right) + \alpha_{instructed}\, \alpha_{+} \delta & \text{if } \delta \geq 0 \\ Q\left(s, a_{instructed}\right) + \frac{\alpha_{-}}{\alpha_{instructed}} \delta & \text{if } \delta < 0 \end{cases} \tag{9}$$

Here, $\alpha_{instructed}$ represents a parameter capturing instruction-biased updating. Neuroimaging studies in young adults have shown that instructions about rewarding outcomes modulate learning-related responses in the striatum (Doll et al., 2009; Li et al., 2011a) and vmPFC (Li et al., 2011a) and that this modulation might be dependent on the prefrontal cortex (Doll et al., 2009, 2011; Li et al., 2011a). This points toward the direction that learning from instructions builds upon the circuit that also supports learning through own experience.

So far, one study compared children, adolescents, and adults with respect to experiential reward learning vs. social instruction in a probabilistic reward learning task using computational RL modeling (Decker et al., 2015). While inaccurate instruction biased adults' estimations of a stimulus value, children and adolescents relied on their own experiences when estimating stimulus values through experience. These data suggest that when explicit instruction conflicts with experiential feedback about the value of an action, children, and adolescents weight their own experience more heavily. The prefrontal-striatal brain circuitry, which instruction learning builds upon, continues to mature into adulthood, which might serve as an explanation for these differences in learning between age groups.

Based on the reviewed developmental differences in instruction-based learning, it would be interesting to investigate how social feedback from different sources affects learning. In Decker et al. (2015), instructions were displayed on the screen without manipulating factors like the age (e.g., peer group vs. adult) or social distance (e.g., family member vs. friend vs. stranger) of the instructor. Such an experimental manipulation would allow fitting different bias parameters $\alpha_{instructed}$ for each social source condition, which could subsequently be compared between age groups. It should be noted, however, that manipulating social information in a laboratory can be very challenging, and the question arises whether the mere presentation of a face on a computer screen is sufficient to count as "social." For future studies, it will be crucial to compare a laboratory situation to settings that are more naturalistic and under "real-life" constraints such as in school or kindergarten.

### Learning about Others' Mind

To understand when and how children develop their capacity to infer other people's mental states (ToM) has long been a "hot topic" in developmental psychology and has recently been extended toward research on lifespan development of social cognition (Henry et al., 2013; Reiter et al., 2017b). One influential idea concerning the implementation of ToM is that humans use and continuously update models for simulating and predicting others' behavior (Yoshida et al., 2008; Boorman et al., 2009; Diaconescu et al., 2014). One particular aspect of ToM is to infer the (potentially time-varying) motives of others during social interaction from their actions in order to determine their fidelity. Such social learning *about* others has recently also been translated into a computational model. In an experiment applied to young adults, participants were required to learn about the intentions of a confederate of whom they received advice to inform their next choice. The confederate's motivation to help or mislead (i.e., his fidelity) changed over time (Behrens et al., 2008; Diaconescu et al., 2014). In such a scenario, in computational terms, players would update an estimate of the confederate‘s fidelity, namely the probability of (un)faithful advice, according to the observed accuracy of the advice by concurrently tracking the congruency of advice and outcome. This idea could be incorporated into RL models; however Bayesian modeling approaches seem to be even better able to account for empirical data in this task (Diaconescu et al., 2014, 2017).

Applying the suggested modeling approaches for learning about other people's motives to developmental questions opens promising avenues for understanding the development of social cognition and social interaction. Tying together findings in young adults that social inference is influenced by uncertainty estimates, and findings from the non-social domain that uncertainty representation changes over the course of the lifespan (Nassar et al., 2016; van den Bos and Hertwig, 2017), it would be very interesting to investigate whether and how changes in uncertainty representation contribute to previously reported developmental differences in social cognition. Moreover, a recent study has demonstrated that distinct social prediction errors are associated with activation in different neuro-modulatory systems, respectively (Diaconescu et al., 2017): Lower-level prediction errors which updated predictions about an adviser's fidelity activated the dopaminergic midbrain, and genotypes favoring higher concentrations of dopamine were related to higher striatal activation associated with fidelity prediction errors. Higher-level prediction errors, updating the volatility of an adviser's intentions were associated with activation in the cholinergic basal forebrain. Notably, both neurotransmitter systems, dopamine, and acetylcholine, undergo marked changes over the course of the lifespan.

## CONCLUSION

In this review, we illustrated how researchers in the field of developmental cognitive neuroscience can make use of computational models to gain a more mechanistic understanding of lifespan differences in learning and decision-making. For both social and non-social settings, RL models provide a powerful technique to formalize the underlying mechanisms. Parameters that are derived from these models can be used to study developmental changes in learning and decision-making as well as the associated neural correlates.

We acknowledge that we are still in the early stages of this research. Some results seem to be inconsistent, possibly due to small sample sizes, differences in the employed paradigms or computational models. For instance, the studies investigating altered neural reward prediction error representations during adolescence (Cohen et al., 2010; van den Bos et al., 2012; Christakou et al., 2013) used different tasks (Iowa Gambling Task and a probabilistic learning task) with or without monetary rewards, and employed RL models that did or did not account for distinct learning rates after relative gains or losses. Future research should aim to identify the important boundary conditions of age-related effects. Furthermore, age-comparative fMRI studies tend to require many resources and therefore often do not involve large sample sizes, which complicates comparisons across studies. Moreover, to our knowledge all studies so far rely on cross-sectional designs, which limits the interpretability of the results. It would be desirable to fill this gap and to track the developmental trajectories of the computational underpinnings for learning and decision-making in a longitudinal manner.

In psychiatry, there is an increasing awareness that a computational understanding of mental illnesses is needed to improve clinical treatments (Montague et al., 2012; Huys et al., 2016; Reiter et al., 2017a). We believe that it is likewise necessary to comprehend the computational groundings of learning and decision-making during healthy development. This would allow us to create better learning environments in educational and occupational settings and adapt them to the specific needs of different age groups. Successful attempts along this direction have already been made. For example, in a study by Raufelder et al. (2016) learning rates and neural prediction error signals in a reversal learning task could be linked to different scholastic motivation types in adolescent pupils. We believe that several aspects of learning and decision-making discussed above also are of great practical relevance, such as learning from negative and positive feedback, the regulation of cognitive effort during (model-based) decision-making or the implications of learning from observations and instructions. Thus, knowing and understanding the cognitive processes involved in different types of learning and how they change with development might finally lead to advancements in lifelong education. Computational models constitute an essential part in this enterprise.

## AUTHOR CONTRIBUTIONS

FB, AR, and BE conceived the theoretical ideas; FB and AR conducted the literature review; FB, AR, and BE wrote the manuscript.

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# False Belief Reasoning in Adults with and without Autistic Spectrum Disorder: Similarities and Differences

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A central diagnostic criteria for autism spectrum disorder (ASD) is the qualitative impairment in reciprocal social interaction and a prominent hypotheses that tried to explain this impairment is the Theory of Mind (ToM) deficit hypotheses. On a behavioral level the critical test for having a ToM, the understanding of false beliefs (FB), is often used for testing ToM abilities in individuals with ASD. Investigating the neural underpinnings several neuroimaging studies revealed a network of areas involved in FB reasoning in neurotypical individuals. For ASD individuals the neural correlates of false belief processing are largely unknown. Using functional magnetic resonance imaging and an adapted unexpected transfer task, that makes it possible to distinguish between the computation of diverging beliefs and the selection of a belief-associated response, we investigated a group of adult high-functioning individuals with ASD ($N = 15$) and an age and IQ matched group of neurotypical adults (NT; $N = 15$). On the behavioral level we found no group differences. On the neural level, results were two-fold: In the story phase, in which participants had to compute whether the character's belief is congruent or incongruent to their own belief, there were no differences between neurotypical participants and those diagnosed with ASD. But, in the subsequent question phase, participants with ASD showed increased activity in the bilateral anterior prefrontal cortex, the left posterior frontal cortex, the left superior temporal gyrus, and the left temporoparietal area. These results suggest that during the story phase in which the participants processed observable actions the neural correlates do not differ between adult individuals with ASD and NT individuals. But in the question phase in which participants had to infer an unobservable mental state results revealed neural differences between the two groups. Possibly, these subtle neural processing differences may contribute to the fact that adult ASD individuals are able to master explicit false belief tasks but fail to apply their strategies during everyday social interaction.

**Keywords: autism spectrum disorder, adults, false belief reasoning, theory of mind, mentalizing**

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## INTRODUCTION

The ability to attribute mental states such as beliefs, intentions, desires, and emotions to oneself and other people is necessary to navigate successfully through the social world and is known as Theory of Mind (ToM) or mentalizing. The understanding of false beliefs is commonly considered to be the critical test for having a ToM. False belief attribution requires a decoupling between a person's mental representation of the world and the real state of the world and enables a person to understand that mental states can misrepresent reality. A classical task for testing false belief understanding is the so-called *unexpected transfer task*, in which a character (e.g., Maxi) leaves an object (chocolate) in one location (e.g., the drawer) and while he or she is outside the room the object is transferred to a new location (Wimmer and Perner, 1983). As a consequence Maxi's subsequent search for the chocolate in the drawer will be unsuccessfully.

In autism, a central diagnostic criteria is a qualitative impairment in reciprocal social interaction. A prominent hypotheses that tried to explain these impairments is the Theory of Mind deficit hypotheses that is based on the observation that individuals with autism spectrum disorders (ASD) show severe deficits in the understanding that in some situations other people have beliefs and other mental states that differ from their own (Baron-Cohen et al., 1985; Senju et al., 2009). As opposed to young neurotypical (NT) children who begin to master false belief tasks at the age of four or five, it is not until the mental age of 6 years that children with ASD pass these tasks (Happé and Frith, 2014). However, from around 12 years of age individuals with ASD and average IQ often show levels of false belief performance that are similar to those of NT children (Happé, 1995). Nevertheless, it seems that adolescents and adults with high-functioning autism or Asperger syndrome fail to employ their knowledge about false beliefs during naturalistic interactions (Ponnet et al., 2004).

Neuroimaging studies that investigated belief reasoning gathered evidence that in healthy adults the posterior part of the medial prefrontal cortex (pMPFC, also referred to as dorsal MPFC), the bilateral temporo-parietal junction (TPJ), the posterior superior temporal sulcus (pSTS) and the precuneus are involved in false belief processing (Saxe and Kanwisher, 2003; Saxe and Powell, 2006; Sommer et al., 2007, 2010; Aichhorn et al., 2009; Scholz et al., 2009; Van Overwalle, 2009; Young et al., 2010; Rothmayr et al., 2011; van der Meer et al., 2011; Döhnel et al., 2012, 2016; Schurz et al., 2013; van Veluw and Chance, 2013; Schuwerk et al., 2014).

There are also some studies that tried to shed light on the neural underpinnings associated with ToM deficits in individuals with ASD. These studies used a variety of different tasks that are supposed to elicit mental state representation resulting in heterogeneous findings (Happé et al., 1996; Castelli et al., 2002; Mason et al., 2008; Kana et al., 2009; Lombardo et al., 2011; Dufour et al., 2013). For example, Kana et al. (2009) investigated adults with autism and control participants during the viewing of animated geometrical shapes. In one condition the movements of the shapes entail the attribution of mental states like thoughts and feelings to the figures. On the behavioral level, neither reaction time nor error rates differed between the two groups. While results revealed no activity differences in posterior ToM regions, like the right pSTS, the ASD group showed lower activation in frontal regions associated with ToM, like the left superior medial frontal gyrus, the left anterior paracingulate cortex, the bilateral anterior cingulate cortex and the left inferior orbitofrontal cortex. Additionally, during the attribution of mental states to animated figures ASD participants compared to controls showed reduced functional connectivity between frontal and posterior (temporal, parietal and occipital) regions and between temporal and occipital areas. The authors suggested that ASD associated difficulties in mentalizing may be the result of a decreased communication and coordination between frontal and other regions of the brain (Kana et al., 2009).

Using a completely different task–making reflective mentalizing or physical judgements about oneself or another person—Lombardo et al. (2011) found that especially the activity of the right temporo-parietal junction (RTPJ) differentiates between adult participants with ASD and control subjects. Behavioral data did not show any group effects, indicating that ASD individuals responded similar to controls while making mentalizing and physical judgements. But, while in controls RTPJ was selectively more responsive to mentalizing than physical judgements, this selectivity was not apparent in ASD individuals. Additionally, individuals with ASD who were more socially impaired had RTPJ responses that were least selective for mental state information, while those who were least socially impaired had RTPJ responses that were relatively more selective for mental state information. Therefore, the authors suggested that the RTPJ is one of the key areas behind the deficits of ASD participants in mental state attribution (Lombardo et al., 2011).

The neural systems that specifically underlie the ability to attribute false beliefs in individuals with ASD were only investigated by Dufour et al. (2013). They compared adult high-functioning individuals with ASD with neurotypical individuals by using verbal stories. In the belief condition the stories described a character who acquired a false belief. These stories were compared to a photo condition in which a physical representation became false, such as an outdated photograph of a map. Behavioral data were not reported, but the fMRI results revealed no differences between neurotypical and autistic individuals, neither in a whole brain analysis nor in a ROI analysis that focused on typical belief-associated areas. The authors suggest that in adults the social cognitive impairments of ASD individuals can occur without differences in activation patterns during the processing of an explicit ToM task.

In sum, results concerning the neural system that underlies ToM deficits in ASD individuals are very heterogeneous. Some authors proposed a lower activity of frontal areas and a decreased functional connectivity between frontal and other areas in ASD individuals as key mechanisms for ToM deficits (Mason et al., 2008; Kana et al., 2009). Other authors emphasized on the role of the RTPJ in the ToM impairment of ASD individuals (Mason et al., 2008; Lombardo et al., 2011). And still others found no activity differences in the brain between ASD and healthy individuals during processing false beliefs (Dufour et al., 2013).

The aim of the current study was to investigate the neurocognitive correlates of false belief reasoning in adult ASD individuals in more detail. In a previous study with healthy adults Schuwerk et al. (2014) adapted the classical unexpected transfer task in order to separate two processing phases: the computation of beliefs and the inference and selection of another's or one's own belief. In neurotypical adults the initial computation phase was associated with activity in the bilateral temporoparietal cortex, the posterior MPFC and the left inferior frontal gyrus (IFG). In the subsequent question phase, conditions in which participants had to consider the other's belief compared to conditions in which they had to respond according to their own belief were associated with activity in the right temporoparietal cortex. Additionally, the authors show that when incongruent beliefs had to be computed activity of the pMPFC inhibited the temporoparietal cortex. These results support suggestions concerning the role of the pMPFC in stimulus-independent processing. Stimulus-independent processing is necessary when the belief of another person becomes false and does not longer correspond to reality (Sommer et al., 2007; Döhnel et al., 2012), e.g., a person's belief that an object is in location A, but meanwhile the object has been transferred to location B. It seems that in these conditions the pMPFC inhibits stimulus-bound processing which helps to process another person's false belief decoupled from one's own perception of reality.

Interestingly, a recent study of the anatomy of white matter networks revealed that ASD individuals compared to NT individuals showed white matter differences in brain areas associated with belief reasoning. White matter differences in ASD were localized to major association and commissural tracts of the frontal lobe (Catani et al., 2016). These tracts connect frontal lobe to more posterior areas of the parietal, limbic and temporal lobe. The results are also in line with functional imaging studies that investigated ToM abilities in individuals with ASD and pointed to a lower degree of synchronization (functional underconnectivity) between MPFC and temporoparietal areas during ToM tasks in adults with ASD compared to neurotypical adults (Mason et al., 2008; Kana et al., 2009; Murdaugh et al., 2012). Interestingly, these areas were also associated with the processing of divergent beliefs in the study by Schuwerk et al. (2014). Therefore, we suggest that the adapted version of the false belief task might be a useful tool to reveal possible differences in the neural correlates associated with false belief processing between individuals with ASD and neurotypical adults. Several behavioral studies have shown, that adults with high-functioning or Asperger autism tend to be just as efficient in understanding explicit false belief tasks as control subjects (e.g., Happé, 1995; Scheeren et al., 2013). With respect to these results we expect no behavioral differences between the two groups. According to our former fMRI study with NT individuals (Schuwerk et al., 2014) we hypothesized that in the NT group the computation of divergent beliefs is related to activity in the temporoparietal cortex and the medial prefrontal cortex. But with respect to studies showing underconnectivity between frontal and temporoparietal areas (e.g., Murdaugh et al., 2012; Catani et al., 2016), we hypothesized that the ASD group will show lower activity in the frontal lobe and in the temporoparietal area. For the question phase we expect higher activity of the right temporoparietal cortex in the NT group compared to the ASD group.

## MATERIALS AND METHODS

### Participants

Fifteen adults with ASD (10 men, mean age = 28.2) and 15 neurotypical (NT) participants (10 men, mean age = 29.87) with no reported history of psychiatric or neurological disorders were included in the study. The ASD participants were recruited through the autism outpatient clinic of the Bezirksklinikum Regensburg, Germany. All participants were diagnosed by specialized psychiatrists and psychotherapists according to the ICD-10 criteria for Asperger syndrome (F84.5, $N = 11$) and autism without intellectual disability (F84.0, $N = 4$) and were tested with a battery of tests including the Wechsler Adults Intelligence Scale-revised (WAIS-R), the Adults Asperger Assessment (AAA, Baron-Cohen et al., 2005; German version Poustka, 2006), Fragebogen zur Sozialen Kommunikation (FSK; the German version of the SCQ; Bölte and Poustka, 2006) the Faux Pas Recognition Test (Baron-Cohen et al., 1999) and the Reading the Mind in the Eyes test (Baron-Cohen et al., 1997).

The groups were matched according to gender, age and IQ measured with the German verbal test Mehrfachwahl-Wortschatz-Test (MWT; Lehrl, 1989) and the non-verbal Grundintelligenztest (CFT 20; Weiß, 1998; see **Table 1** for details). All of the participants gave written informed consent prior to their participation and received payment for participating. The study was approved by the local ethics committee of the University Medical Center Regensburg.

### Task

The present task was a version of the object transfer false belief paradigm (Baron-Cohen et al., 1985), adapted from a prior fMRI-paradigm (Schuwerk et al., 2014). Each Trial consisted of two phases (see also **Figure 1**). In the initial story phase participants watched a 4 s long animation depicted a room with a boy flanked by a dark-brown and light-brown box, which are standing on a wooden floor. Underneath the floor there was an empty basement. In the beginning of each trial a self-propelled-moving ball fell in one of the two open boxes. Then the boxes closed and two events simultaneously happened: the ball bounced into the basement through a hidden trap door, what not could be seen by the story character, and the boxes switched their places, witnessed by the story character. In the congruent-beliefs condition the ball fell into the basement but bounced right back into the same box and was transferred inside the box to the character's other side. In this condition the story character and the participant's belief about the location of the ball were congruent. In the incongruent-beliefs condition, the ball fell into the basement, however, bounced back with a short

**TABLE 1** | Demographic characteristics.

| | ASD group ($N = 15$) | | NT group ($N = 15$) | | | |
|---|---|---|---|---|---|---|
| | M | SD | M | *SD* | *t*-value | *p*-value |
| Age | 28.2 | 10.4 | 29.9 | 12.2 | 0.40 | 0.69 |
| Verbal IQ (MWT) | 113.5 | 10.1 | 112.8 | 13.9 | 0.17 | 0.87 |
| Non-verbal IQ (CFT 20) | 122.3 | 8.7 | 125.2 | 11.0 | 0.81 | 0.43 |

*M, means; SD, standard deviation; ASD, autism spectrum disorder; NT, neurotypical.*

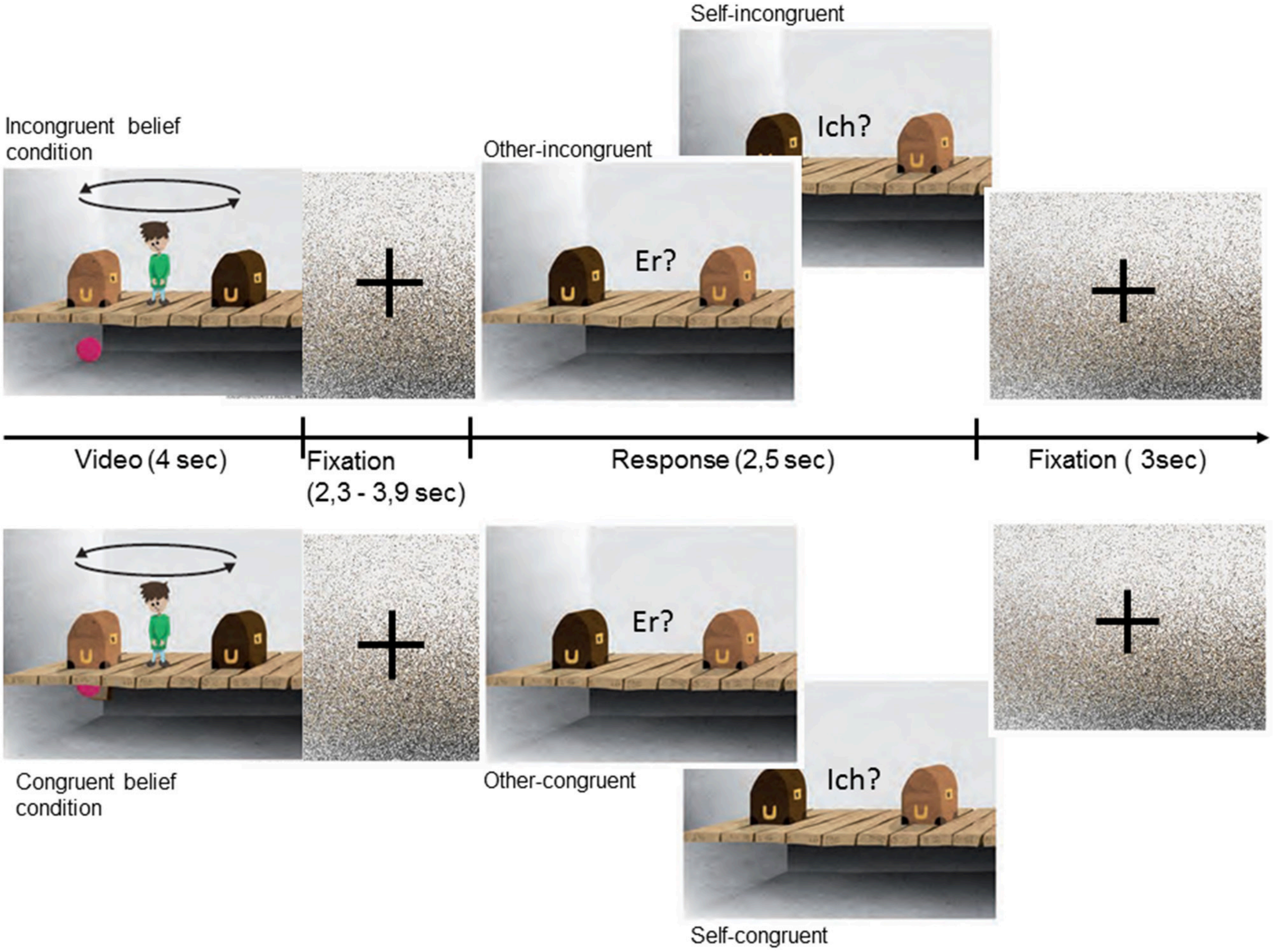

**FIGURE 1 |** Experimental design: Each trial started with the presentation of a video, in which the protagonist compared to the participant either ended up with an incongruent belief (**Top**) or a congruent belief (**Bottom**) about the location of the ball. The story phase was followed by a fixation picture of scrambled pixels with jittered duration. In the following question phase the participants had to respond either according to their own belief ("Ich?") or according to the belief of the protagonist ("Er?") about the ball's location. Response was given via button press. The trial ended with a second fixation picture.

time delay and entered the other box after they had switched. In this condition the story character's belief and the participant's belief are incongruent. The character believes that the ball was transferred inside the box it initially entered, the participant knows that the ball was not transferred and is now in the other box.

After the initial story phase a fixation picture of scrambled pixels was presented for a varying time interval (jitter) in order to control for possible overlapping BOLD signal responses to stimuli (2.3–3.9 s). Then in the following question phase a still frame was presented for 2.5 s. On this picture the character was replaced and a written test question was presented. Either participants were asked in which one of the two boxes the story character thinks the ball is located (in German: "Er?," in English: "He?") or in which box the participant thinks the ball is located (in German: "Ich?," in English: "I?"). Depending on the prior condition, reasoning about the character's false belief (other-incongruent) or true belief (other-congruent) or reasoning about one's own belief, either diverging from the character's belief (self-incongruent) or corresponding with it (self-congruent), was required. The task of the participants was to respond as fast and accurately as possible. Reaction time (RT) was measured from picture onset until one of two buttons of a five-button fMRI-compatible response pad (LUNItouch, Photon Control Inc., Burnaby, Canada) was pressed. Between trial a fixation picture of scrambled pixels was presented for 3 s.

The animations were controlled for type, number, order, and laterality (ball enters the left or right box first) of events. Question pictures were identical across conditions, showing only the two closed boxes without any social stimuli. After being given a standardized instruction and some practice trials outside the scanner, subjects completed 120 trials, 30 per condition, in a pseudo-randomized order. Presentation software was used for stimulus presentation and response recording (Neurobehavioral Systems Inc., Albany, CA).

## Statistical Analysis of the Behavioral Data

In order to analyze reaction times (RT) and response accuracy (percentage of correct responses) a repeated measures analysis (ANOVA) with within-subject factors of perspective (other vs. self) and congruency of beliefs (incongruent vs. congruent) and the between-subject factor group (ASD, Control) was performed. The significance level for the analyses was set at $P \leq 0.05$.

## Image Acquisition

A 3-Tesla Siemens Allegra Head Scanner (Siemens Inc., Erlangen, Germany) located at the University Medical Center Regensburg was used to record the imaging data. The scanner acquired echo-planar-imaging (EPI) sequences using fast gradients. During T2* data acquisition, we recorded 32 axial slice in interleaved order with a Time-to-Repeat (TR) of 2.0 s, a Time-to-Echo (TE) of 0.95 s, a flip angle of 90°, a Field of View (FoV) of 192 x 192 mm and a voxel size of $3 \times 3 \times 3$ mm. A total of 767 functional images were recorded in the entire experiment.

A structural image was recorded from every subject at the end of functional data acquisition. These T1-weighted images were obtained using a MPRAGE (Magnetization Prepared Rapid Acquisition Gradient Echo) pulse sequence (TR = 2.25 s, TE = 0.026 s, TI = 0.9 s, FoV = 256 mm), scanning 160 slices with voxel size of $1 \times 1 \times 1$ mm$^3$.

The entire scan session lasted approximately 35 min.

## Functional Imaging Data

All images were analyzed with SPM8 (Wellcome Department of Imaging Neuroscience, London, UL) run in Matlab 7.0 (Math Works Inc., Nattick, MA).

Individual subjects' data were slice-timed corrected using the middle slice as a reference. Images were spatially realigned to the first volume by rigid body transformation to correct for head movements. After coregistration to the tructural $T_1^*$ –weighted images, data were normalized to the functional template contained in SPM8 (Montreal Neurological Institute template, MNI) with a voxel size of $2 \times 2 \times 2$ mm$^3$ and smoothed with a 8 mm full-width at half maximum Gaussian kernel.

All statistical analyses were based on functional activity obtained from the whole brain. In the first level analysis, a fixed-effects analysis was computed for each participant based on the general linear model (GLM). The analyses focused on amplitude changes in the hemodynamic response function (HRF) associated with the different mentalizing conditions. For each condition, correctly answered trials were modeled as a boxcar function convolved with the HRF. In the story phase, the two regressors for the incongruent-belief and the congruent-belief condition comprised the last 2 s of the 4 s long video. The events in the video were timed so that exactly after 2 s it became clear whether the story character's belief was congruent or incongruent to that of the participant. In the question phase, which started with the onset of the question and lasted for 2.5 s a regressor for each of the four conditions of interest (other-incongruent, other-congruent, self-incongruent, self-congruent) was modeled. In addition to the regressors of interest, the realignment parameters, the mean constant over scans, and a non-hit parameter (incorrect responses and misses) were included as regressors of no interest. The data were high-pass filtered with a frequency cutoff at 128 s.

Statistical parametric maps (SPMs) were generated for each subject by t-statistics derived from contrasts utilizing the HRF (Friston et al., 2002). To identify brain activity associated with the processing of incongruent vs. congruent beliefs in the story phase, we contrasted the two conditions incongruent-beliefs vs. congruent beliefs.

In order to detect brain activity associated with divergent beliefs in the question phase, we analyzed the main effect of congruency of beliefs [(other-incongruent + self-incongruent) vs. (other-congruent + self-congruent)]. Additionally, the main effect considered person was calculated [(other-incongruent + other-congruent) vs. (self-incongruent + self-congruent)]. Further we analyzed the interaction effect between the considered person and congruency of beliefs [(other-incongruent–other-congruent) > (self-incongruent–self-congruent)] and vice versa.

For group analyses single-subjects' first-level contrasts were introduced in second-level random-effect analysis. First, one-sample *t*-tests for all contrasts were conducted separately for ASD and controls. Second, in order to test the influence of autism we investigated the interaction between group (ASD and Controls) and condition in the story phase (congruency) as well as in the question phase (congruency, perspective). Additionally, we explored whether common brain regions are associated with processing incongruent beliefs in the story phase and in the question phase. Separately for the NT and the ASD group, we computed a conjunction analysis (based on the Minimum statistic compared to the Null Conjunction; Nichols et al., 2005) on the contrasts (story phase: incongruent > congruent beliefs) and [question phase: (self-incongruent + other-incongruent) > (self-congruent + other-congruent)]. The resulting set of significant voxel values for each contrast constituted SPM maps that were thresholded at $p < 0.001$ (uncorrected, 10 or more contiguous voxels). Reported significant voxels survived a statistical FWE (family-wise error)-corrected threshold of $p < 0.001$ for multiple comparisons on cluster level. The activated brain regions were overlaid on the MNI template and labeled according to the Talairach atlas (http://www.bioimagesuite.org/Mni2Tal).

# RESULTS

## Behavioral Results

Regarding accuracy, the ANOVA revealed a significant main effect for congruency of beliefs [$F_{(1,\,28)} = 11.90$, $p < 0.01$]. Participants gave more correct answers when they were asked for congruent beliefs ($M = 97.44$, $SD = 3.30$) compared to incongruent beliefs ($M = 93.67$, $SD = 5.61$). There was no influence of group for congruency [congruency × group: $F_{(1,\,28)} = 0.09$, $p = 0.76$]. For perspective neither the main effect [$F_{(1,\,28)} = 0.09$, $p = 0.78$] nor the interaction perspective × group[$F_{(1,\,28)} = 1.07$, $p = 0.31$] were significant. Also the interaction congruency × perspective [$F_{(1,\,28)} = 0.15$, $p = 0.7$] was not significant. Only the interaction congruency × perspective × group interaction [$F_{(1,\,28)} = 4.64$, $p < 0.05$] shows a significant effect.

The analysis of RT revealed a similar picture. Only the main effect congruency [$F_{(1, 28)} = 136.74$, $p < 0.001$] was significant. RT were slower when incongruent beliefs had to be processed ($M = 1366.10$ ms, $SD = 249.96$ ms), compared to processing congruent beliefs ($M = 977.67$ ms, $SD = 194.49$ ms). There were no significant effects for the interaction congruency x group[$F_{(1, 28)} = 0.02$, $p = 0.89$], the main effect perspective [$F_{(1, 29)} = 0.02$, $p = 0.88$], the interaction perspective x group [$F_{(1, 28)} = 1.62$, $p = 0.21$], the interaction congruency x perspective [$F_{(1, 28)} = 0.66$, $p = 0.42$], the interaction congruency x perspective x group [$F_{(1, 28)} = 1.03$, $p = 0.32$]. Altogether behavioral data show no group differences and no influence of the considered perspective. For both groups mean RT and response accuracy for each experimental condition are shown in **Table 2**.

## Brain Imaging Results

### Story Phase

In the story phase, for the participants it became clear whether the character's belief is congruent or incongruent to their own belief. However, they did not know whether they have to respond in respect to their own or the characters' belief. The analyses of this phase focused on brain regions engaged in the processing of emerging incongruent beliefs by contrasting incongruent vs. congruent beliefs (see **Figure 2** and **Table 3** for more details).

The full factorial ANOVA design with the two factors "group" (ASD/NT) and "congruency" (incongruent/congruent) revealed no significant main effect for "group" or a significant interaction between "group and congruency." But there was a significant main effect "congruency." Further t-contrasts revealed that the processing of incongruent compared to congruent beliefs induced activity in a network of brain areas, including the posterior medial prefrontal cortex (BA6), the bilateral posterior/inferior frontal cortex (BA 6/44), the bilateral middle temporal gyrus (BA 22), the bilateral inferior temporal gyrus (BA 19/7/37) and the left thalamus.

The analyses of the separated groups revealed rather similar results. In the control group of NT participants the processing of incongruent beliefs in contrast to congruent beliefs were associated with activity in the posterior medial prefrontal cortex (BA 6), the left posterior/inferior frontal gyrus (BA 6/44), the bilateral middle temporal gyrus (BA 22), the right inferior temporal gyrus (BA 19/40) and the left thalamus.

**TABLE 2 |** Mean reaction time and response accuracy.

| | ASD group | | NT group | |
|---|---|---|---|---|
| | **RT (ms)** | **PCR (%)** | **RT (ms)** | **PCR (%)** |
| | **M (SD)** | **M (SD)** | **M (SD)** | **M (SD)** |
| Other-incongruent | 1410.1 (258.1) | 91.6 (7.2) | 1308.2 (270.0) | 95.3 (6.9) |
| Other-congruent | 1053.1 (189.8) | 97.1 (3.5) | 911.7 (195.9) | 97.8 (3.9) |
| Self-incongruent | 1418.6 (233.0) | 94.0 (5.7) | 1328.9 (279.2) | 93.8 (5.9) |
| Self-congruent | 1007.1 (169.9) | 96.7 (3.1) | 938.5 (221.1) | 98.2 (4.5) |

*RT, reaction time; PCR, percentage of correct responses; M, means; SD, standard deviation; ASD, autism spectrum disorder; NT, neurotypical.*

In the ASD group incongruent beliefs compared to congruent beliefs induced more activity in posterior medial prefrontal gyrus (BA 6), the middle and left posterior/inferior frontal gyrus (BA 6/44), the left inferior frontal gyrus (BA 44) and the right inferior temporal gyrus (BA 19/37).

In both groups, for the reverse contrast, congruent-beliefs condition over incongruent-beliefs condition, no brain area showed significantly increased activity.

### Question Phase

The question phase focused on identifying brain regions related to processing a response conflict due to diverging mental states. Results based on the full factorial design with the factors perspective (self/other), congruency (congruent/incongruent) and group (ASD/NT) revealed no main effect for perspective, the interaction perspective x group, the interaction perspective x congruency or the interaction congruency x group. However, there was a main effect for congruency associated with activity in the anterior MPFC/anterior cingulum (BA 10/32). Further analysis revealed that the activity was induced by responses to congruent compared to incongruent beliefs and was independent of group. Results also showed a main effect of group. The comparison between the two groups revealed that in the NT group compared to the ASD group the processing of the response was associated with more activity in the middle occipital gyrus (BA 19/17/18). ASD individuals showed more activity during the question phase in several areas, including the bilateral anterior prefrontal cortex (BA 10/11), the left posterior frontal gyrus (BA 6/8), the thalamus, the left superior temporal gyrus (BA 41/21) and the left temporoparietal area (BA 39/40; see also **Figure 3**). There were no brain regions in which NT compared to ASD individuals showed significantly increased activity.

We then examined the functional activity within each of the two groups. In the control group, the comparison between the other-condition in which the participants had to consider the other's belief with the self-condition in which the subjects had to respond according to their own belief showed no significant activity. However, independently of perspective, incongruent compared to congruent beliefs were associated with activity in the right inferior fontal gyrus (BA 47) and the right inferior temporal gyrus (BA 19). Congruent beliefs compared to incongruent beliefs induced more activation in the anterior MPFC (BA 10/11), the bilateral posterior frontal gyrus (BA 8), the right temporoparietal area (BA40) and the precuneus.

Also in the ASD group there was no influence of perspective (self, other). But in individuals with ASD the response to congruent beliefs compared to the response to incongruent beliefs induced more functional activity in the anterior MPFC (BA10). There were no significant effect for the reverse contrast incongruent > congruent beliefs (for more details see **Table 3**).

### Common Activity in the Story and Question Phase

The whole brain conjunction analysis of the contrasts (story phase: incongruent > congruent beliefs) and [question phase: (self-incongruent + other-incongruent) > (self-congruent + other-congruent)] showed only for the ASD group on a lower cutoff for FEW-corrected results ($P_{\text{FWE-corr}} = 0.021$, cluster

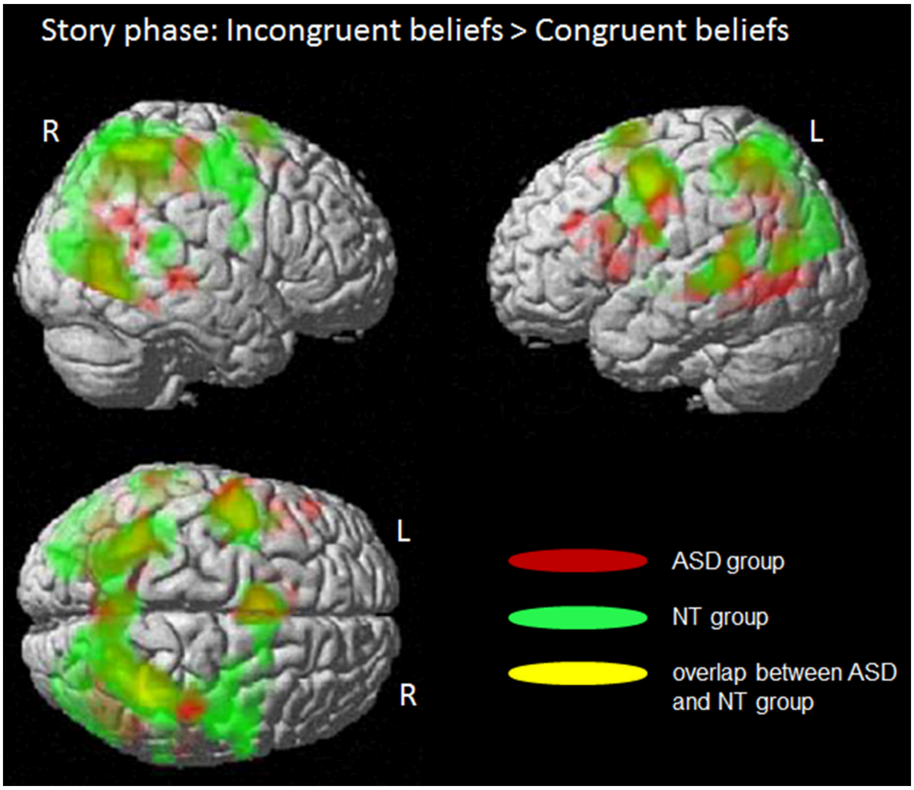

**FIGURE 2 |** Story phase: Processing of incongruent beliefs compared to congruent beliefs. Whole brain fMRI findings for the ASD group (in red) and the NT group (in green). Common activity in both groups is shown in yellow; L, left side; R, right side. Colored regions indicate significantly activated voxels with $T > 5.0$, $P_{FWE-corr} \leq 0.001$, cluster level. There were no significant group differences.

level) commonly increased functional activity of the posterior medial prefrontal cortex (BA 6) associated with the processing of incongruent beliefs in both the story and the question phase. For the NT group the conjunction analysis revealed no common functional activity.

## DISCUSSION

Autistic symptoms in adult individuals are highly heterogenous and vary considerably with many different aspects like clinical severity, psychiatric impairments, language abilities and intellectual abilities (Howlin et al., 2004). However, in everyday situations deficits in understanding other person's behavior on the basis of their mental states are present in all individuals with ASD and represent a significant barrier to social integration (Howlin et al., 2004; Frith and de Vignemont, 2005). This observation is in line with experimental behavioral studies showing that children and adults with high-functioning or Asperger autism are able to master explicit ToM tasks (Ponnet et al., 2004; Scheeren et al., 2013), but that they show subtle ToM impairments in more complex mentalizing tasks (Begeer et al., 2012; Backer van Ommeren et al., 2015).

Studies that investigated the neural underpinnings of mentalizing in ASD individuals revealed a rather heterogeneous picture. Whereas, some results pointed to lower activity of frontal areas and a decreased functional connectivity between frontal and other areas (Mason et al., 2008; Kana et al., 2009) or to decreased activity of the RTPJ during the processing of ToM tasks (Mason et al., 2008; Lombardo et al., 2011) in ASD individuals, other studies found no activity differences in the brain between ASD and healthy individuals during mentalizing (Dufour et al., 2013). These studies used a variety of tasks that require very different mentalizing abilities, such as the attribution of mental states to moving geometrical shapes or making judgements about another person on the basis of descriptions.

The aim of the present study was to investigate the neural correlate of a very basic ability necessary for mentalizing, the false belief understanding, in adults with and without ASD. We know from several neuroimaging studies that in neurotypical individuals the posterior MPFC, the bilateral TPJ, the middle temporal gyrus and the precuneus are involved in false belief processing (Sommer et al., 2007; Meinhardt et al., 2011; Rothmayr et al., 2011; Döhnel et al., 2012). And we know from ToM studies with ASD individuals that there might be an anatomic and functional underconnectivity between two brain areas that are centrally involved in false belief processing, the MPFC and the temporo-parietal junction (Mason et al., 2008; Kana et al., 2009; Murdaugh et al., 2012).

**TABLE 3 |** Whole brain imaging results for the neurotypical (NT) group, the autism spectrum (ASD) group and the whole group: Significant clusters ($P_{FWE\text{-corr}} \leq 0.001$, cluster level) of functional activity: **(A)** Story phase: peak activation associated with the processing of incongruent beliefs, **(B)** Question phase: peak activation associated with the selection of incongruent and congruent beliefs, **(C)** peak activation associated with group differences during the processing of the question phase, and **(D)** conjunction of story and question phase: peak activation commonly associated with the processing of incongruent beliefs.

| | | MNI coordinates | | | | |
|---|---|---|---|---|---|---|
| **Contrast / Brain region** | **BA** | ***x*** | ***y*** | ***z*** | **Cluster size**[a] | ***T*-value**[b] |
| **(A) Story phase: incongruent > congruent beliefs** | | | | | | |
| **NT GROUP** | | | | | | |
| Posterior medial prefrontal cortex (pMPFC) | 6 | 8 | 8 | 66 | 795 | 7.60 |
| Left posterior/inferior frontal gyrus (IFG) | 6/44 | −40 | 0 | 42 | 1,680 | 14.91 |
| Left middle temporal gyrus (MTG) | 22 | −64 | −32 | 2 | 1,069 | 7.21 |
| Right middle temporal gyrus (MTG) | 22 | 50 | −40 | 14 | 530 | 6.18 |
| Right inferior temporal gyrus | 19/39 | 48 | −58 | −8 | 12,712 | 11.59 |
| Left Thalamus | | −8 | −28 | −2 | 316 | 4.19 |
| **ASD GROUP** | | | | | | |
| Posterior medial prefrontal gyrus (pMPFC) | 6 | −8 | 6 | 66 | 515 | 4.66 |
| Left posterior/inferior frontal gyrus (IFG) | 6/44 | −50 | −10 | 42 | 1000 | 7.00 |
| Left inferior frontal gyrus (IFG) | 44 | −42 | 18 | 24 | 504 | 4.44 |
| Right inferior temporal gyrus | 19/37 | 42 | −66 | −6 | 7,789 | 9.78 |
| **WHOLE GROUP** | | | | | | |
| Posterior medial prefrontal cortex (pMPFC) | 6 | −6 | 6 | 66 | 429 | 10.08 |
| Left posterior/inferior frontal gyrus (IFG) | 6/44 | −46 | −4 | 44 | 727 | 10.03 |
| Right posterior/inferior frontal gyrus (IFG) | 6/4 | 50 | −2 | 34 | 253 | 5.45 |
| Left middle temporal gyrus (MTG) | 22 | −60 | −26 | 0 | 535 | 7.79 |
| Right middle temporal gyrus (MTG) | 22 | 52 | −38 | 16 | 96 | 6.60 |
| Left inferior temporal gyrus | 19/7 | −40 | −68 | 8 | 1,308 | 10.05 |
| Right inferior temporal gyrus | 37/19 | 46 | −60 | −8 | 3,058 | 11.60 |
| Left Thalamus | | −8 | −28 | −2 | 28 | 6.47 |
| **(B) Question phase: Incongruent (self-incongruent + other incongruent) > congruent (self-congruent + other congruent)** | | | | | | |
| **NT GROUP** | | | | | | |
| Right inferior frontal gyrus[c] (IFG) | 47 | 42 | 20 | −6 | 208 | 4.84 |
| Right inferior temporal gyrus[d] | 19 | 42 | −44 | 2 | 289 | 5.53 |
| **ASD GROUP** | | | | | | |
| Posterior medial prefrontal gyrus[e] (pMPFC) | 6 | −4 | 6 | 64 | 238 | 5.44 |
| Right inferior frontal gyrus[f] (IFG) | 44 | 32 | 28 | 10 | 258 | 5.12 |
| **Question phase: Congruent (self-congruent + other congruent) > incongruent (self-incongruent + other incongruent)** | | | | | | |
| **NT GROUP** | | | | | | |
| Anterior medial prefrontal cortex (aMPFC) | 10/11 | 14 | 40 | −14 | 882 | 6.03 |
| Right posterior frontal gyrus | 8 | 26 | 24 | 54 | 263 | 6.03 |
| Left posterior frontal gyrus | 8 | −20 | 26 | 54 | 280 | 5.67 |
| Right temporoparietal area | 40 | 68 | −24 | 26 | 416 | 7.11 |
| Precuneus | 31 | 12 | −56 | 26 | 526 | 5.01 |
| **ASD GROUP** | | | | | | |
| Anterior medial prefrontal cortex (aMPFC) | 10 | −6 | 54 | −10 | 2109 | 9.61 |
| **(C) Question phase: group differences** | | | | | | |
| **NT > ASD** | | | | | | |
| Middle occipital gyrus | 19/18 | −12 | 80 | 18 | 4,103 | 9.24 |
| | | 14 | −56 | −2 | | 7.81 |
| **ASD > NT** | | | | | | |
| Left anterior prefrontal gyrus | 10/11 | −22 | 52 | 0 | 2,119 | 7.53 |
| Right anterior prefrontal gyrus | 10/11 | 38 | 48 | −12 | 904 | 6.94 |
| Left posterior frontal gyrus | 6/8 | −42 | 4 | 60 | 629 | 6.89 |
| Left superior temporal gyrus | 41/21 | −40 | −30 | 8 | 498 | 6.23 |
| Left temporoparietal area | 39/40 | −58 | −46 | 36 | 612 | 5.58 |
| **(D) Conjunction of story and question phase: (incongruent>congruent beliefs) and [(self-incongruent + other-incongruent) > (self-congruent + other-congruent)]** | | | | | | |
| **ASD GROUP** | | | | | | |
| Posterior medial prefrontal cortex (pMPFC)[c] | 6 | −4 | 8 | 64 | 295 | 5.42 |

*Brodmann areas (BAs) are approximate.*

[a] *Number of activated voxels per cluster.*

[b] *Peak T-value in activated cluster.*

[c] $P_{FWE-corr} = 0.021$*, cluster-level.*

[d] $P_{FWE-corr} = 0.005$*, cluster-level.*

[e] $P_{FWE-corr} = 0.015$*, cluster-level.*

[f] $P_{FWE-corr} = 0.011$*, cluster-level.*

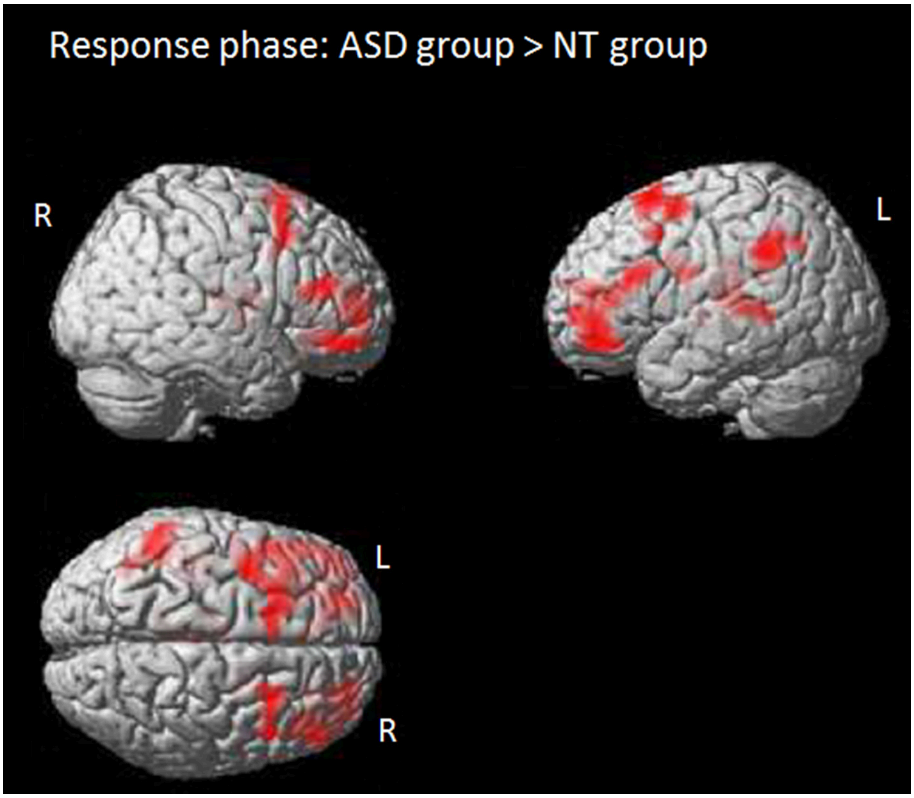

**FIGURE 3 |** Response phase: activation maps for the contrast ASD group > NT group. Colored regions indicate significantly activated voxels with $T > 5.0$, $P_{FWE-corr} \leq 0.001$, cluster level.

In order to investigate, if the possible underconnectivity between MPFC and temporo-parietal areas might play a role in false belief processing in individuals with ASD, we used an adapted version of the classical unexpected transfer task (Schuwerk et al., 2014) that enables a separation between the computation of diverging beliefs and the consideration of another's or one's own belief.

As expected, the behavioral results of the present study revealed no differences between the two groups. The ASD as well as the NT adults performed very well with over 90% of right answers in all conditions. This result is in line with former behavioral studies showing that individuals with high-functioning or Asperger autism are able to compensate mentalizing deficits in explicit false belief tasks (Happé, 1995; Scheeren et al., 2013).

## Story Phase: Computing Diverging Beliefs

In contrast to our hypothesis, the fMRI results for the story phase, in which participants had to compute divergent beliefs, showed no differences in brain activity between neurotypical participants and those diagnosed with ASD. In both groups the processing of incongruent beliefs was associated with activity in the pMPFC, the left inferior frontal gyrus and the right inferior temporal gyrus. The activation pattern of the whole group is very similar to that of our previous study (Schuwerk et al., 2014) and is also in line with findings from earlier studies on false belief reasoning (Sommer et al., 2007; Rothmayr et al., 2011; van der Meer et al., 2011; Döhnel et al., 2012; van Veluw and Chance, 2013). In the story phase participants had to compute if reality (and therefore their own belief) becomes discrepant from the belief of the story protagonist. The involvement of the pMPFC especially in this phase of the task indicates that the region plays a central role in the processing of incongruent beliefs (Schuwerk et al., 2014). Activity of the bilateral middle temporal gyrus was also associated with computing another's discrepant belief. The region seems to play an important role in the processing of mental states that can be deduced from perceived actions (for an overview see Beauchamp, 2015). In the story phase of the present task it was very important to track the movement of the ball (did the ball jump back into the boxes before the boxes switched or did it jump in the other box after the position change of the boxes?). Based on the ball's movement, the participants had to build their own internal mental model. In the incongruent beliefs condition the movement of the ball led to diverging mental models (the own belief in contrast to the other's false belief), in the congruent condition there were no differences between the mental model of the participant and the mental model of the story character.

## Question Phase: Considering and Selecting Own or Another's Belief

In the question phase, in order to give a correct response participants had to select the previously encoded own or other's belief. Neither for the ASD nor for the NT group an effect of perspective was found. This result contradicts our previous study in which Schuwerk et al. (2014) found increased functional brain activity in the temporoparietal junction for conditions in which the other's belief had to be considered in contrast to conditions in which subjects were asked for their own belief. In contrast, in the present study we found differences in the functional activity rather associated with the processing of congruency than of perspective. These diverging results may be associated with the necessary adaptations of the used paradigm. Schuwerk et al. (2014) used another fixation picture (a picture of the two boxes) and intermixed filler trials with experimental trials in order to prevent habituation. For ASD individuals the scanning procedure with the noise and the narrowness of the scanner is very stressing therefore we reduced the scanning time by skipping the filler trials.

Also results revealed no significant interaction between group and congruency. On a more liberal threshold, in both groups responses to incongruent beliefs compared to congruent beliefs were associated with activity in the right inferior frontal gyrus. Activity of the IFC has been observed in many ToM studies (Mar, 2011) and was primarily found in the response phase of a task (Samson et al., 2005; Sommer et al., 2007; Aichhorn et al., 2009; Döhnel et al., 2012). As a basic process, the right IFG has been observed to be associated with response inhibition (Aron, 2007; Aron et al., 2014). Consistent with this view, the IFC is involved in false belief tasks putting high vs. low demands on self-perspective inhibition (Samson et al., 2005; van der Meer et al., 2011). During false belief reasoning, in order to correctly indicate the location where the protagonist will search for an object, participants have to inhibit their own knowledge about the object's location. By contrast, in a true belief task, the participant's perspective and the perspective of the story character are the same. With respect to the current study, it is argued that the highest demands for response control were required when participants had to inhibit their self-perspective on the ball's location in the incongruent belief condition, in which their knowledge about the ball's location did not match with the knowledge of the story character.

Responses to congruent beliefs compared to responses to incongruent beliefs induced in both groups increased activity in the anterior MPFC. This finding is consistent with Döhnel et al. (2012) and Sommer et al. (2007) who also observed aMPFC activity for the contrast true over false belief reasoning. The aMPFC does play an important role in ToM (Carrington and Bailey, 2009; Frank, 2011). Additionally, the area is also discussed to be a core region of the brain's default network, that is centrally involved in processing self-referential thoughts (Raichle, 2015). Meta-analysis reported an overlap in aMPFC activity associated with ToM processing and the default network (Schilbach et al., 2008; Spreng and Grady, 2009). In our congruent belief condition participants have to respond according to their own knowledge about reality, this might have resulted in activity of the aMPFC, an area which is centrally involved in self-referential thoughts.

# CONCLUSION

In contrast to our hypothesis that group differences would be observable in the story phase, results revealed significant differences between individuals with ASD and neurotypical individuals only in the question phase. These activity differences were independent of perspective or congruency. During the question phase the ASD group compared to the NT group showed increased activity in the bilateral anterior prefrontal gyrus, the left posterior frontal gyrus, the left superior temporal gyrus and the left temporoparietal area. The anterior prefrontal gyrus is associated with episodic retrieval and the integration of diverse information content (Reynolds et al., 2006), a process generally necessary in contextualizing stimuli and planning (Koechlin et al., 1999; Koechlin and Summerfield, 2007). And the superior temporal gyrus as well as the temporo-parietal area is not only involved in belief based perspective taking during ToM tasks (Aichhorn et al., 2009; Döhnel et al., 2016), but also in directing the attentional focus toward behaviorally relevant objects (Corbetta et al., 2008). Interestingly, the activity increase in the ASD group is not influenced by the congruency of the beliefs.

Although the autistic participants executed the belief task as well as the neurotypical participants fMRI results indicate that there are differences between autistic and neurotypical individuals on the neural level. This result contradicts the study of Dufour et al. (2013) that investigated also belief reasoning but found no group differences between individuals with ASD and NT individuals. But in contrast to our study, they did not differentiate between the computation and question or response phase. We found differences between ASD and NT individuals only in the question phase, in which participants had to refer to a previously encoded observable story line (the movement of the ball and the boxes) in order to infer an unobservable belief. It might be that ASD individuals compared to NT individuals have to recruit a broader network of brain areas in order to respond adequately to questions concerning beliefs. Additionally, also the conjunction analysis of common functional activity associated with the processing of incongruent beliefs in the story and the question phase may point to subtle differences in the neural processing between ASD and NT individuals. By using a more liberal threshold the ASD group showed increased activity in the pMPFC in both phases during processing incompatible beliefs. Possibly, these differences in the neural processing play no role in a belief task executed under scientific, and for the participants' predictable conditions. But they may have an influence on the deficits of ASD individuals to infer mental states in ongoing social situations in everyday life.

It is important to note that our sample size was rather small which may reduce the chance to detect neural differences between ASD and NT individuals during the processing of different beliefs and may increase the risk that results in neuroimaging studies are not reproducible. However, the revealed activity of the whole group during story processing was very similar to our previous study (Schuwerk et al., 2014). And also Dufour et al. (2013) found no differences in brain activation during a false belief task in adults with and without autism. Additionally, the behavioral data showed that the ASD group performed equally well on the unexpected transfer task as the NT group. Therefore, for future research it could be very interesting to investigate how individuals with ASD compensate their mentalizing deficits in such tasks.

## SUMMARY

The current study was the first one that used the classic unexpected transfer task in order to investigate the neural correlates of false belief reasoning in high-functioning and Asperger adults. Our adapted version of the task makes it possible to separate a phase in which diverging beliefs have to be computed from a phase in which participants have to respond either due to a diverging belief or to a belief that corresponds with their own belief and reality. According to former studies we found no differences between our ASD participants and our NT participants on a behavioral level. On the neural level both groups showed similar activation patterns during the processing of the story, but during the response phase ASD individuals showed increased activity in fontal and temporoparietal areas. Possibly, these subtle processing differences may contribute to the fact that adult ASD individuals are able to master explicit false belief tasks (Ponnet et al., 2004; Scheeren et al., 2013) but fail to apply their strategies during naturalistic social interactions.

## AUTHOR CONTRIBUTIONS

MoS: substantial contributions to the conception and design of the work; the acquisition, analysis, and interpretation of data for the work; writing the manuscript; KD, IJ, and VN: substantial contributions to the conception and design of the study; the acquisition of the patients and the analysis of the data; TS, LB, MaS, and RR: substantial contributions to the conception and design of the work; the acquisition and Interpretation of the data and the revising the manuscript. MoS, KD, LB, MaS, VN, TS, and RR: final approval of the manuscript to be published; Agreement to be accountable for all aspects of the work.

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# Itsy Bitsy Spider…: Infants React with Increased Arousal to Spiders and Snakes

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Attention biases have been reported for ancestral threats like spiders and snakes in infants, children, and adults. However, it is currently unclear whether these stimuli induce increased physiological arousal in infants. Here, 6-month-old infants were presented with pictures of spiders and flowers (Study 1, within-subjects), or snakes and fish (Study 1, within-subjects; Study 2, between-subjects). Infants' pupillary responses linked to activation of the noradrenergic system were measured. Infants reacted with increased pupillary dilation indicating arousal to spiders and snakes compared with flowers and fish. Results support the notion of an evolved preparedness for developing fear of these ancestral threats.

**Keywords: infants, pupillary dilation, arousal, fear, evolution**

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## INTRODUCTION

Although clinical fears of spiders and snakes have a prevalence rate of 1–5 percent (Fredrikson et al., 1996), a strong dislike of these animals is reported by more than a third of the child population (Muris et al., 1997) and the adult population (Davey, 1991), the latter from which even entomologists are not exempt (Vetter, 2013). Fear of spiders and snakes are the most reported specific phobias, even though these animals hardly pose a threat to humans today (Russell, 1991; Fredrikson et al., 1996). Venomous spiders and snakes have, however, been dangerous for our ancestors for 40–60 million years of co-existence, possibly allowing primates to evolve mechanisms to quickly detect these potential threats (New and German, 2015).

Seligman (1971) proposed that primates possess an evolved preparedness to associate ancestral threats such as spiders and snakes with fear, thus explaining the high occurrence of specific phobias for these stimuli. Poulton and Menzies (2002) even suggested the existence of evolved fears of snakes and spiders that do not require fear-learning in ontogeny. These fears may, however, be extinguished through safe exposure and habituation in normal development explaining why specific phobias do not occur at an even higher prevalence rate. Evidence for arousal in response to snakes and spiders in early ontogeny would support the notion that an evolved mechanism underlies specific fears of ancestral threats in humans. In the present study, we therefore test whether young infants react with increased pupillary dilation to spiders and snakes.

Several studies have demonstrated rapid detection of spiders and snakes in visual search tasks with adult participants (Öhman et al., 2001), especially in patients with specific phobias (Pflugshaupt et al., 2005). Furthermore, adults are able to detect a single briefly presented task-irrelevant spider (but they less often detect houseflies or modern threats such as hypodermic needles) suggesting that the human visual system retains biases to reflectively direct attention toward this ancestral threat (New and German, 2015). There is also considerable evidence supporting the view that humans preferentially associate ancestral threats with fear. For instance, participants associate snakes and spiders more readily with aversive stimuli (e.g., mild electric shocks) than other stimuli, such as flowers, in fear conditioning experiments (see Öhman and Mineka, 2001, for a review). In addition, fear-associations with ancestral threats seem to be more robust and less prone to extinction than associations with non-threatening stimuli (Cook et al., 1986; Öhman and Mineka, 2001). However, these studies were conducted with adult participants, making it hard if not impossible to rule out the influence of prior socio-cultural learning experiences. In order to gain a better understanding of the origins of specific fears it is therefore important to test very young participants with limited prior learning opportunities.

Recent research has confirmed visual attention biases for stimuli representing an ancestral threat in infants as young as 5 months of age (Rakison and Derringer, 2008; LoBue and DeLoache, 2010). Similar to older children and adults (LoBue and DeLoache, 2008), infants are able to detect ancestral threats more quickly compared to non-threat-related images (LoBue and DeLoache, 2010). There is also some evidence that infants are prone to associate vocal and facial fear-expressions with spiders and snakes, but these effects were limited to girls in one study (Rakison, 2009) and dynamic stimuli showing snakes in motion in a second study (Deloache and LoBue, 2009). In another study, 9-month-old infants increased their attention to spiders (but not to flowers) when they were paired with fearful facial expressions, but showed an increased attention to snakes compared to fish regardless of the emotional context (Hoehl and Pauen, 2017). Thus, there are currently some hints, but no conclusive evidence for an evolved preparedness for building fear-associations with spiders and snakes in early human development.

The above-mentioned studies used measures of attention allocation (e.g., looking times) to test for early attention biases in human infants. In addition, physiological measures of arousal may be useful, as arousal is intricately linked with fear-conditioning and episodic memory consolidation (see Phelps and LeDoux, 2005, for a review). For instance, explicit memory of images rated as emotional (but not neutral) is enhanced through arousal induced by pain stimulation immediately after presentation of the images (Cahill et al., 2003). Thus, memory consolidation seems to be modified by arousal especially for stimuli that are predisposed to induce an emotional reaction. If evolutionary threats lead to increased arousal from early on in development, this might substantially support learning fear of these stimuli.

To our knowledge, only two studies on early biases for ancestral threats used arousal measures in infants. In the first study Erlich et al. (2013) found that 9-month-olds react with enhanced heart rate deceleration (indicating attentional orienting), larger startle eye-blinks and more visual orienting when listening to evolutionary fear-relevant sounds including angry voices, fire, and snake hissing, compared to modern fear-relevant sounds and pleasant sounds. However, this study did not control for all low-level properties of these sounds, making it difficult to separate a fear response from attention to, or processing of, a large array of other stimulus properties (i.e., to some extent results may reflect the perceived salience of stimuli based on acoustic cues such as dissonance, pitch, spectral tilt, and disharmonic fluctuations of pitch and loudness, rather than the perceived valence of equally salient stimuli).

Thrasher and LoBue (2016) measured 6- to 9-month-olds' heart rate and startle eye blink response to videos of moving snakes or elephants paired with a happy or fearful voice. Infants' heart rate was lower for snakes paired with a fearful voice compared to a happy voice while no such difference was found for elephants. Unexpectedly, startle magnitude was lower for snakes than for elephants, especially when paired with a fearful voice, making the results difficult to interpret. Furthermore, snakes and elephants were not matched for visual properties such as luminance and color.

Together, these two studies provide inconclusive evidence. This is partly due to the fact that startle eye-blink seems to be of limited use when working with infants as Erlich et al. (2013) report great difficulties obtaining these data. More conclusive evidence is still needed from a study using stimuli that control for low-level perceptual features and employing a physiological measure that can be readily applied with infant populations.

One way to achieve this is to measure physiological arousal via pupillary dilations. Pupillary responses, other than those of adjusting to ambient light, indicate activity of the noradrenergic system and therefore an aspect of the stress response (Laeng et al., 2012). Only a few studies looking at infants' pupillary responses to negative or threatening stimuli exist in the literature and these focused on emotional expressions. In one recent study, 14- to 17-month-olds showed increased pupil dilation to negative (fearful and sad) vs. positive or neutral facial expressions, indicating sensitivity to the valence of facial expressions in this age group (Aktar et al., 2016). Similarly, Gredebäck et al. (2012) report a trend for increased pupillary responses for fearful vs. neutral and happy faces in 14-month-olds. Six and twelve month old infants also reacted with increased pupillary dilation when seeing and hearing a peer in distress compared to a neutral condition (Geangu et al., 2011). In contrast to these findings, Jessen et al. (2016) found increased pupillary responses to happy vs. fearful facial expressions when using very short presentation times in 7-month-old infants. The authors attribute the discrepancy of their findings with previous research on differing presentation modes and stimulus durations. Finally, Hepach and Westermann (2013) report that 14- but not 10-month-old infants respond with increased pupillary dilation to actions that are incongruent with an actor's expressed emotions, i.e., a tender action accompanied by an angry facial expression and an aggressive action accompanied by a happy expression, suggesting that between 10 and 14 months infants become sensitive to the congruence of other people's actions and emotional expressions. In sum, previous research confirms that pupillary measures are a useful tool to investigate arousal in response to emotional stimuli in infants, with a specific sensitivity of infant pupillary dilation to negative stimuli.

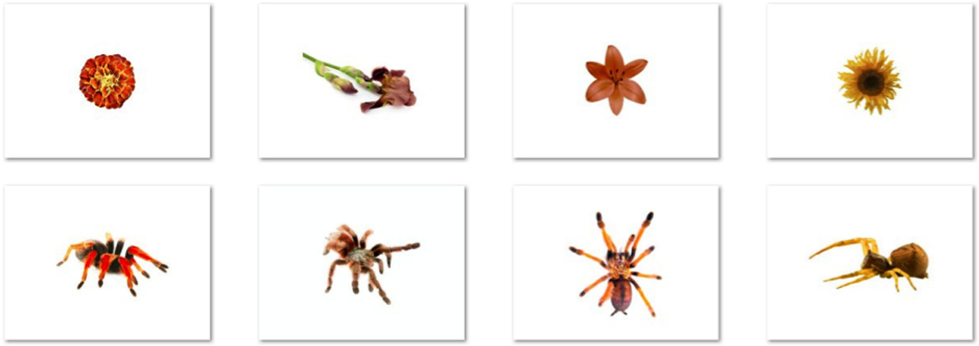

**FIGURE 1 |** Four pairs from the total of eight color-matched pairs of flowers **(Top)** and spiders **(Bottom)** used in Study 1. Each item from the spider category has a corresponding color-matched flower item.

Here, we use pupillary dilation to investigate whether 6-month-old infants react to visual displays of spiders and snakes with increased arousal compared to fear-irrelevant images matched for color, luminance, and size. Assuming an evolved preparedness to develop fear for ancestral threats (Seligman, 1971), we predict increased pupillary dilation for spiders and snakes when compared to visually matched control stimuli that do not represent an ancestral threat to humans (i.e., flowers and fish).

## STUDY 1

We conducted two studies with 6-month-old infants measuring pupillary dilation using a Tobii T120 near infrared eye tracker. In Study 1 infants saw pictures of spiders and flowers (spider-flower experiment) and pictures of snakes and fish (snake-fish experiment). The order of both experiments was counterbalanced across participants and stimuli from the two categories within each experiment were presented intermixed in a pseudorandom order. Pupillometric data from the spider stimulus category were compared with the neutral flower stimulus category, and snake stimulus category data were compared with fish stimulus category. All experiments were conducted with the understanding and written and oral informed consent of each participant's parent. The local ethics committee declared this study exempt. The committee stated that it would not consider the application since it does not need ethical approval. All experiments were conducted with the understanding and informed consent of each participant's parent in accordance with the Declaration of Helsinki.

## Materials and Methods

### Participants

Sample sizes ($N = 16$ per study/experiment) were pre-determined based on *a priori* power analysis (G*Power: Faul et al., 2007) given a level of significance of 0.05, power of 0.8 and expected (moderate) effect size of $f = 0.25$. Study 1 included 16 6-month-old infants (*M* age = 183 days, *SD* = 3.7, 11 boys). All participants were included in the final analysis. All participants were recruited by means of their parents responding to an invitation letter sent to families with children of appropriate age living in Uppsala, a medium-size Swedish city.

### Material and Apparatus

Two sets of items were used, one consisting of eight photographs each of spiders and flowers (16 total), and one consisting of eight photographs each of snakes and fish (16 total). Flowers and fish were chosen for comparison because they can be relatively easily matched in terms of low-level properties with spiders and snakes, respectively, due to similar morphology and surface properties. Each item in both sets had a corresponding color-matched item from the other category (**Figures 1**, **2**).

The color-matching was performed firstly by choosing appropriate pairings from the original coloring of the photographs, and secondly using photo editing software to apply the color content of one of the photographs onto the other. Thereby, the color content of one photograph was duplicated onto the other, rendering them pair-wise identical in regards to color. Across all pairs in both sets, the size of each item on screen was adjusted to be identical (60,000 pixels; ± 1,000 pixels). Lastly, the luminosity was leveled to ensure that brightness (and the confounding light-induced pupillary constriction) was even across each set (245 luminosity units). This was to ensure that the total amount of light in each item was identical.

Items from the two sets were presented once each in counter-balanced orders on a Tobii T120 near infrared eye tracker (sampling rate = 60 Hz, accuracy = 0.5 degrees, monitor size = 17 inches; Tobii, Stockholm, Sweden).

### Procedure

Study 1 was conducted in two phases with a short break in between, to make sure that the infant was not fatigued. The content of each phase was counter-balanced, i.e., half of the participants received the spider-flower experiment in the first phase and the snake-fish experiment in the second phase, the other half received experiments in the reversed order. Within each set order, the first stimulus presented in the pseudo-randomized (pre-determined) order was equally often a snake or a spider as it was a fish or a flower. Per condition, 8 trials

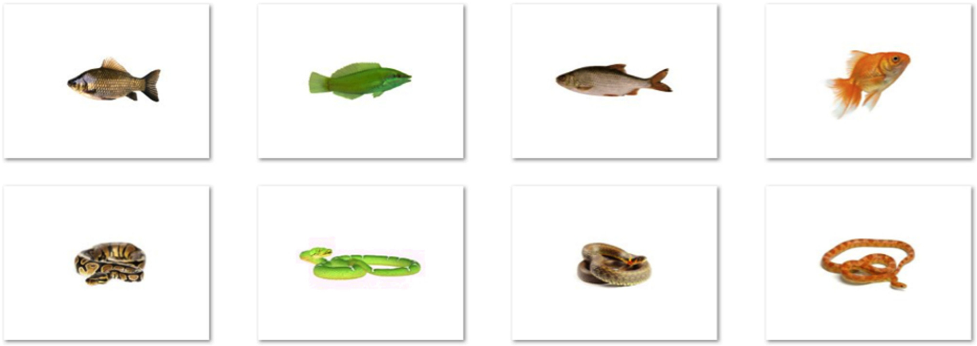

**FIGURE 2 |** Four pairs from the total of eight color-matched pairs of fish **(Top)** and snakes **(Bottom)** used in Studies 1 and 2. Each item from the snake category has a corresponding color-matched fish item.

were run, each featuring a different exemplar of the respective category, presented individually. Each stimulus was presented for 5 s. Prior to each stimulus there was a 3 s long white screen.

All experiments were conducted in the same window-less room with constant ambient light across all participants. Infants were seated in their parent's lap with a distance of 60 cm from the eye-tracker's screen. Parents were required to wear opaque glasses (sunglasses covered with a non-transparent plastic sheet) to ensure that they did not see the stimuli. They were told beforehand what the pictures would contain and were shown example images after the experiment.

The experiment started directly after a short 5-point gaze calibration after which infants were already attending the screen. Upon the experiment's start, trials were presented regardless of infants' gaze direction and therefore a short attention grabber to keep the infant's attention was placed in between every fourth item. Attention grabbers consisted of a starry sky with stars moving randomly and birds that popped out and chirped (total duration about 3 s).

A total of 50% gaze data in each trial (from −500 ms until the end of the analysis window) was required for inclusion. In Study 1 infants on average contributed 5.75 trials (from a maximum of 8) in the spider condition, 5.63 trials in the flower condition, 5.31 trials in the snake condition, and 5.38 trials in the fish condition. Participants with 1–3 valid trials in one condition were still included because mixed models control for an uneven distribution of trials.

## Data Analysis

Data was imported into TimeStudio[1] (Nyström et al., 2016), an open source analysis environment for eye tracking data and general time series analysis accessible from MATLAB. Spurious data samples were removed based on the second derivate and minor gaps in the data were interpolated (max 5 samples at 60 Hz). A moving average filter (width 5 samples at 60 Hz) was applied and data was baseline corrected based on the average pupil size for the first 100 ms of the stimulus presentation. The analysis interval ranged from 2.5 to 3.5 s after stimulus onset; during this time the mean pupil dilation was assessed. The selected time-window is consistent with pupil dilation effects found in previous infant studies occurring or starting around 2 s after stimulus onset (e.g., Geangu et al., 2011; Gredebäck et al., 2012; Sirois and Jackson, 2012). The analysis script including all data (from Study 1), settings and scripts can be downloaded using uwid ts-429-125 inside the TimeStudio environment. Running this uwid will recreate **Figure 3**.

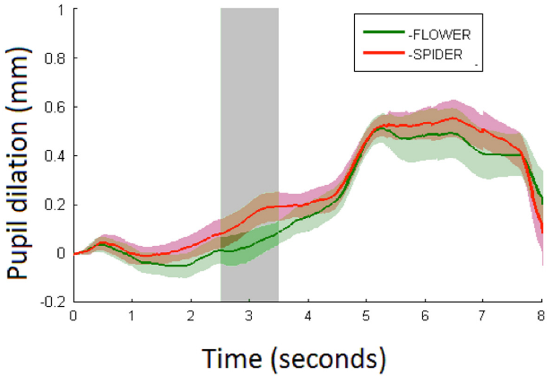

**FIGURE 3 |** Average pupil dilation (mm) for spiders (red) and flowers (green) over 8 s with shaded areas showing the standard errors. Stimulus onset is at 0 s with a duration of 5 s at which a white screen onsets. The analysis time period is marked in light gray.

Statistical analysis was performed using a linear mixed model in R version 3.0.2 (Ihaka and Gentleman, 1996) using lmer in the lme4 package (Bates et al., 2015). In all analyses we used pupil dilation as dependent variable, trial number as a continuous predictor (1–8), experiment as a categorical predictor (spider vs. flower, respectively, snake vs. fish), and participant as random factor. The *p*-values of the fixed factors are based on Satterthwaite approximation of degrees of freedom. The spider-flower experiment and the snake-fish experiment in Study 1 were conducted within-participants, but will be reported with separate analyses due to luminance differences between the category-pairs preventing a direct statistical comparison.

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[1] www.timestudioproject.com

**TABLE 1 |** Fixed effects of condition, trial, and condition × trial on pupil dilation.

| | β | Std. Error | *t*-value | *p* |
|---|---|---|---|---|
| Intercept | −0.22 | 0.11 | 1.93 | 0.06 |
| Condition | 0.18 | 0.07 | 2.63 | <0.01** |
| Trial | 0.05 | 0.03 | 1.68 | 0.10 |
| Condition × trial | −0.02 | 0.02 | −1.40 | 0.16 |

$^{*}p < 0.05$, $^{**}p < 0.01$.

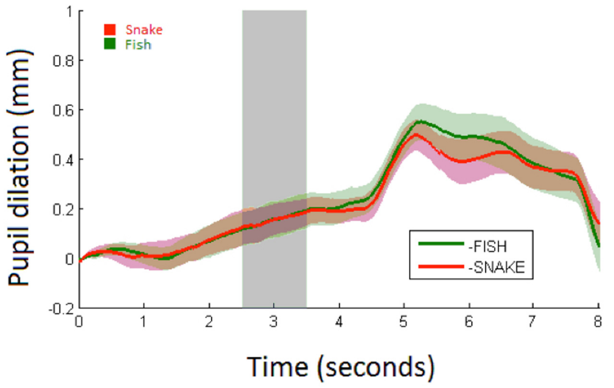

**FIGURE 4 |** Average Pupil dilation (mm) for snakes (red) and fish (green) over 8 s with shaded areas showing the standard errors. Stimulus onset is at 0 s with a duration of 5 s at which a white screen onsets. The analysis time period is marked in light gray.

**TABLE 2 |** Fixed effects of condition, trial, and condition × trial on pupil dilation.

| | β | Std. Error | *t*-value | *p* |
|---|---|---|---|---|
| Intercept | 0.08 | 0.12 | 0.65 | 0.52 |
| Condition | 0.15 | 0.08 | 0.63 | 0.53 |
| Trial | 0.03 | 0.03 | 0.87 | 0.39 |
| Condition x trial | −0.02 | 0.02 | −0.99 | 0.32 |

## Results

### Spiders vs. Flowers

Pupillary responses are depicted in **Figure 3**. The linear mixed model (**Table 1**) demonstrates a main effect of condition ($p < 0.01$) with larger pupil dilations for spiders (mean = 0.14 mm, $\mathrm{CI}_{95}$ = 0.08–0.19) than flowers (mean = 0.03 mm, $\mathrm{CI}_{95}$ = −0.03–0.09). No effect of trial or interaction between condition and trial was observed. Results speak to increased arousal in response to spiders compared with flowers in 6-month-old infants.

Snake vs. Fish. Pupillary responses are depicted in **Figure 4**. The linear mixed model (**Table 2**) did not show a significant main effect of condition ($p = 0.53$; mean pupil dilation for snake = 0.16, $\mathrm{CI}_{95}$ = 0.04–0.27, and fish = 0.16, $\mathrm{CI}_{95}$ = 0.06–0.25), trial, or an interaction between condition and trial.

## Discussion

Results of the spiders-flowers experiment were in line with our hypothesis of increased pupillary dilation for ancestral threats compared to non-threatening stimuli in infants. As pupillary dilation reflects arousal, this early physiological response may contribute to the increased probability for forming fear-associations with spiders compared to neutral stimuli such as flowers and mushrooms reported in human adults (Öhman and Mineka, 2001; Mineka and Öhman, 2002) and infants (Rakison, 2009; Hoehl and Pauen, 2017).

However, results of the snake-fish experiment suggest that there was minimal difference in infants' physiological arousal in response to these stimulus categories. Although a direct comparison between category pairs is not possible as we matched luminance across stimuli only within pairs, it is notable that infants' pupillary responses for snakes and fish were very similar to their responses to spiders and thus higher than their responses to flowers in the spider-flower experiment. This could indicate either that infants react with increased arousal to animate stimuli in general (hinting at a possible "life detector" mechanism) or that their responses to snakes generalized to the perceptually matched fish in this within-participant study. In Study 2 we therefore measure infants' responses to snakes and fish using a between-participant design in order to rule out potential carry-over effects.

# STUDY 2

In Study 2 pupillometric data from one group of participants viewing only snakes were compared with pupillometric data from another group viewing only fish.

## Materials and Methods

### Participants

Study 2 included 32 6-month-old infants (*M* age = 184 days, *SD* = 2.82, 9 boys), i.e., 16 infants per experiment. All participants were included in the final analysis. As in Study 1, participants were recruited by means of their parents responding to an invitation letter sent to families with children of appropriate age.

### Material and Apparatus

Stimuli from the snake-fish experiment from Study 1 were used.

### Procedure

Procedures were the same as in Study 1, with the exception that each infant only saw pictures from one stimulus category. Infants on average contributed 5.56 trials in the snake condition and 5.31 trials in the fish condition.

## Results

### Snake vs. Fish

Pupillary responses are depicted in **Figure 5**. The linear mixed model (**Table 3**) demonstrated a significant main effect of condition ($p = 0.04$; mean pupil dilation for snake = 0.29, $\mathrm{CI}_{95}$ = 0.25–0.33, and fish = 0.17, $\mathrm{CI}_{95}$ = 0.14–0.20). No significant effects were observed for trial or interaction between condition and trial.

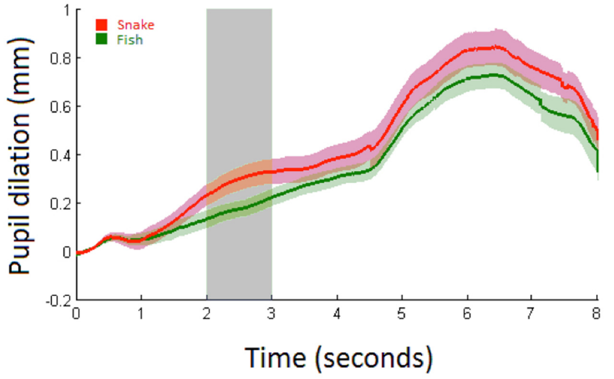

**FIGURE 5 |** Average pupil dilation (mm) for snakes (red) and fish (green) in Study 2 over 8 s with shaded areas showing the standard errors. Stimulus onset is at 0 s with a duration of 5 s at which a white screen onsets. The analysis time period is marked in light gray.

**TABLE 3 |** Fixedeffects of condition, trial, and condition × trial on pupil dilation.

| | β | Std. Error | *t*-value | *p* |
|---|---|---|---|---|
| Intercept | 0.06 | 0.09 | 0.64 | 0.52 |
| Condition | 0.12 | 0.06 | 1.99 | 0.04* |
| Trial | > −0.01 | <0.01 | −0.07 | 0.95 |
| Condition × trial | > −0.01 | <0.01 | −0.02 | 0.99 |

*$^{*}p < 0.05$, $^{**}p < 0.01$.*

## GENERAL DISCUSSION

We measured 6-month-old infants' pupillary responses when viewing stimuli representing ancestral threats (spiders and snakes) and visually matched neutral control stimuli (flowers and fish). Infants responded with increased pupillary dilation to pictures of spiders and snakes when compared with pictures of flowers and fish. Sympathetic pupillary dilation is directly linked to activity in the noradrenergic system (Gilzenrat et al., 2010), arousal and increased focused attention (Laeng et al., 2012). In summary, our results support the notion of an evolved mechanism that is sensitive to spiders and snakes. Six month old infants react with increased physiological arousal to these ancestral threats compared to non-threatening control stimuli.

In Study 1, we found larger pupil dilation for spiders than for luminance- and color-matched flowers in 6-month-olds. Though in line with a previous study showing that infants look longer toward spiders than non-threatening control-stimuli (Rakison and Derringer, 2008), this finding is novel in that it provides first evidence that infants respond to the sight of a spider with increased arousal. We contrasted spiders with flowers in order to keep in line with previous research (Rakison and Derringer, 2008; Rakison, 2009). However, this means that infants' arousal to spiders might also be attributed to the detection of an animate being, thus possibly hinting at a mechanism responsive to animals in general. We therefore contrasted snakes with fish in another experiment.

In the within-participants snake-fish experiment in Study 1 we observed no differences in infants' pupillary dilation to both categories. Responses to snakes and fish were similar to infants' responses to spiders. In line with a potential "life detector" mechanism, one possible explanation is that our participants did not differentiate between snakes and fish and that animals in general elicit arousal in infants. Alternatively, infants in the snake-fish experiment may have been aroused specifically by the snake stimuli but this response carried over to the visually closely matched fish which were shown intermediately in randomized sequence. This, of course, would imply that some form of generalization can take place from ancestral threats to perceptually similar non-threatening stimuli. In order to distinguish between both interpretations we carried out Study 2 with fish and snakes shown to separate groups of infants in a between-participants design to avoid potential carry-over effects.

In Study 2 infants in the snake condition reacted with significantly increased pupillary dilation compared to infants in the fish condition speaking to a specific sensitivity to snakes as an ancestral threat in 6-month-old infants. Although luminance differences across category pairs impede direct statistical comparisons, it is notable that across experiments infants showed the smallest pupillary response to flowers (0.03 mm) followed by spiders (0.14 mm) and fish (and snakes in Study 1:0.16 mm) with a particularly increased response to snakes presented in isolation (0.29 mm in Study 2). Thus, infants seem to be aroused by images of animals, but ancestral threats, especially snakes, elicit a particularly strong reaction. To what extent a life-detector mechanism potentially explains pupil dilation remains a question for future research. However, Study 2 also specifically shows that pupil dilation is greater for snakes than fish

Our results extend earlier findings of quicker visual detection of snakes compared to flowers in 8- to 14-month-old infants (LoBue and DeLoache, 2010). Not only do infants allocate visual attention more quickly to snakes than other stimuli, they also react to snakes and spiders with physiological arousal indicating involvement of the noradrenergic system. This result is also in line with the finding of an enhanced startle eye blink response when infants listen to evolutionary fear-relevant sounds including snake hissing compared to modern threats or pleasant sounds (Erlich et al., 2013).

Taken together, findings from this and several other studies (Rakison, 2009; LoBue and DeLoache, 2010; Erlich et al., 2013; Hoehl and Pauen, 2017) provide growing cumulative evidence for an evolved mechanism that ensures special attention and facilitated fear-learning for ancestral threats in early human ontogeny (Seligman, 1971). It is notable, though, that there is little evidence for 18- to 36-month-old toddlers displaying fear to or spontaneously avoiding live snakes and spiders (Lobue et al., 2013). Thus, there is currently limited evidence for an evolved full-fledged fear response as suggested by Poulton and Menzies (2002), unless one assumes that by 18 months most infants have already habituated to snakes and spiders. Rather, most researchers seem to agree that early attention biases and arousal to ancestral threats predispose humans to develop specific fears of these stimuli given appropriate direct or vicarious learning opportunities (Rachman, 1977) in the sense of an evolved probabilistic cognitive mechanism (Bjorklund and Ellis, 2014; Bjorklund, 2015).

Some limitations of the current study should be noted. First, although the number of stimulus exemplars used in the current study (8 per category) is consistent with or even higher than in previous behavioral research on the same topic (Rakison, 2009), categories should be represented more comprehensively in future studies. Though stimuli were matched in a range of relevant low-level features, the spider and flower stimuli in particular were not perfectly matched in terms of features and complexity, as the use of ecological stimuli was of great importance to us in the current study. Future research may address this issue by using a set of stimuli based on schematic illustrations of spider-like vs. not spider-like arrangements of a "body" and "legs" or "petals" (e.g., New and German, 2015). Furthermore, due to the relative novelty of using pupillary dilation in infancy research, it is difficult to interpret some of the characteristics of the response such as its latency. It is conceivable that the timing of pupillary reactions will prove informative on infants' cognitive processes in the future, but it is necessary to acquire more data in different paradigms in order to be able to draw firm conclusions on this. Finally, although we deem 6-month-olds unlikely to have been exposed to spiders and/or snakes or experienced direct fear-conditioning or social learning of specific fears, we cannot know for sure that infants included in our study were unaffected in their responses by prior experience.

## CONCLUSION

We provide evidence that infants at 6 months of age respond with increased arousal, as indicated by pupillary dilation, to spiders and snakes compared with flowers and fish. We suggest that stimuli representing an ancestral threat to humans induce a stress response in young infants. These results speak to the existence of an evolved mechanism that prepares humans to acquire specific fears of ancestral threats.

## AUTHOR CONTRIBUTIONS

SH and GG conceived of the experiments. KH and MJ performed the experiments and data analyses. All authors contributed to the interpretation of the results. SH wrote an initial version of the manuscript; all authors provided comments and approved of the final version.

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# The Moderating Effect of Self-Reported State and Trait Anxiety on the Late Positive Potential to Emotional Faces in 6–11-Year-Old Children

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**Introduction:** The emergence of anxiety during childhood is accompanied by the development of attentional biases to threat. However, the neural mechanisms underlying these biases are poorly understood. In addition, previous research has not examined whether state and trait anxiety are independently associated with threat-related biases.

**Methods:** We compared ERP waveforms during the processing of emotional faces in a population sample of 58 6–11-year-olds who completed self-reported measures of trait and state anxiety and depression.

**Results:** The results showed that the P1 was larger to angry than neutral faces in the left hemisphere, though early components (P1, N170) were not strongly associated with child anxiety or depression. In contrast, Late Positive Potential (LPP) amplitudes to angry (vs. neutral) faces were significantly and positively associated with symptoms of anxiety/depression. In addition, the difference between LPPs for angry (vs. neutral) faces was independently associated with state and trait anxiety symptoms.

**Discussion:** The results showed that neural responses to facial emotion in children with elevated symptoms of anxiety and depression were most evident at later processing stages characterized as evaluative and effortful. The findings support cognitive models of threat perception in anxiety and indicate that trait elements of anxiety and more transitory fluctuations in anxious affect are important in understanding individual variation in the neural response to threat in late childhood.

**Keywords: emotion, faces, LPP, anxiety, depression, children**

## INTRODUCTION

Understanding emotions from facial expressions plays an important role in children's socio-emotional competence (Trentacosta and Fine, 2010). Recent studies have focused on associations between emotion processing of threatening (vs. neutral) stimuli and experiences of anxious affect in children and adolescents (review by Dudeney et al., 2015). Developmental research has been guided by conceptual models of attention and anxiety which have proposed that attention biases for threat stimuli are evident in early (automatic) information processing stages and these processes cause or maintain anxious affect (e.g., Bar-Haim et al., 2007). While some theoretical frameworks suggest that information processing is a function of *current* emotional state such as state anxiety (e.g., Bower, 1981); most have argued that positive associations between anxious affect and attention to threat reflects elevated trait anxiety that interacts with state anxiety (Mogg and Bradley, 1998, 2016; Bar-Haim et al., 2007). In support, studies have found positive associations between self-reported trait anxiety symptoms in a community sample of children aged 9–12 years and reactions times to probes that followed angry vs. neutral faces, indicating an attentional bias for threat in late childhood (Waters et al., 2010). Similar results have been shown for children aged 5–13 years diagnosed with social phobia (Waters et al., 2011). Furthermore, in an eye movement task children aged 11–12 years diagnosed with pediatric anxiety disorder showed shorter saccade latencies to angry faces, compared to a healthy age-matched control group (Mueller et al., 2012).

Although theoretical models have suggested that processing biases to threat are best understood in the context of elevated symptoms of trait and state anxiety (e.g., Williams et al., 1997), few studies have directly compared the independent effect of trait anxiety, state anxiety, and depression symptoms on emotion processing biases. Concurrent state anxiety has been argued to exacerbate the effects of trait anxiety in an interactive way (Broadbent and Broadbent, 1988; Farrin et al., 2003). Some studies have shown that state anxiety is associated with attentional biases to threat only in individuals with high trait anxiety (Egloff and Hock, 2001), while the results of other studies suggest that state anxiety and trait anxiety contribute independently to attentional biases (Mogg et al., 1990). It remains unclear how state and trait anxiety symptoms contribute to threat-related attentional biases in children.

While behavioral and eye movement data have provided some support for cognitive models of anxiety, event-related potential (ERP) paradigms allow a clearer analysis of the time course associated with the processing of emotional stimuli and the identification of neural markers of anxiety-related attentional processes in children and adolescents. Developmental research has found that the P1 (reflecting early sensory processing) has been observed over parietal-occipital sites around 190 ms in response to happy and fearful faces early in development (Nelson and de Haan, 1996; Taylor et al., 2004). The N170 is an occipitotemporal negative potential occurring at 170 ms post stimulus onset linked to sensitivity in processing information from human faces (Bentin and Carmel, 2002). Research has shown larger N170 amplitudes for negative (i.e., angry) compared to positive (i.e., happy) and neutral faces in 14- to 15-year-olds (Batty and Taylor, 2006). In addition, the Late Positive Potential (LPP) is a positive parietal-occipital component that is evident from around 300 ms and that is proposed to signify elaborative or effortful processing of emotional stimuli (Schupp et al., 2000; Hajcak et al., 2010). The LPP has been found to be sensitive to the emotional content of human faces from the 1st months of life (Leppänen et al., 2007) and its amplitude is larger to positive and negative (compared to neutral) stimuli in 5–8-year-olds (Hajcak and Dennis, 2009; Solomon et al., 2012). Consistent with adult research, the LPP was larger following angry (vs. happy) faces in 7-year-old children (Kestenbaum and Nelson, 1992) and larger for sad compared to neutral faces at occipital sites in a passive viewing paradigm in 6-year-olds (Kujawa et al., 2012a). The LPP is also elicited in adults by non-affective, but task relevant, stimuli that require effortful cognitive processing (Matsuda and Nittono, 2015). Some studies using facial stimuli have shown small emotion effects on LPP amplitudes in children (Kujawa et al., 2012a,b). Similar research has found greater LPP amplitudes for pictorial stimuli (i.e., negative and positive images) compared with faces in children and adolescents (Kujawa et al., 2012b).

Considering the moderating effect of anxiety on ERP components, research supports the proposition that individuals with increased anxious affect allocate attention to threat at early processing stages. For example, a community sample of adult individuals with high trait anxiety showed increased P2 amplitudes and faster latencies in the occipital region when viewing centrally presented angry faces (Bar-Haim et al., 2005). In addition, O'Toole et al. (2013) found that increased N170 amplitudes to angry (vs. happy) faces in young children predicted the development of anxiety symptoms 2 years later. Further studies indicate that later ERP components (i.e., the LPP) are also potential neural markers of increased attention to threat (MacNamara and Hajcak, 2010). A study using an emotional flanker task, for example, found enhanced LPPs to angry (vs. happy) target faces in non-referred high socially anxious adults (Moser et al., 2008). A recent study showed that increased processing of unpleasant compared to neutral pictures (reflected by the posterior LPP) was associated with parent-rated child anxiety in a community sample of 5–7-year olds (DeCicco et al., 2012). However, this study used pictorial stimuli in a reappraisal task and has not examined trait and state anxiety and depression. A second study, using a passive viewing paradigm found that the degree to which unpleasant compared to neutral pictures elicited larger late anterior LPPs was associated with inhibited and fearful behavior in a community sample of 5–7-year olds (Solomon et al., 2012). Recently, Kujawa et al. (2015) also found enhanced LPPs to angry and fearful faces during an emotional face-matching task in 7–19-year-old adolescents diagnosed with social anxiety, separation anxiety and generalized anxiety disorders (compared to controls). This study, however, included a limited range of depressive symptoms and did not measure state anxiety.

Whereas early components (e.g., P1) are thought to be a marker of relatively automatic attention to emotional stimuli, later components (e.g., LPP) are argued to reflect more deliberate processing and allocation of attention to emotional stimuli (Foti and Hajcak, 2008). It has been suggested that the greater deployment of attentional processing resources to emotionally salient stimuli may occur due to feedback from the amygdala to visual cortical areas (Pessoa et al., 2002; Amaral et al., 2003; Vuilleumier et al., 2004). Early components (e.g., P1 and N170) represent a useful measure of preferential processing of threat. In anxious individuals threatening (e.g., angry) faces rapidly and automatically heighten awareness and recruit attentional resources (Eysenck, 1992; Hadwin et al., 2009; Hadwin and Field, 2010). Late positivities (e.g., LPP) may indicate more deliberate processing based on the elaborated meaning of facial stimuli (Hajcak et al., 2010). Research has shown that the LPP is sensitive to emotion regulation strategies such as directed reappraisal (Foti and Hajcak, 2008; MacNamara et al., 2016). The LPP is modulated by a brain network composed of cortical and subcortical structures, such as the amygdala, associated with visual and emotional processing (Liu et al., 2012). Research examining reappraisal and the LPP suggests that children are able to effectively use reappraisal to modulate how they process unpleasant emotional stimuli, as measured via the LPP, and that changes in the LPP are associated with individual differences in mood and anxiety (Dennis and Hajcak, 2009). These models have suggested that increased elaborate processing in response to unpleasant stimuli (as indicated by increasing amplitude of the LPP) may index enhanced attention to negative information in anxiety whereas decreased elaborative processing of unpleasant stimuli (as indicated by decreased amplitude of the LPP) may reflect a mechanism of avoidance of threat (Weinberg and Hajcak, 2011). Based on this model, individual differences in attention to threat may reflect a propensity to maintain or develop symptoms of anxiety in children. Identifying a biomarker for this type of biased processing (e.g., P1 and N170) can help us understand the development of anxiety and identify 'at risk' individuals.

While there is an emerging picture in developmental research highlighting the role of individual differences in both negative affect and the processing of emotional stimuli, research has not explored associations between state and trait anxiety symptoms on ERPs to facial emotion processing, despite evidence from adult studies showing larger LPP amplitudes to unpleasant compared to neutral stimuli in individuals with higher state anxiety (MacNamara and Hajcak, 2009). Similar research with adults has further shown that individual differences in state anxiety moderate the amygdala response to fearful faces (Bishop et al., 2004). It is not clear whether neural alterations underlying children's processing of threatening information are associated with enduring personality characteristics (trait anxiety) or more temporary anxious state regardless of the personality trait (or their interaction).

Recent studies in adults have aimed to examine the differential effects of anxiety and depression symptoms on the LPP to emotional stimuli. Research has shown that anxiety and depression may have opposing associations with the LPP; while anxiety was associated with *enhanced* LPP to threat, depression was linked to *reduced* LPP to threat (MacNamara et al., 2016). For example, an increased number of self-reported depressive symptoms was associated with reduced LPPs to angry faces in a group of 7–19-year-olds diagnosed with an anxiety disorder during an emotional face-matching task (Kujawa et al., 2015). The finding of a blunted/reduced emotional response (as reflected by the LPP) is consistent with theories suggesting disengagement from emotional stimuli more generally in depression (Proudfit et al., 2015). The findings are also consistent with results from behavioral studies which have found that anxiety and not depression is characterized by increased attention to threat (e.g., Hadwin et al., 2003; Waters et al., 2010).

The present study aimed to extend previous research to explore associations between child self-reported anxiety and depression symptoms and the processing of threat (angry faces), and positive (happy faces) vs. neutral (neutral faces) stimuli measuring ERP responses. It considered whether links between early and late ERPs to emotional information are associated with elevated state and trait anxiety symptoms (and their interaction) in young children. In particular, we investigated whether trait anxiety and depression symptoms would explain variance in ERP amplitude to angry vs. neutral faces above and beyond that explained by state anxiety. We included self-reported data on children's anxiety and depression, because parents have been shown to be relatively poor at reporting accurately on their child's internalizing symptoms (Choudhury et al., 2003). We used facial stimuli because human faces represent unique social signals that elicit differential ERP responses (Kujawa et al., 2012b). Following theoretical models of anxiety and empirical research, we explored the possibility that anxiety would be linked to early visual processing of threat (as indicated by increased amplitude of early ERP components; e.g., P1 and N170), as well as later elaborative processes (i.e., increased amplitude of the later LPP component). The inclusion of happy faces allowed some exploration of whether this pattern of neural activity would be specific to threat stimuli. We further anticipated that associations between trait and state anxiety symptoms and their interaction on threat processing would be clearer than those with depression. Based on theoretical models of depression (Armstrong and Olatunji, 2012) and previous literature (Foti et al., 2010; MacNamara et al., 2016) we predicted that depression symptoms would be associated with reduced/blunted LPP amplitudes to threat.

## MATERIALS AND METHODS

### Participants

A hundred and eight children were approached via primary schools which agreed to forward a letter of information and consent to parents. Parents of 75 children gave consent for their child to participate in the study. Of those, pilot data from 5 children and data from 12 children (mean age = 7.50 years, *SD* = 1.20, age range 6–9 years) were excluded from analyses due to incomplete data and ERP artifacts. Complete ERP and behavioral data were available from 58 children (mean age = 8.80 years, *SD* = 1.60 years, age range 5.50–11.80, 37 boys). The study was approved by the Psychology Ethics Committee.

### Facial Expression Stimuli

Stimuli consisted of a standardized set of emotional facial expressions from two adult female models (Ekman and Friesen, 1976; Young et al., 2002) displaying prototypical anger and happiness and a neutral expression. We conducted a behavioral validation study of the facial stimuli in a separate community sample of 65 6–11-year-old children (mean age = 8.31 years, *SD* = 1.55, age range 6.00–10.75 years, 31 boys) recruited as above.

Children viewed facial expressions one at a time (Angry, Happy, and Neutral, 12 trials per emotion), and were asked to identify the emotion in the face and press one of the three buttons with the labels 'angry,' 'happy,' or 'neutral' to indicate their response. The mean percentage of trials classified correctly was as follows: Angry: $M = 94.10$, $SD = 14.56$, Happy: $M = 90.51$, $SD = 19.75$, Neutral: $M = 62.70$, $SD = 30.90$. Accuracy was above-chance for all emotion types, with chance defined as 33.3% given the three response options. Age was significantly positively associated with accuracy for angry ($r = 0.27$, $p < 0.05$) but not happy ($r = 0.08$, $p > 0.05$) or neutral ($r = 0.07$, $p > 0.05$) faces. Accuracy for one emotion was correlated with accuracy for the other emotions ($r > 0.27$ and $p < 0.05$).

## Experimental Paradigm and Procedure

The experimental paradigm consisted of 180 experimental trials (60 trials per emotion type/30 trials per actor) presented in two blocks of 90 trials each. Children participated in 12 practice trials (four presentations of each emotion). Each trial began with the presentation of a central fixation cross (500 ms) followed by stimulus presentation (1000 ms) and a blank screen until participants responded, with a 1000 ms inter-trial interval. Emotion stimulus presentation was randomized across participants to prevent more than two faces of the same emotional category from appearing consecutively. Children viewed facial expressions one at a time (Angry, Happy, and Neutral), and were asked to identify the emotion in the face. Children were instructed to respond with their dominant hand and press one of three response buttons on a keyboard with the labels 'angry,' 'happy,' and 'neutral' to indicate their response. At the end of the session, children completed self-reported measures of anxiety and depression symptoms (see section "Symptoms of Trait and State Anxiety and Depression").

## Symptoms of Trait and State Anxiety and Depression

Because the aim of the study was to examine individual differences in anxiety and depression, the sampling strategy employed aimed to identify the full range of clinical representation of children's internalizing symptoms from no symptoms through to symptoms. The vast heterogeneity of internalizing symptoms imposed a continuous as opposed to categorical measure of child psychopathology. Self-report measures of trait anxiety and depression were taken via the DOMINIC (see Valla et al., 2000 for details on predictive validity), a DSM-IV based pictorial interview designed to assess a range of current psychiatric symptoms in 6- to 11-year-old children. In the DOMINIC, items are presented in the form of an interview via pictures accompanied by questions read to the children. The pictures illustrate the emotional and behavioral content of the DSM-IV (American Psychiatric Association, 2000) Axis I symptomatology. We used the generalized anxiety (14 items; 'Do you worry a lot about not having friends?') and depression (18 items; 'Do you often feel like crying?') scales. For each sentence there was a picture that described the character (DOMINIC) in the picture. Test–retest reliability for the DOMINIC is satisfactory with Kappa ranging from 0.40 to 0.70 (Valla et al., 2000). Cronbach's alpha for child-reported anxiety and depression in the present study was >0.70 for both scales. Questions require a 'yes' (score 1) or 'no' (score 0) answer to create a total score with possible ranges of 0–14 and 0–18 for anxiety and depression, respectively. Parent-reports of symptoms were also collected using the DOMINIC but not included in analyses due to low reliability (for both scales Cronbach's alpha < 0.20).

In addition, we asked children to report symptoms of state anxiety using the state anxiety questions from the State-Trait Anxiety Inventory for Children (STAIC; Spielberger, 1973). This consists of a 20-item 4-Likert-type scale (e.g., 'I feel tense') scored from (1) not at all, (2) somewhat, (3) moderately so and (4) very much so to generate a score range of 20–80 ($\alpha = 0.90$ in the current sample).

## Electrophysiological Recording and Processing

Electroencephalographic (EEG) data were recorded from an electrode cap (Easycap, Herrsching, Germany) containing 66 equidistant silver/silver chloride (Ag/AgCl) electrodes using Neuroscan Synamps$^2$ 70 channel EEG system. Cap electrodes were referenced to the nose. The EEG data were sampled at 250 Hz with a band pass filter at 0.1–70 Hz and recorded from 19 sites. The equidistant montage with the sites used in EEG recording and analyses is shown in **Figure 1**. Analyses focused on nine sites at parietal (sites 12, 13, 14, 24, and 26) and occipital (sites 37, 38, 39, and 40) areas consistent with previous research (Batty and Taylor, 2006). A ground electrode was fitted midway between the electrode at the vertex and frontal site 32. Vertical electro-oculogram (vEOG) was recorded from two bipolar electrodes placed directly beneath the left and right eyes and two electrodes placed above the right and left eye included within the electrode cap. Impedances for vEOG, reference and cap electrodes were kept below 5 kΩ. The ERP epoch was defined as 100 ms pre-stimulus to 900 ms post-stimulus and was filtered with a low-pass filter down 48 dB at 32 Hz. An ocular artifact reduction procedure (Semlitsch et al., 1986) based on vEOG activity was used to remove the influence of blink and other eye movement; epochs were rejected if amplitudes exceeded $\pm 150\ \mu V$ at any EOG or scalp site included in analyses or if participants responded incorrectly. Average ERPs were calculated for each emotion type. A minimum of 20 artifact free epochs for each emotion type were used for calculating ERP averages. The mean and SD of the number of epochs for each emotion were as follows: Angry: $M = 44.24$, $SD = 10.65$, Happy: $M = 44.17$, $SD = 10.70$, Neutral: $M = 42.90$, $SD = 11.46$ (see Supplementary Material 1).

A mean amplitude method was followed for the P1 (110–200 ms), N170 (170–320 ms) and the LPP at parietal and occipital sites (see **Figure 1**). The LPP was observed in both early (LPP1: 430–520 ms) and late (LPP2: 520–610 ms) windows. Selection of this epoch length for the LPP was informed by

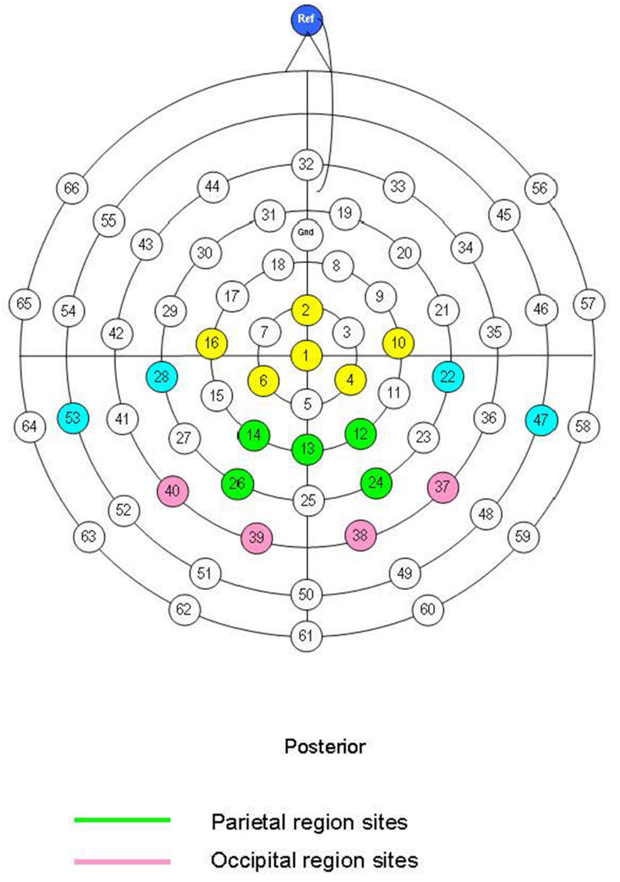

**FIGURE 1 |** Montage with 19 sites used in EEG recording highlighted in yellow, blue, green, and pink. Sites used in analyses highlighted in green and pink for the parietal and occipital regions, respectively.

previous literature in adults (Schupp et al., 2000) and children (Solomon et al., 2012; Kujawa et al., 2012a) indicating that the effects of emotion on the LPP are evident from 300 to 750 ms and become less stable at later windows. We also explored a later LPP window (610–900 ms) overlapping with the beginning of a negative slow wave but there were no significant main effects of emotion or emotion × group interaction effects for this window and these data are not reported further. Similarly, we explored the P300 amplitudes in a 340–430 ms window and found no significant main effects of emotion, emotion × laterality effects or associations with anxiety/depression. We chose to focus on 19 sites at parietal-occipital areas because the main components of interest in this study were maximal in posterior regions. This is consistent with previous literature showing that effects of emotion on LPP amplitudes become less stable in central and anterior scalp regions in children (Solomon et al., 2012). In addition, frontal channels are affected by ocular artifacts in children which can affect the number of clean epochs per condition and compromise the reliability of the ERPs. The mean amplitude was initially calculated for each individual site and then for each ERP component as a combined score for a number of electrode sites ('scalp regions'-see **Figure 1**) to increase the reliability of measurement (see Dien and Santuzzi, 2005).

## DATA ANALYSIS

### Performance Data

Discrimination accuracy was computed for each target emotion using 'hits' (i.e., number of happy, angry, or neutral expressions classified correctly) according to the two-high-threshold model (Corwin, 1994; see Chronaki et al., 2012, 2013). Discrimination accuracy (Pr) is defined as sensitivity to discriminate a particular emotional expression and is given by the following equation: $\text{Pr} = [(\text{number of hits} + 0.5)/(\text{number of targets} + 1)] - [(\text{number of false alarms} + 0.5)/(\text{number of distractors} + 1)]$ (Corwin, 1994). In other words, the Pr reflects the difference between the Hit rate and False Alarm rate, with values tending to 1, 0, and $-1$ for accuracy at better than chance, close to chance and worse than chance, respectively. Note that transformations are added in the above formulae (i.e., $+0.5$) to prevent divisions by zero. For example, in our task with 60 trials for each of the three conditions: angry, happy, and neutral, if a child classified 40 angry faces as angry but he/she also classified as angry 10 neutral faces and 10 happy faces, then his/her accuracy for angry faces would be: $[(40 + 0.5)/(60 + 1)] - [(10 + 10 + 0.5)/(120 + 1)] = 0.49$, suggesting that accuracy is better than chance. Spearman's correlations examined the relationship between accuracy and trait anxiety symptoms (as measured by DOMINIC), depression and a composite score of 'anxious/depressed' symptoms (see below). To examine the effect of emotion type on accuracy, accuracy scores were entered in Friedman's ANOVA with emotion as within-subject factor and paired Wilcoxon follow up tests. Mann–Whitney tests examined gender differences in accuracy for the three emotions.

### ERP Data

Preliminary analyses examined associations between child age and ERP amplitudes at each region. Independent-samples $t$-tests examined gender differences in ERP amplitudes. Preliminary analyses also examined the effect of (i) face model and (ii) task period on ERP amplitudes (see section "Preliminary ERP Analyses"). The trait anxiety and depression scales were highly intercorrelated ($r = 0.80$, $p < 0.001$), therefore, we created a composite score of 'Anxious/Depressed Symptoms' by summing anxiety and depression scores and we used the composite score in further analyses. For all analyses, the results were the same for combined or separate anxiety and depression scores. We created a High and Low 'Anxious/Depressed Symptoms' group (henceforth 'Anx/Dep' group) from a tertile split (i.e., the lowest and highest third of participant symptoms) of Anxious/Depressed symptom scores. We compared the 'High' ($n = 19$)' and 'Low' ($n = 19$) groups from this tertile split in ERP analyses. The whole-sample correlations between ERPs and anxiety/depression scores were generally consistent with the pattern of results from the ANOVA analysis based on the high vs. low anxious/depressed groups. To facilitate the interpretation of the findings we report the high vs. low group analyses alongside the Pearson's correlations in the whole sample between ERPs and anxiety/depression as continuous variables.

Repeated measures ANOVA was conducted including emotion (Angry, Happy, and Neutral) and laterality (Right and Left) as within-subjects factors and group (Low Anx/Dep and High Anx/Dep) as a between subjects factor to examine the main effects of emotion, group and group × emotion interaction effects on ERPs amplitude for each region (parietal and occipital), component (P1, N170, and LPP) and for the LPP only, time window (early-LPP1 and late-LPP2). Where there was a significant effect or interaction, these were followed-up with planned contrasts. In all analyses, planned contrasts compared angry and happy faces with neutral faces. We compared the right and left hemisphere after combining sites per region belonging to each hemisphere for the ERPs as follows: Right Parietal (sites 12, 24), Left Parietal (sites 14, 26), Right Occipital (sites 37, 38), Left Occipital (sites 39, 40). Finally, we ran hierarchical multiple regression analyses to explore whether trait anxiety/depression symptoms explained variance in LPP amplitude to angry vs. neutral faces above and beyond that explained by state anxiety symptoms. For these analyses we calculated scores for processing differences between angry and happy faces vs. neutral faces and where increased LPP scores indicated increased amplitudes for emotional vs. neutral faces.

# RESULTS

The mean scores for self-report anxiety and depression from the DOMINIC were 5.00 ($SD = 2.84$) and 5.50 ($SD = 3.40$), respectively; 17.2% (scores > 8) and 13.8% (scores > 9) of the respective scores fell in the atypical (elevated) range (see Valla et al., 2000). The mean for the 'Anxiety/Depression Symptoms' composite score (see section "ERP Data") was 10.60 ($SD = 5.94$). The mean state anxiety score was 26.70 ($SD = 3.36$) and was positively associated with the anxiety/depression composite score ($r = 0.33$, $p = 0.012$). The Low Anx/Dep group and High Anx/Dep group differed significantly in composite anxiety/depression scores [$F(1,36) = 228.06$, $p < 0.001$; Low: $M = 4.20$, $SD = 1.68$, High: $M = 17.50$, $SD = 3.45$] and state anxiety scores [$F(1,36) = 8.66$, $p < 0.01$; Low: $M = 25.60$, $SD = 3.05$, High: $M = 28.60$, $SD = 3.10$]. Child age was not associated with trait or state anxiety, depression or the composite score ($rs < -0.17$, $ps > 0.18$). There was no significant difference in anxiety or depression symptoms between males and females ($ps > 0.05$).

## Performance

Mean accuracy for all emotions are shown in **Table 1**. Accuracy values were not normally distributed due to ceiling effects, and could not be transformed, therefore, non-parametric tests were used. There was no significant gender difference in accuracy ($U = 587$, $Z = -0.37$, $p > 0.05$, $r = -0.04$). There was a tendency toward an effect of emotion on accuracy [$\chi^2(2) = 5.45$, $p = 0.06$] with higher accuracy scores for angry ($T = 463$, $p < 0.05$, $r = -2.60$) and happy ($T = 511$, $p < 0.05$, $r = -2.50$) compared to neutral faces. Spearman's correlations between accuracy and trait anxiety, depression or the composite score were not significant ($rs < -0.15$, $ps > 0.24$). Spearman's correlations between ERPs and accuracy showed that accuracy for happy faces was significantly correlated with occipital P100 to angry, happy and neutral faces ($r > 0.30$, $p < 0.05$).

## Preliminary ERP Analyses

**Figure 2** plots the grand mean averages to each emotion and region in the whole sample. Means and standard deviations for the ERP data are presented in **Table 2**. Child age was not associated with P1 or N170 amplitudes ($rs < -0.08$, $ps > 0.55$). Age was positively associated with parietal LPP amplitudes to happy and neutral faces for the early and late window ($rs > 0.30$, $ps < 0.01$). For this reason, LPP analyses for the early and late windows parietally were carried out with and without child age as a covariate. There was no significant difference in ERPs amplitude between males and females [$t(56) < 1.7$, $p > 0.08$].

Preliminary analyses examined the effects of face model on ERPs and a time on task effect on ERP amplitudes to assess habituation of stimulus repetition. We conducted a repeated measures ANOVA with model (model 1 and model 2), task period (first half vs. second half) and emotion (Angry, Happy, and Neutral) as within-subject factors and ERP amplitude as the dependent measure. The results revealed no significant main or interaction effects (in all cases $Fs < 3.20$ and $ps > 0.08$, see Supplementary Material 2 for details). Because there was no significant main effect of model or model × emotion interaction on ERPs amplitudes, ERP amplitudes to the two models were averaged for further analyses.

## ERP Analyses and Individual Differences

P1 and N170: The results showed a significant main effect of laterality on the P1 amplitudes in the parietal [$F(1,36) = 19.73$, $p < 0.001$, $\eta_p^2 = 0.35$] and occipital [$F(1,36) = 18.20$, $p < 0.001$, $\eta_p^2 = 0.34$] region. Planned contrasts showed larger P1 amplitudes in the right compared to the left hemisphere in the parietal [$F(1,36) = 19.70$, $p = 0.002$, $\eta_p^2 = 0.24$] and occipital [$F(1,36) = 18.20$, $p < 0.001$, $\eta_p^2 = 0.33$] region. In addition, there was a significant emotion × laterality × group interaction effect on occipital P1 [$F(2,72) = 3.90$, $p = 0.025$, $\eta_p^2 = 0.09$] but not on the parietal P1 [$F(2,72) = 1.86$, $p = 0.16$, $\eta_p^2 = 0.05$]. To break down this interaction for the occipital P1, contrasts were performed comparing angry with neutral and happy with neutral across each level of hemisphere (right vs. left) for the High Anx/Dep vs. Low Anx/Dep group. Planned contrasts revealed a significant difference between the two groups when

**TABLE 1** | Mean percentage (SD) of trials classified correctly (in bold) and misattributions.

| | Facial expression | | |
|---|---|---|---|
| **Identified as** | **Angry** | **Happy** | **Neutral** |
| Angry | **92.27 (9.35)** | 3.04 (4.90) | 3.53 (4.50) |
| Happy | 3.30 (4.60) | **92.18 (8.70)** | 3.80 (5.70) |
| Neutral | 5.48 (8.70) | 3.82 (6.40) | **88.50 (14.30)** |

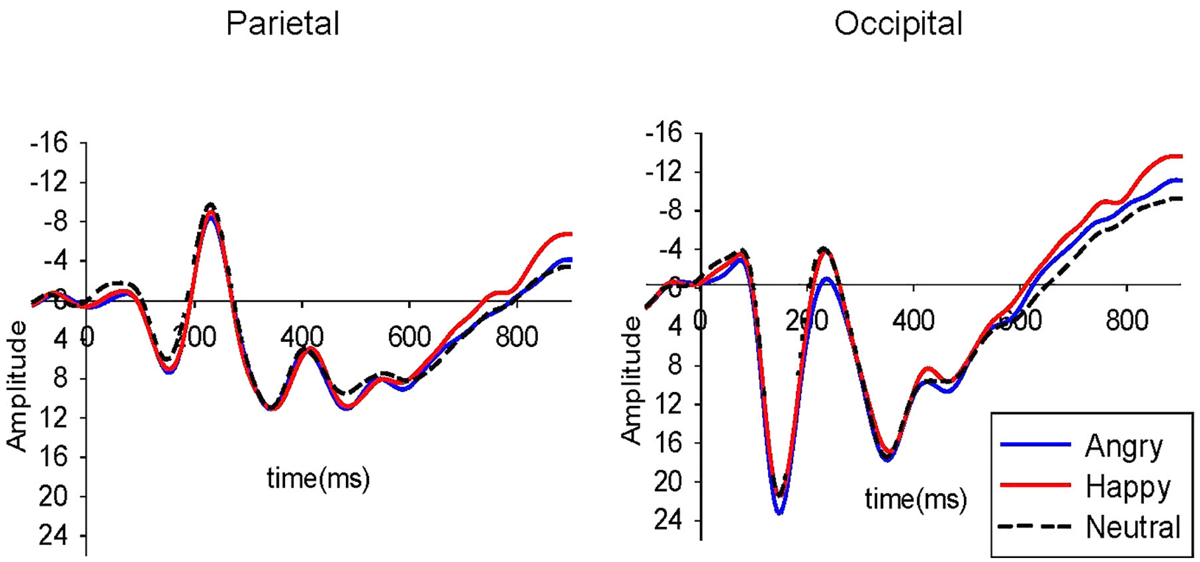

**FIGURE 2 |** Grand mean ERPs to angry, happy, and neutral faces in the parietal and occipital region in the whole sample ($N$ = 58). Amplitude (μV) and time (ms) are marked at the parietal and occipital regions with a pre-stimulus baseline of –100 ms. Scale is –16 to +25 μV.

**TABLE 2 |** Means (SD) for the ERP components in the whole sample in the parietal and occipital region.

| | Angry | Happy | Neutral |
|---|---|---|---|
| **Parietal** | | | |
| P100 | 9.74 (7.00) | 9.90 (7.00) | 9.08 (5.90) |
| N170 | −11.35 (8.70) | −11.47 (9.27) | −11.87 (8.00) |
| LPP1 | 9.80 (8.75) | 9.60 (9.27) | 9.50 (10.24) |
| LPP2 | 9.00 (9.20) | 8.55 (10.27) | 8.52 (10.58) |
| **Occipital** | | | |
| P100 | 25.35 (9.20) | 24.50 (10.40) | 24.60 (8.86) |
| N170 | −6.30 (9.60) | −7.80 (10.80) | −7.40 (9.76) |
| LPP1 | 9.45 (7.87) | 8.70 (9.25) | 9.90 (9.70) |
| LPP2 | 3.96 (8.77) | 2.87 (10.20) | 4.28 (10.27) |

comparing angry and neutral for the left compared to the right hemisphere [$F(1,36) = 11.20$, $p = 0.002$, $\eta_p^2 = 0.24$]. Specifically, there were significantly larger occipital P1 amplitudes to angry compared to neutral faces in the high compared to the low anxiety group for the left hemisphere. Finally, there was a significant laterality × group interaction effect on the parietal N170 amplitudes [$F(1,36) = 7.20$, $p = 0.01$, $\eta_p^2 = 0.17$]. To break down this interaction, contrasts were performed comparing right with left hemisphere for the High Anx/Dep and Low Anx/Dep groups. Planned contrasts revealed a significant difference between the two groups for the left compared to the right hemisphere [$F(1,36) = 7.20$, $p = 0.01$, $\eta_p^2 = 0.17$]. In particular, children with low anxiety/depression showed larger N170 amplitudes in the left compared to the right hemisphere, whereas children with high anxiety/depression showed larger N170 amplitudes in the right compared to the left hemisphere. When a Bonferroni correction was applied with an alpha level of 0.05/8 = 0.006 adopted, the emotion × laterality × group interaction effect on occipital P100 amplitudes remained significant. Results from the Pearson's correlations showed significant positive associations between parietal and occipital P100 to angry-neutral amplitude difference scores and symptoms of state anxiety ($ps > 0.30$, $p < 0.05$). When a Bonferroni correction was applied with an alpha level of 0.05/12 = 0.004 adopted, the associations between the parietal ($r = 0.38$, $p = 0.003$) and occipital ($r = 0.40$, $p = 0.003$) P100 to angry–neutral amplitude difference scores and state anxiety remained significant. Associations between parietal ($r = 0.33$, $p = 0.010$) and occipital ($r = 0.28$, $p = 0.034$) N170 to angry–neutral amplitude difference scores and state anxiety were less strong and did not survive correction for multiple comparisons. Results are presented in **Table 3** (see also Supplementary Table S1 in Supplementary Material 3).

LPP: The results showed a significant emotion × group interaction effect on the occipital LPP1 [$F(2,72) = 3.68$, $p = 0.030$, $\eta_p^2 = 0.09$] and occipital LPP2 [$F(2,72) = 4.85$, $p = 0.010$, $\eta_p^2 = 0.12$] amplitudes. There was also a significant emotion x group interaction effect on the parietal LPP2 amplitudes [$F(2,72) = 4.50$, $p = 0.014$, $\eta_p^2 = 0.10$]. To break down these interactions, contrasts were performed comparing angry with neutral and happy with neutral for the High Anx/Dep vs. Low Anx/Dep group. Planned contrasts revealed a significant difference between the two groups when comparing angry and neutral for the occipital LPP1 [$F(1,36) = 6.30$, $p = 0.017$, $\eta_p^2 = 0.15$], occipital LPP2 [$F(1,36) = 8.70$, $p = 0.006$, $\eta_p^2 = 0.19$] and parietal LPP2 [$F(1,36) = 8.40$, $p = 0.006$, $\eta_p^2 = 0.18$]. Specifically, the LPP amplitudes were significantly larger to angry compared to neutral faces in the high Anx/Dep group compared to the Low Anx/Dep group (see **Table 4**). Results are presented in **Figures 3**, **4**. In addition, there was an emotion × laterality interaction effect on the LPP2 in the occipital [$F(2,72) = 6.70$,

**TABLE 3 |** Pearson correlations between child-report symptoms of negative affect (depression, trait and state anxiety) with Angry–Neutral and Happy–Neutral P1 and N170 amplitude difference scores in the parietal and occipital region in the whole sample ($n$ = 58).

| Symptoms | Angry–Neutral | | | | Happy–Neutral | | | |
|---|---|---|---|---|---|---|---|---|
| | Parietal | | Occipital | | Parietal | | Occipital | |
| | P1 | N170 | P1 | N170 | P1 | N170 | P1 | N170 |
| Trait anxiety | 0.07 | 0.15 | 0.09 | 0.17 | −0.05 | −0.03 | 0.00 | −0.07 |
| State anxiety | 0.38** | 0.33** | 0.40** | 0.28* | 0.26* | 0.06 | 0.26* | 0.18 |
| Depression | 0.12 | 0.17 | 0.15 | 0.10 | 0.07 | 0.05 | 0.05 | −0.02 |

*$p < 0.05$, **$p < 0.01$, ***$p \leq 0.001$. Associations between the state × trait interaction term and ERPs were non-significant ($ps > 0.08$).

**TABLE 4 |** Summary of 3 emotion (angry, happy, and neutral) × 2 Anxiety/Depression group (High and Low) effects on LPP1 and LPP2 amplitudes at the parietal and occipital region.

| | Contrast | Details | *F*-value | Significance |
|---|---|---|---|---|
| **Parietal** | | | | |
| LPP1 | Angry vs. Neutral | High Anx/Dep:7.30 vs. 3.60<br>Low Anx/Dep:11.20 vs. 12.70 | 4.45 | 0.040 |
| LPP2 | Angry vs. Neutral | High Anx/Dep: 6.80 vs. 2.70<br>Low Anx/Dep: 9.20 vs. 11.45 | 8.40 | 0.006 |
| **Occipital** | | | | |
| LPP1 | Angry vs. Neutral | High Anx/Dep:7.30 vs. 3.80<br>Low Anx/Dep:10.00 vs. 12.50 | 6.30 | 0.017 |
| LPP2 | Angry vs. Neutral | High Anx/Dep:2.50 vs. −0.98<br>Low Anx/Dep :4.38 vs. 6.80 | 8.70 | 0.006 |

*For parietal LPP1, although the contrast comparing angry with neutral in the two groups was significant the top level emotion × group interaction effect was not significant (p = 0.06).*

$p = 0.002$, $\eta^2_p = 0.16$] and parietal [$F(2,71) = 8.20$, $p = 0.001$, $\eta^2_p = 0.18$] region. To break down this interaction, contrasts were performed comparing angry with neutral and happy with neutral across each level of hemisphere (right vs. left). Planned contrasts revealed a significant difference between the two hemispheres for angry compared to neutral for the LPP2 in the occipital [$F(1,36) = 4.70$, $p = 0.037$, $\eta^2_p = 0.10$] and parietal [$F(1,36) = 7.26$, $p = 0.010$, $\eta^2_p = 0.17$] region. Specifically, the occipital and parietal LPP2 amplitudes were significantly larger to angry compared to neutral faces for the right compared to the left hemisphere.

There was also a marginally significant emotion × laterality × group interaction effect on the occipital LPP2 amplitudes [$F(2,72) = 3.08$, $p = 0.050$, $\eta^2_p = 0.08$]. Contrasts were used to break down this interaction. The first contrast compared occipital LPP2 scores of the high and low anxiety group for angry compared to neutral faces and right compared to left hemisphere. This contrast revealed a significant difference between the high and low anxiety group when comparing angry to neutral faces and right to the left hemisphere [$F(1,36) = 4.38$, $p = 0.040$, $\eta^2_p = 0.10$]. This showed that for the left hemisphere occipital LPP2 amplitudes were higher to angry compared to neutral faces for the high anxiety group, whereas for the low anxiety group LPP2 amplitudes were higher to neutral, compared to angry faces. For the right hemisphere, however, there was no difference between the groups in LPP2 amplitude to angry vs. neutral faces (see **Figure 6**). The second contrast revealed a non-significant difference between the two groups when comparing happy to neutral faces when the right hemisphere was compared to the left hemisphere [$F(1,36) = 0.90$, $p = 0.75$, $\eta^2_p = 0.003$].

When a Bonferroni correction was applied with an alpha level of 0.05/8 = 0.006 adopted, only the effects related to the LPP2 remained significant. Results from the Pearson's correlations showed significant positive associations between parietal and occipital LPP to angry-neutral amplitude difference scores and symptoms of state anxiety, trait anxiety and depression ($ps > 0.38$, $p < 0.01$). Results are presented in **Figure 5**. When a Bonferroni correction was applied with an alpha level of 0.05/12 = 0.004 adopted, the associations between the occipital LPP2 to angry-neutral amplitude difference scores and trait anxiety ($r = 0.40$, $p = 0.002$) and depression ($r = 0.39$, $p = 0.002$) remained significant. Associations between the parietal LPP2 to angry-neutral amplitude difference scores and state anxiety ($r = 0.39$, $p = 0.003$) and depression ($r = 0.40$, $p = 0.002$) also remained significant. However, associations between parietal and occipital LPP1 to angry-neutral amplitude difference scores and anxiety/depression did not remain significant ($ps > 0.009$). Results are presented in **Table 5** (see also Supplementary Table S2 in Supplementary Material 3).

Furthermore, hierarchical multiple regression analyses were run to directly test whether trait anxiety/depression symptoms explained variance in LPP amplitude to angry vs. neutral faces above and beyond that explained by state anxiety symptoms. The parietal and occipital LPP amplitudes were entered as

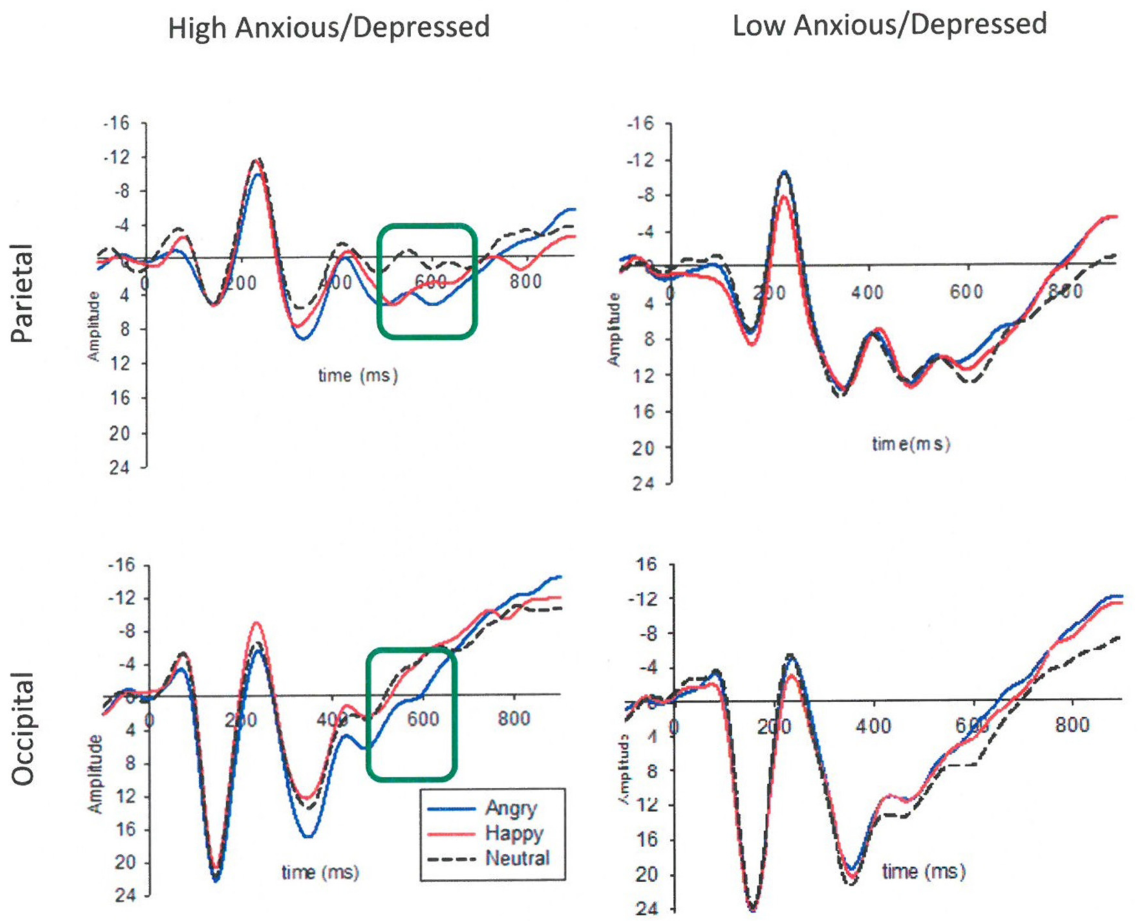

**FIGURE 3 |** Grand mean ERPs to angry, happy and neutral faces in the High and Low Anxious/Depressed group using a tertile split. Larger LPP2 (520–610 ms) responses to the angry compared to neutral faces in the High Anxious/Depressed group in the parietal and occipital region are marked in the green box. Amplitude (μV) and time (ms) are marked with a pre-stimulus baseline of −100 ms. Scale is −15 to +26 μV.

the outcome variable. Predictor variables included state anxiety entered in the first block, the trait anxiety/depression composite score and the interaction with state anxiety in the second block[1]. The results showed that state anxiety explained 13% of the variance in the occipital LPP2 amplitudes to angry relative to neutral faces [$F(1,56) = 8.17$, $p < 0.01$, $R^2 = 0.13$, $R^2_{\text{Adjusted}} = 0.11$]. When trait anxiety/depression composite score and the state × trait anxiety interaction term were added as predictors (model 2), this increased to 26% of the total variance [$F(3,54) = 6.48$, $p = 0.001$, $R^2 = 0.26$, $R^2_{\text{Adjusted}} = 0.22$]. In model 2, there was a significant association between trait anxiety/depression composite score and the occipital LPP2 to angry vs. neutral face ($p < 0.05$), suggesting that trait anxiety/depression explained variance in the LPP amplitudes to angry vs. neutral faces above and beyond that explained by state anxiety. No other association with angry or happy vs. neutral scores was significant; see **Table 6** and **Figures 3–6**.

## DISCUSSION

The current study examined the association between the neural processing of angry and happy (vs. neutral) facial stimuli with child report symptoms of trait and state anxiety and depression in 6–11 year old children. The results showed that the P1 was larger to anger than neutral faces in the left hemisphere, though early components (P1, N170) were not strongly associated with anxiety and depression symptoms. In contrast, anxiety/depression symptoms were positively associated with LPP amplitudes to angry (vs. neutral) faces. Finally, the differences between LPP amplitudes for angry vs. neutral faces were independently associated with measures of state and trait anxiety/depression symptoms.

The early components (P1, N170) did not show sensitivity to facial emotion in our study, consistent with previous research in children (Todd et al., 2008; Dennis et al., 2009). The LPP to

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[1] ERPs for neutral faces were subtracted from those for angry faces to create a difference score. Higher scores indicated greater amplitudes for angry relative to neutral faces. This was repeated for the happy faces. The interaction term between state and trait anxiety was created by multiplying centered variables.

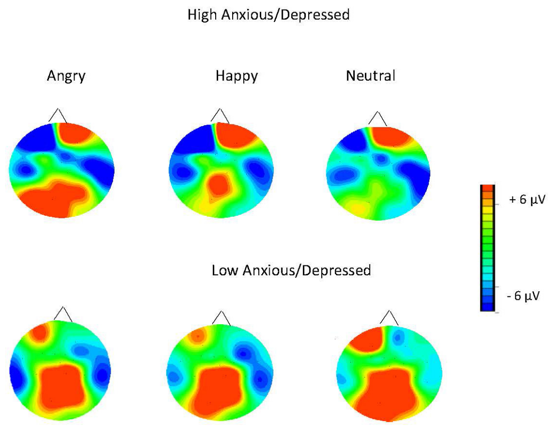

**FIGURE 4 |** Topographic maps for the mean voltage distribution for the angry, happy, and neutral faces for the LPP2. Maps indicate larger posterior positivity (LPP2) in response to angry faces in the High Anxious/Depressed group compared to the Low Anxious/Depressed group. Scalp values represent the ends of the color scale in µV for the LPP2. Dark blue = negativity, red = positivity.

emotional and neutral stimuli emerged in similar time windows (~350 to 750 ms) and scalp regions as reported in previous studies (e.g., Schupp et al., 2000; Hajcak and Dennis, 2009).

Children with high anxiety/depression displayed larger LPP amplitudes to angry (vs. neutral) faces. This effect was clearest for the second LPP time window in parietal and occipital regions. These results are consistent with previous research showing increased processing of angry compared to neutral stimuli (reflected by the LPP) in highly anxious adults (Holmes et al., 2008) and children during reappraisal tasks (DeCicco et al., 2012). Finally, our study found larger P100 amplitudes to angry (vs. neutral) faces in the left hemisphere in the high compared to the low anxiety group, possibly suggesting greater early, sensory processing of threat in anxiety/depression. Findings extend previous work in a community sample of adults with high trait anxiety who have shown larger amplitudes of early latency components (e.g., P2) when viewing angry faces (Bar-Haim et al., 2005).

The stronger effects in the current study related to the angry compared to neutral faces. Neutral expressions are argued to be highly ambiguous and potentially threatening for children (Melfsen and Florin, 2002; Yoon and Zinbarg, 2007). This interpretation is consistent with the lower accuracy scores for neutral compared to angry and happy expressions in our study. Similar research has shown that children displayed greater amygdala activation in response to neutral than fearful faces (Thomas et al., 2001). In contrast, adults showed increased left amygdala activity for fearful faces relative to neutral faces in the same study. Findings highlight the need to address the specificity of differential neural responses by employing positive stimuli and different types of negative stimuli (e.g., anger and fear) in future studies.

Our study showed differential effects of anxiety/depression symptoms for early (P100/N70) compared to late (LPP) components. This pattern of results may reflect differential functional locus of anxiety effects in evaluative compared to perceptual domains of processing social signals of threat. While the present study did not support broader links between anxiety and attentional biases toward threat at early stages of perceptual processing it is possible that neural patterns of early biases observed in adults (Bar-Haim et al., 2005; Eldar et al., 2010) are not developmentally evident in middle childhood. Alternatively, recent conceptualizations of attention in anxiety suggest that attention to threat in anxiety is clearest when presenting stimuli that compete for attention and at relatively short stimulus presentation durations (review by Richards et al., 2014). This raises the possibility that face categorization tasks (and when presented for longer periods) are more sensitive to evaluative cognitive processes in anxiety. The exact mechanisms that underlie the neural development of early processing biases toward threat and sensitivity of individual differences to different experimental paradigms in childhood anxiety require further investigation.

In addition, this study extended previous research to demonstrate that both elevated state and trait anxiety symptoms

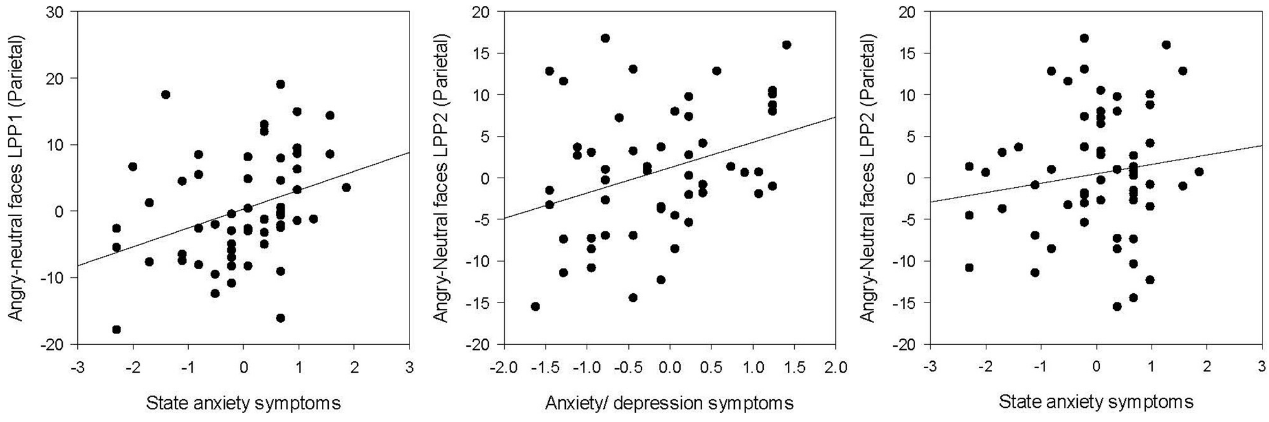

**FIGURE 5 |** Associations between the LPP1 and LPP2 amplitudes in the parietal region for trait anxiety/depression and state anxiety.

**TABLE 5 |** Pearson correlations between child-report symptoms of negative affect (depression, trait and state anxiety) with Angry–Neutral and Happy–Neutral LPP amplitude difference scores in the parietal and occipital region in the whole sample (*n* = 58).

| Symptoms | Angry–Neutral | | | | Happy–Neutral | | | |
|---|---|---|---|---|---|---|---|---|
| | Parietal | | Occipital | | Parietal | | Occipital | |
| | LPP1 | LPP2 | LPP1 | LPP2 | LPP1 | LPP2 | LPP1 | LPP2 |
| Trait anxiety | 0.20 | 0.33* | 0.29* | 0.40** | 0.19 | 0.22 | 0.19 | 0.19 |
| State anxiety | 0.34** | 0.39** | 0.35** | 0.36** | 0.18 | 0.15 | 0.18 | 0.13 |
| Depression | 0.27* | 0.40** | 0.29* | 0.39** | 0.28* | 0.21 | 0.17 | 0.11 |

**p < 0.05, **p < 0.01, ***p ≤ 0.001. Associations between the state x trait interaction term and ERPs were non-significant (ps > 0.08).*

contributed independently to variation in the LPP amplitude to angry compared to neutral faces. These findings are consistent with the proposition that state anxiety and trait anxiety can contribute independently to attentional biases (Mogg et al., 1990). Specifically the difference between amplitudes to angry vs. neutral faces was positively associated with state anxiety in the first LPP time window and subsequently with both increased trait anxiety/depression symptoms and state anxiety in the second LPP time window across parietal and occipital regions. The findings support cognitive models of attention to threat in anxiety (Mogg and Bradley, 1998) and demonstrate that state and trait anxiety contribute independently to the neural response to threat during childhood. This pattern of results was observed with angry, but not happy stimuli suggesting that the neural development of information processing biases in childhood anxiety is specific to threat rather than emotionally arousing stimuli in general. It is important to note that although ERPs can show differences between groups of subjects that can elucidate mechanisms of development of developmental disorders, because of their variability ERPs are less helpful in determining whether an individual child is developing abnormally (Picton and Taylor, 2007). One should consider carefully the variability of ERPs in terms of latency and amplitude in groups of children and average ERPs across participants (Picton et al., 2000).

**TABLE 6 |** Hierarchical multiple regression examining the independent contribution of state anxiety, trait anxiety/depression composite score and state × trait anxiety interaction on the occipital LPP2 to angry vs. neutral faces.

| | Occipital LPP2 | | | |
|---|---|---|---|---|
| | *b* | *SEB* | β | *p* |
| **Model 1** | | | | |
| State anxiety | 0.80 | 0.27 | 0.35 | 0.006 |
| **Model 2** | | | | |
| State anxiety | 0.50 | 0.27 | 0.24 | 0.056 |
| Trait anxiety/depression | 0.37 | 0.16 | 0.30 | 0.020 |
| State × trait anxiety | 1.67 | 1.03 | 0.20 | 0.110 |

*$R^2$ = 0.13 for Model 1: $R^2$ = 0.26 for Model 2, $\Delta R^2$ = 0.13 for Model 2.*

Several studies have explored the role of state anxiety on attentional biases to threat stimuli (e.g., Fox et al., 2001; Quigley et al., 2012; Nelson et al., 2014). Fox et al. (2001) found that individuals with elevated state anxiety showed difficulties disengaging from threatening (angry) faces compared to those with low state anxiety. More recent research has explored attentional processes to simultaneously presented emotional (threat or happy) vs. neutral images in state anxiety before an attention task (baseline state) and after experiencing an anxious mood manipulation (elevated state; Quigley et al., 2012). They found that individuals with increased baseline and elevated symptoms of state anxiety viewed threat (vs. neutral) images for

**FIGURE 6 |** Line graph with error bars showing the occipital LPP2 amplitudes per emotion and hemisphere in the two groups. Emotion × laterality × group interaction shows that for the left hemisphere occipital LPP2 amplitudes were higher to angry compared to neutral faces for the high anxiety group, whereas for the low anxiety group LPP2 amplitudes were higher to neutral, compared to angry faces.

a greater proportion of the time. Consistent with the findings of Fox et al. (2001), Quigley et al. (2012) showed that elevated state anxiety was also linked to increased time spent looking at threat images on first fixation (indicating some difficulties with disengagement). Quigley et al. (2012) argued that these findings link to Bower's (1981) proposition that individuals are predisposed to attend to and recall "mood-congruent" (p.138) information. Bower's (1981) emotion network theory highlights emotion-relevant attentional processes in chronic negative emotional states, like anxiety. Quigley et al. (2012) further highlight that these results support brain imaging studies that have found links between state anxiety with increased amygdala activation to fearful stimuli (e.g., Bishop et al., 2004). Consistently, a recent eye movement study showed that children aged 9–11 years who reported elevated symptoms of neuroticism showed increased latencies to move their eyes away from angry faces to identify a target stimulus, supporting difficulties with disengagement (Pavlou et al., 2016).

Importantly, the above effects were not specific to anxiety symptoms but also generalized to depression symptoms, suggesting common neural substrates of information processing biases in childhood internalizing symptomatology. Recent work suggests that anxiety and depression may have opposing associations with the LPP; while anxiety is associated with *enhanced* LPP to threat, depression is associated with *reduced* LPP to threat (MacNamara et al., 2016). It is further suggested that blunted/reduced LPP emotional response in depression persists even when controlling for the presence of generalized anxiety (MacNamara et al., 2016). Our results support a pattern of *enhanced* LPP to threat linked to *both* anxiety and depression symptoms, suggesting that anxiety and depression may share overlapping cortical mechanisms to threat biases. This similarity in underlying emotional brain circuits may explain the similarity of behavioral manifestations of symptoms in the two conditions. However, because child report symptoms of anxiety and depression were highly inter-correlated in this study, it was not possible to disentangle their independent effects. Future studies should employ pure and comorbid groups of childhood anxiety and depression to understand key emotional processes associated with childhood internalizing psychopathology and aid the identification of causal mechanisms and treatment targets (Kring, 2010).

In summary, this study extends previous research to identify neurobiological markers of attentional biases in children with state and trait anxiety and depression symptoms. The results are consistent with theoretical models of anxiety to highlight increased processing of threat in individuals with elevated trait anxiety (e.g., Mogg and Bradley, 1998; Bar-Haim et al., 2007). The findings are therefore relevant to the development of interventions that focus on emotion regulation and attentional control in this group of children. Consistent with the notion of mood congruent processing (Bower, 1981), our results also indicate that when children report temporary feelings of anxiety, as expressed in state anxiety measures, biases for the processing of threatening information are also evident. A significant limitation in the study is the high correlations between anxiety and depression; however, this is a common problem in the literature (Holmes et al., 2008). The conclusions are also limited by the properties of the stimuli used. Complex emotional images may be more effective in eliciting larger LPPs to emotional compared to neutral stimuli in children. Future studies would also benefit from a more diverse stimulus set of female models. Moreover, effects of anxiety and depression on the LPP were observed in a small time window (520–610 ms) and although we also explored a later LPP window (610–900 ms) we did not observe effects of anxiety on this late LPP. Future research should replicate the present findings in clinical samples of children with anxiety and depression, taking into account measures of state anxiety. Future research should also aim to employ larger sample sizes and examine attention bias using dot-probe tasks which can more readily examine potential behavioral biases. Despite the above limitations, the present study provided novel evidence that neural abnormalities underlying the processing of threat-related stimuli in childhood state and trait anxiety/depression occur at later, more evaluative and effortful processing stages rather than earlier, perceptual processing stages.

## AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2018.00125/full#supplementary-material

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# The Influence of Emotional Material on Encoding and Retrieving Intentions: An ERP Study in Younger and Older Adults

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Prospective memory is a cognitive process that comprises the encoding and maintenance of an intention until the appropriate moment of its retrieval. It is of highly relevance for an independent everyday life, especially in older adults; however, there is ample evidence that prospective memory declines with increasing age. Because most studies have used neutral stimuli, it is still an open question how emotional factors influence age-related differences in prospective remembering. The aim of the study was to investigate the influence of emotional material on prospective memory encoding, monitoring, maintaining, and retrieval in younger and older adults using behavioral and electrophysiological measures. We tested 24 younger adults ($M$ = 26.4 years) and 20 older adults ($M$ = 68.1 years) using a picture one-back task as ongoing activity with an embedded prospective memory instruction. The experimental task consisted of three sessions. In each session, participants had to encode series of images that represented the prospective memory cues for the consecutive block. The images were either of pleasant, unpleasant, or neutral valence. The pictures used in the ongoing task were likewise of pleasant, unpleasant, or neutral valence. Event-related potentials (ERPs) were recorded to assess the neural correlates of intention encoding, maintenance, and self-initiated retrieval. We did not find age differences between younger and older adults on the behavioral level. However, the ERP results revealed an interesting pattern that suggested for both age groups elevated attentional processing of emotional cues during encoding indicated by an elevated LPP for the emotional cues. Additionally, younger adults showed increased activity for unpleasant cues. During the maintenance phase, both age groups engaged in strategic monitoring especially for pleasant cues, which led to enhanced sustained positivity. During retrieval, older adults showed increased activity of ERP components related to cue detection and retrieval mainly for pleasant cues indicating enhanced relevance for those cues. In conclusion, emotional material may influence prospective remembering in older adults differently than in younger adults by supporting a mixture of top-down and bottom-up controlled processing. The results demonstrated a negativity bias in younger adults and a positivity bias in older adults.

**Keywords: prospective memory, aging, partial least square analysis, emotion, EEG**

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# INTRODUCTION

Remembering to buy bread on the way home and remembering to do the taxes on the weekend are typical examples of prospective memory tasks in everyday life. Prospective memory describes the ability to remember and execute delayed intentions in the future (Kliegel et al., 2008a). Although remembering to buy bread on the way home is a relatively easy task, it still might be forgotten when we are stressed by work or excited to go to birthday drinks after work. Based on everyday life experience, it is comprehensible that emotions cannot only interact but also interfere with planned intentions and goals. Surprisingly, studies on emotional influences on prospective memory emerged only recently leaving still lots of open questions, especially with respect to the influence of emotions on age differences in prospective memory. The present study investigated how emotional material modulates the encoding, maintaining, and retrieving of intentions in younger and older adults.

## Prospective Memory and Aging

Remembering a delayed intention consists of four different processes with each relying on different cognitive functions (Kliegel et al., 2011). In a first step, the intention has to be encoded and planned for later execution; planning abilities are implied in this phase (e.g., Hering et al., 2014). In the following, the intention has to be maintained in memory while people are engaged in background activities – so-called ongoing tasks – until the appropriate moment for intention retrieval. The retrieval can be cued either by a certain moment in time labeled time-based prospective memory (e.g., remembering to take the pizza out of the oven after 20 min) or by a specific event labeled event-based prospective memory (e.g., remembering to withdraw money at the next cash maschine; Einstein and McDaniel, 1990). The retrieval and execution of intentions has mainly been associated with controlled cognitive functions such as task switching and inhibition (Schnitzspahn et al., 2013; Zuber et al., 2016). We have to interrupt the ongoing task and switch to the prospective memory task for its execution before returning to the ongoing activity. Conceptually, Kliegel et al. (2011) argued that a mismatch between the task demands in each of the four phases of prospective remembering and the available cognitive resources required for that specific phase determines age-related performance differences.

Several meta-analyses showed a general decline of prospective memory with increasing age across adulthood in laboratory prospective memory tasks (Henry et al., 2004; Kliegel et al., 2008b; Cona et al., 2012a; Ihle et al., 2013). Moreover, Ihle et al. (2013) showed that prospective memory tasks that rely on strategic monitoring are especially impaired in older adults. Strategic monitoring describes the allocation of attentional resources to detect the prospective memory cue within the ongoing task (McDaniel and Einstein, 2007a). In older adults, prospective memory decrements are accompanied by decrements in attentional and cognitive control capacities (e.g., Park and Reuter-Lorenz, 2009), resulting in decreases in strategic monitoring and reduced prospective memory performance (e.g., Smith and Bayen, 2006).

However, McDaniel and Einstein (2000) suggested an alternative route of prospective memory retrieval besides the top-down strategic monitoring. They argue that the retrieval of an intention can be triggered by the cue in a spontaneous and reflexive fashion due to processes of familiarity, distinctiveness, or discrepancy (McDaniel and Einstein, 2007b). For example, McDaniel and Einstein (2007b) hypothesized that if the prospective memory cue is very salient or distinct within the ongoing task, it is likely to provoke a spontaneous retrieval of the associated action. Similarly, very familiar cues and cues that are highly discrepant of the ongoing task will result in spontaneous retrieval because these cues capture attention more easily.

Moreover, spontaneous retrieval is based on bottom-up processing (Bugg et al., 2013) and thus, it should be spared of decrements in older adults (Cherry et al., 2001; Cohen et al., 2003). For example, Cohen et al. (2003) used perceptually distinct cues and showed benefits on prospective memory performance in older adults. Importantly for the present purposes, we argue that using emotional material can also increase the distinctiveness of the prospective memory cue and eliminate age differences. This idea was first tested by Altgassen et al. (2010) who compared emotional prospective memory cues with neutral cues in younger and older adults and showed that older adults performed comparably to younger adults with both pleasant and unpleasant cues, but they performed worse than younger adults with neutral prospective memory cues indicating that emotional valence increases the distinctiveness of prospective memory cues. However, the emerging literature of emotional influences on prospective memory and in particular on age differences in prospective memory demonstrates some contradictory findings, especially regarding the underlying mechanisms.

## The Role of Emotions on Age-Related Differences in Prospective Memory

So far, only a handful of studies have addressed the role of emotional material on prospective memory in older adults (Altgassen et al., 2010; Rendell et al., 2011; Schnitzspahn et al., 2012; Ballhausen et al., 2015; May et al., 2015). Interestingly, the studies showed diverging results regarding the beneficial or disadvantageous influence on prospective memory performance, whereas the study by Ballhausen et al. (2015) found worse prospective memory retrieval for pleasant and unpleasant prospective memory cues compared to neutral cues; Altgassen et al. (2010), Rendell et al. (2011), and Schnitzspahn et al. (2012) showed that older adults improved their prospective remembering with emotional material.

More precisely, in the study by Ballhausen et al. (2015), participants encoded a semantic category (e.g., animals) as prospective memory cues along with emotional examples to manipulate the valence of encoding; however, the later actual cues within the task were of neutral valence (Experiment 2). The results showed that older adults performed worse with the emotional prospective memory cue examples than with neutral ones. The authors conducted another experiment, where they manipulated the valence of the actual prospective memory cue within the task (Experiment 1). Here, older adults showed no differences between pleasant, neutral, and unpleasant prospective memory cues at retrieval. Overall, the study suggested that emotional material might not always enhance prospective memory performance in older adults. Furthermore, emotional material seemed to be more relevant at the encoding phase than the retrieval phase.

The studies showing a beneficial effect of emotional material, however, vary in the magnitude of the effect. In the first study by Altgassen et al. (2010), age differences between younger and older adults were eliminated in prospective memory performance for pleasant and unpleasant prospective memory cues compared to neutral cues. The study by Schnitzspahn et al. (2012) only found that age differences between younger and older adults were attenuated for emotional prospective memory cues compared to neutral ones. Finally, Rendell et al. (2011) did only find an emotional enhancement effect for pleasant material in older adults.

However, when comparing these three studies to the findings reported by Ballhausen et al. (2015), differences in task design between the studies suggest already possible underlying mechanisms regarding the influence of emotional material on prospective memory. Ballhausen et al. (2015) manipulated the valence of the prospective memory cue either at encoding or at retrieval but not in both phases, whereas the other studies used emotional prospective memory cues at encoding and retrieval. This leads to the assumption that especially the encoding of emotional material is relevant for the modulating effects.

Taken together, the empirical evidence on the influence of emotional material on age effects in prospective memory indicates a beneficial effect of emotional material in older adults. It is assumed that the emotional material enhances the salience of the prospective memory cues, and thus supports the detection of the prospective memory cues within the ongoing task (Altgassen et al., 2010; Schnitzspahn et al., 2012). Furthermore, May et al. (2015) argued that the beneficial effect of emotional material does not lead to more strategic monitoring for the cue but rather supports cue detection by the more salient emotional cues *per se* and thus enhancing spontaneous retrieval. Support for this conclusion comes from a study investigating emotional influences on prospective memory in younger adults only (May et al., 2012). The authors found an advantage in prospective memory performance for pleasant and unpleasant prospective memory cues compared to neutral cues, but they did not find indication for elevated monitoring. To the contrary, the authors even reported less monitoring in the emotional conditions compared to the neutral one. However, the heightened effect of emotional material is not always found. Similar to Ballhausen et al. (2015), Clark-Foos et al. (2009) found a deteriorating influence of emotional material on prospective memory performance in younger adults. The authors argue that emotional material might increase task-irrelevant thinking and has a distracting influence toward cue detection.

In sum, although the majority of studies suggested a beneficial influence of emotional material, there is also contradictory evidence in younger and older adults (e.g., Ballhausen et al., 2015). Attempts to identify the underlying mechanisms focused on the role of emotional material either in enhancing the cue saliency and fostering spontaneous retrieval or in boosting the relevance of the cues and fostering strategic monitoring. So far, the evidence supports rather the first assumption (e.g., Altgassen et al., 2010; May et al., 2012; but see Cona et al., 2015a for more monitoring with emotional material). However, the debate of possible underlying mechanisms is mainly led on the behavioral level, which clouds the identification of relevant processes. One study addressed the issue by including electrophysiological measures from the electroencephalogram (EEG) to investigate the neural correlates of emotional cue effects in younger adults (Cona et al., 2015a). The EEG shows high temporal resolution that allows for a precise investigation of underlying neural processes with respect to the presentation of stimuli and to responses.

## Prospective Memory, Emotion, and EEG

The study by Cona et al. (2015a) examined event-related potentials (ERPs) for the different phases of prospective remembering and how these phases were modulated by emotional material. Participants had to encode either pleasant, neutral, or unpleasant prospective memory cues. For the ongoing task, participants worked on a picture one-back task that consisted of pleasant, neutral, and unpleasant ongoing task trials. The design allowed investigating ERPs at encoding, maintaining, and retrieving intentions by crossing the three levels of emotional valence in both tasks.

For the encoding phase, the authors found elevated activity for the late positive potential (LPP) for emotional compared to neutral prospective memory cues. The LPP is a centro-parietal sustained positivity that starts around 300 ms after stimulus onset and can last for 1000–2000 ms and that is increased for emotional material. It is assumed that the LPP reflects sustained attention toward the emotional material (Hajcak et al., 2011). Respectively, the elevated LPP in the study by Cona et al. (2015a) indicated that more attentional resources were recruited for encoding of emotional (pleasant and unpleasant) intentions. During the maintenance phase, the authors found sustained activity in the LPP mainly for pleasant ongoing task trials in blocks where participants had to remember pleasant prospective memory cues. The finding suggests a rather specific allocation of monitoring resources to the more relevant ongoing task trials (pleasant ongoing task trials), as the prospective memory cues that had to been detected were pleasant as well.

A similar effect was expressed on the behavioral level. The authors found increased reaction times for the ongoing task stimuli that had the same valence as the prospective memory cue. This effect is labeled stimulus specific interference effect (SSIE; Cohen et al., 2012) and suggests increased strategic monitoring in situations where the task material for prospective memory cues and the ongoing task overlap and thus increase interference between the two task demands. Cohen et al. (2012) could show that the SSIE can be explained theoretically by the two processes model of strategic monitoring (Guynn, 2003). The model suggests that strategic monitoring for the prospective memory cue consists of two processes, (1) being in a retrieval mode and (2) checking for the target. The retrieval mode describes a general preparedness for the prospective memory cue to arrive. In other words, attentional resources are allocated to monitor for the prospective memory cue. Target checking describes the flexible comparison of the stimulus in the environment with the representation of the prospective memory (target) cue. When there is a high match between these two, monitoring increases resulting in higher reaction times (Cohen et al., 2012). Accordingly, if the emotional valences between prospective memory cues and ongoing task stimuli match (e.g., both being pleasant pictures), reaction times should be higher and monitoring should increase as it was shown by Cona et al. (2015a) for pleasant material.

For the retrieval phase of prospective memory, there are two component complexes discussed in the literature [for a review, see West (2011)]. The two components refer to the cue detection and the retrieval of the intention. For cue detection, West et al. (2001) identified a negativity – the N300 – at occipital sites around 300–500 ms after stimulus onset that distinguishes between prospective memory cues and ongoing task trials. Along with the N300, there is a frontal positivity that is also associated with cue detection. The second component is the parietal positivity that is associated with the retrieval of the intention. The parietal positivity occurs at parietal electrodes around 400–1200 ms after stimulus onset and consists of three subcomponents (West, 2011). The three subcomponents are the P3b that is linked to task-relevant evaluation of the prospective memory cues (e.g., Hering et al., 2016); the old–new effect that is linked to the retrieval from memory (e.g., West and Ross-Munroe, 2002); and the prospective positivity that reflects the switching between the ongoing task and the prospective memory task (e.g., Bisiacchi et al., 2009). Cona et al. (2015a) found in their study that the emotional material modulated especially the frontal positivity and the parietal positivity. The greater frontal positivity for emotional material seemed to reflect more automatic, bottom-up processing to detect the prospective memory cue (i.e., FN400). The elevated parietal positivity, which was the result of the P3b and the parietal old–new effect, suggested an engagement of top-down strategic resources to retrieve the intention from memory. Based on this pattern of modulations, the results by Cona et al. (2015a) seem to indicate that emotional material not only triggers an automatic, bottom-up capture of attention but also boosts a greater allocation of top-down strategic processes.

However, it remains an open question if that would also hold true for older adults. Older adults show usually performance decreases in tasks that need strategic monitoring, whereas tasks that rely on spontaneous retrieval seemed to be spared of age-related performance decreases. They also show rather attenuated activity for the N300 and the parietal positivity compared to younger adults (e.g., West and Covell, 2001; West and Bowry, 2005). Similarly, it has been found that older adults show smaller LPPs (e.g., Wood and Kisley, 2006).

### The Present Study

The present study followed up on that previous study with the main objective of investigating the influence of emotional material on prospective memory in younger and older adults on distinct phases composing prospective remembering using ERPs. The study aimed to clarify the contradictory findings regarding emotional prospective memory tasks in older adults (Altgassen et al., 2010; Ballhausen et al., 2015) by investigating the underlying mechanisms. Therefore, we replicated the study by Cona et al. (2015a) and applied the paradigm in a group of younger and older adults.

Following the previous literature, we expected that older adults should perform worse than younger adults for neutral prospective memory cues reflecting the general (non-emotional) decline in prospective memory performance. For pleasant and unpleasant cues, age differences should be smaller or even eliminated, if older adults benefit from the emotional saliency of the cues.

On the neural level, we expected attenuated activity in older adults compared to younger adults for the LPP at encoding and retrieval and for the prospective memory-related ERPs. Furthermore, older adults tend to show a positivity bias that might be detectable in elevated activity for pleasant cues compared to neutral and unpleasant cues (Mather and Carstensen, 2005). The positivity bias (or positivity effect) in older age is a motivational cognitive processing style that is grounded in the socioemotional selectivity theory (Carstensen, 2006). This theory suggests that due to the perceived limited time in older adults, there is a shift of goals from future-oriented goals such as seeking new information toward more present-oriented goals such as emotional regulation to increase well-being. The positivity bias describes the preference for pleasant or positive information in attention and memory tasks in older adults (see Reed et al., 2014 for meta-analytical evidence).

The neural correlates for the maintenance phase might elucidate the role of emotional material on prospective memory in older adults. If emotional material boosts the attentional processing of the cues, it should also increase monitoring processes. Thus, we would expect smaller monitoring ERP activity in older adults compared to younger adults due to decrements in attentional capacities. However, if emotional material would foster the distinctiveness of prospective memory cues, following McDaniel and Einstein (2000), older adults would rather rely on spontaneous retrieval and should not show monitoring activity during the maintenance phase.

## MATERIALS AND METHODS

### Participants

Forty-four participants took part in the study. Among them, 24 participants belonged to the younger adults' group (*M* = 26.42 years; range = 21–52 years; 12 males) and 20 participants belonged to the older adults' group (*M* = 68.05 years; range = 60–80 years; 8 males). The younger adults were recruited from the University of Geneva and participated for course credits. The older adults were recruited at local senior associations and libraries and received 20 CHF in reimbursement for their time. To assess general cognitive abilities, we administered the matrices' subtest and the vocabulary subtest from the Wechsler Adult Intelligence battery (WAIS 4; Wechsler, 2011). The two age groups did not differ regarding fluid intelligence assessed with the matrices subtest [$t(42) = 1.846$; $p = 0.072$; $M_{young} = 20.63$; $SD_{young} = 3.51$; $M_{old} = 18.65$; $SD_{old} = 3.51$] and verbal abilities assessed with the vocabulary subtest [$t(42) = 1.313$; $p = 0.196$; $M_{young} = 43.83$; $SD_{young} = 6.28$; $M_{old} = 46.05$; $SD_{old} = 4.58$]. All participants reported normal or corrected to normal vision and hearing, no history of neurological or major psychiatric diseases, and were not currently taking any psychoactive medication. All participants reported to be right-handed and were fluent in French or have spoken French for more than 5 years. Furthermore, we screened all older adults for their general cognitive status with the modified version of the French Telephone Interview for the Cognitive Status (F-TICS-m; Vercambre et al., 2010) and included only participants that scored higher than a value of 26 ($M_{old} = 36.50$; $SD_{old} = 3.30$). Given the study material, participants with specific phobias (e.g., blood phobia and snake phobia) were excluded. The study was approved by the ethic commission of the faculty of psychology and educational sciences of the University of Geneva. All participants signed an informed consent prior to the testing.

## Material

We used a prospective memory paradigm that was previously published by Cona et al. (2015a). The task consisted of emotional stimulus material from the International Affective Picture System (Lang et al., 2005); 228 pictures were selected for the task among them 76 pleasant, 76 unpleasant, and 76 neutral pictures. The selected pictures varied in their normative valence ratings to create the three different emotional conditions (pleasant pictures: $M = 7.3$; $SD = 0.6$; unpleasant pictures: $M = 2.8$; $SD = 0.6$; and neutral pictures: $M = 5.0$; $SD = 0.2$). Regarding the arousal of the three conditions, pleasant and unpleasant pictures did not differ from each other (pleasant pictures: $M = 5.1$; $SD = 0.6$; unpleasant pictures: $M = 5.2$; $SD = 0.4$; $p > 0.05$), but showed higher arousal ratings than neutral pictures (neutral pictures: $M = 3.3$; $SD = 0.6$; all $p < 0.05$). Pictures were chosen from four categories: persons, animals, landscape, and objects and represented a wide range of semantic categories to avoid biases for specific pictures. For more details on the picture selection, see Cona et al. (2015a). For each valence condition, 25 pictures were chosen that served as prospective memory cues and the remaining pictures were used as ongoing task material. Prospective memory cues and ongoing task stimuli were matched regarding valence and arousal ratings. The pictures were presented in the center of the computer screen in front of a black background.

The prospective memory task consisted of a one-back ongoing task with an embedded prospective memory instruction. For the ongoing task, participants had to judge if the presented picture on the screen was the same or a different picture as the previous one by pressing the corresponding keys. Participants had to press with the index and middle fingers of their right hand on the keys “G” or “H” of a French-Swiss keyboard for the same/different judgment. The response-key mapping for the same/different keys was counterbalanced across participants. On each trial, the picture appeared for 2000 ms or until a response was made, followed by a black screen with a fixation cross that pseudo-randomly lasted for 1200, 1400, or 1600 ms. The pictures were of pleasant, neutral, and unpleasant valence. In total, 24% of the ongoing task stimuli were one-back hits.

For the prospective memory instruction, participants had to press the “A” key with their left index finger after answering the ongoing task when seeing a previously encoded prospective memory cue. Before each block, participants had to encode five different pictures of the same valence with each picture presented for 2000 ms followed by a black screen for 1000 ms. Prospective memory cues were never one-back hits.

## Procedure

After signing the informed consent, the testing session started with the assessment of the general cognitive abilities and participants performed the matrices subtest and the vocabulary test. Afterward, the electrodes were applied on the head and in the face of the participants. The preparation for the EEG recording took approximately 15 min. The participants were installed in a noise shielded cabin in front of a computer, where the prospective memory task was administered.

The task instructions were displayed on the screen and participants were asked to explain all instructions in their own words to ensure understanding. The task started with a practice block to familiarize participants with the ongoing task (39 trials with 13 trials per valence). If they performed at least 85% correct, they could continue with the next block; otherwise, the instructions were explained again and participants could repeat the practice block. Following the practice, participants performed a baseline block for the ongoing task consisting of 198 trials.

Afterward, participants worked on three prospective memory sessions that represented the three valence conditions pleasant, neutral, and unpleasant referring to the respective valence of the prospective memory cues. The three sessions were counterbalanced across participants. The valence of the prospective memory cues in each session defined the valence condition (pleasant, neutral, or unpleasant prospective memory cues). The ongoing task stimuli in each session were pictures from all three valences. Each session consisted of five blocks of 55 ongoing stimuli and 5 prospective memory cues (in total 300 stimuli per session). The ongoing task stimuli were presented in a pseudo-randomized way. We created three randomized orders of the ongoing task stimuli, one for each prospective memory session. In each block, 24% of the ongoing task stimuli were one-back hits. Each block started with the encoding phase of prospective memory cues followed by a summary of the task instructions before the respective block started. The three prospective memory sessions were presented in a counterbalanced order between participants to control for possible order effects.

At the end of the experiment, participants worked on a recognition task to assess retrospective memory for the prospective memory cues. Participants were asked to recognize the prospective memory cues. The task consisted of 75 former prospective memory cues (25 cues per session) and 75 ongoing stimuli as distractors. Participants had to press either the key “N” or “M” to indicate if the picture was a former prospective memory cue or an ongoing stimulus. The response-key mapping was counterbalanced across participants. The experiment was run using the software Eprime 2.0 (Psychology Software Tools).

## Recording of the Electrophysiological Data

The electrophysiological data was recorded continuously for the baseline block, the three prospective memory sessions, and the recognition block using the Active-Two BioSemi system with 32 AG/AgCl active scalp electrodes. Electrodes were distributed on the head according to the 10–20 system using head caps with electrode holders (Fp1, Fpz, Fp2, F7, F3, FZ, F4, F8, FC3, FCZ, FC4, T7, C3, CZ, C4, T8, CP3, CPZ, CP4, P7, P3, PZ, P4, P8, PO3, POZ, PO4, O1, OZ, O2, left mastoid, right mastoid). Additionally, we applied six facial electrodes near the outer canthi as well as below and above the pupils to record eye movements (LO1, LO2, IO1, IO2, SO1, SO2). Data were recorded with the ActiView BioSemi software (BioSemi Active-Two, V.O.F., Amsterdam, Netherlands) and digitized at a sampling rate of 2048 Hz in a bandwidth filter of 0–417 Hz. All electrode offsets were held between ±20 μV. Processing of the data was accomplished using the EEGlab 14.1.1 toolbox (Delorme and Makeig, 2004) for Matlab (Version R2016, MathWorks, Natick, MA, United States). The data were downsampled to 512 Hz and low-pass filtered with 30 Hz. Following, the data were further downsampled to 256 Hz and high-pass filtered with 0.1 Hz. In the next step, the data were segmented in epochs of 200 ms before stimulus onset and 2400 ms after stimulus onset. Artifact rejection was performed using independent component analysis (ICA) algorithm from the EEGlab toolbox. Afterward, epochs were re-segmented from 200 ms before stimulus onset until 1400 ms after stimulus onset for stimuli with correct responses. Baseline correction was applied using the 200 ms pre-stimulus interval. Epochs showing activity above of ±75 μV were excluded. All electrodes were re-referenced offline to the average of the two mastoid electrodes. ERPs were averaged for each subject and condition for ongoing task trials, prospective memory cues and hits and recognition trials. We obtained the following numbers of artifact-free trials for the average: prospective memory cues at encoding per session $M = 24.50$, $SD = 1.82$ (younger adults: $M = 24.19$, $SD = 2.42$; older adults: $M = 24.82$, $SD = 0.63$); ongoing task trials per valence $M = 87.44$; $SD = 11.19$ (younger adults: $M = 84.82$, $SD = 14.83$; older adults: $M = 90.33$, $SD = 2.29$); prospective memory hits per session $M = 20.07$, $SD = 5.11$ (younger adults: $M = 20.46$, $SD = 4.65$; older adults: $M = 19.61$, $SD = 5.60$); and recognition trials per task type and valence $M = 18.75$, $SD = 5.85$ (younger adults: $M = 19.09$, $SD = 5.46$; older adults: $M = 18.33$, $SD = 6.30$). We had to exclude two younger adults and one older adult from the electrophysiological analyses due to bad signal.

## Data Analysis

### Behavioral Data Analysis

The behavioral data were analyzed separately for the prospective memory task and the ongoing task performance. We conducted mixed ANOVAs with age group (two: younger adults and older adults) as between-subjects' factor and valence of the prospective memory session (three: pleasant, neutral, and unpleasant) and valence of the ongoing task stimuli (three: pleasant, neutral, and unpleasant) as within-subject factors. The ANOVAs were conducted separately for the accuracy rates and the reaction times of prospective memory hits (i.e., correct response after detecting the prospective memory cue) and ongoing task hits (i.e., correct same/different judgment). Greenhouse-Geisser corrections were applied whenever necessary and degrees of freedom were adapted accordingly. Alpha level was set to 0.05. Significant main effects and interactions were explored using *post hoc* $t$-tests. *Post hoc* tests were corrected for multiple testing using the Bonferroni adjustment: for the subsequent $t$-tests, all $p$-values were multiplied by the number of comparisons made (indicated as $p_{adj}$).

### Electrophysiological Data Analysis

The electrophysiological data were analyzed with partial least square (PLS) analysis (Lobaugh et al., 2001; McIntosh and Lobaugh, 2004). PLS is a multivariate statistical technique that identifies latent differences in ERP amplitudes between experimental conditions across time and space. As input, PLS analyzes the cross-block covariance between a set of orthonormal contrasts reflecting the experimental design of the study and the ERP data, with ERP data consisting of averaged signals per subject and condition in rows and the amplitudes of all time points and electrodes (i.e., 0–1400 ms) in the columns. We used the 30 head electrodes without mastoids for the analyses. PLS was conducted using the PLSGUI for Matlab[1]. The PLS yields a relation between a cohesive pattern of ERP activity over the scalp and a specific experimental effect, which is represented by the optimal contrast across the task conditions, or design scores. In particular, the following three outputs were analyzed and interpreted: (1) task-related variance of latent variables (LVs), (2) ERP saliences, and (3) design scores. The singular value for an LV corresponds to the covariance of the ERP activity with the experimental conditions, expressed in terms of design scores. Each LV explains a progressively lower percentage of the total covariance pattern, until all the covariance is explained. The significance of the LVs values was calculated using a permutation test (1000 replications). An LV was considered as significant at $p < 0.05$. The second and third outputs characterize the structure of the LVs. The design scores describe the contrast between the experimental conditions. Importantly, a greater difference among the distinct design scores reflects a greater difference in the ERP pattern among the relative experimental conditions captured by the corresponding LV. The electrode saliences show where in time (i.e., at which temporal intervals of the epochs) and space (i.e., at which electrodes) the contrast is expressed (Lobaugh et al., 2001; West and Krompinger, 2005). To reduce the bias of possible outliers and to provide a standard error, all data were bootstrapped by randomly resampling participants with replacement 200 times, therefore, allowing to determine the reliability of the saliences identified by the LVs. Bootstrap ratios > 3 were chosen as the cut off for stable non-zero saliences.

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[1] https://www.rotman-baycrest.on.ca

We conducted four separate PLS analyses to analyze the ERP effects for the four phases of prospective remembering in younger and older adults:

(1) The first analysis referred to the *encoding phase* and considered ERPs elicited by pleasant, neutral, and unpleasant prospective memory cues that resulted in a later correct response (prospective memory hit). One younger subject had to be excluded because of not enough data points.

(2) The second analysis referred to the *maintenance phase* and considered ERPs elicited by pleasant, neutral, and unpleasant ongoing task hits in the three prospective memory sessions. This analysis comprised nine conditions by crossing the three valence levels of the prospective memory sessions and the three different valence conditions of the ongoing task stimuli.

(3) The third analysis referred to the *retrieval phase* and considered ERPs elicited by prospective memory cues and by ongoing task hits. The valence for prospective memory cues and ongoing task hits was matched comparing the same emotional valence for the different trials (pleasant, neutral, and unpleasant). The analysis included six conditions because ongoing stimuli valence and prospective memory session valence was matched. We had to exclude one older participant due to too few prospective memory hits in some of the conditions.

(4) The fourth analysis referred to the *recognition task* and considered the ERPs elicited by prospective memory trials and ongoing task trials in the recognition task. The analysis considered six conditions by crossing the two task types (prospective memory cues and ongoing task stimuli) with the three valence levels (pleasant, neutral, and unpleasant). We had to exclude one younger and three older adults because of missing electrophysiological data.

# RESULTS

## Behavioral Results

**Table 1** depicts the descriptive measures for the behavioral performance rates in younger and older adults.

### Prospective Memory Performance

First, we conducted an ANOVA on accuracy rates for the prospective memory hits including the factors age group (two: younger adults and older adults) and prospective memory session (three: pleasant, neutral, and unpleasant). The ANOVA did not reveal significant main effects for age group [$F(1,42) = 0.491$; $p = 0.487$] or prospective memory session [$F(1.71,71.93) = 1.525$; $p = 0.226$]. There were no performance differences between younger and older adults as well as between the three different valence conditions of the prospective memory cues. The interaction did not reach significance [$F(1.71,71.93) = 2.783$; $p = 0.077$] but showed descriptively that younger and older adults differed in their performance for negative prospective memory cues with younger adults performing better than older adults.

In a second step, we analyzed the reaction times for prospective memory hits. Although younger adults performed descriptively faster than older adults, the ANOVA revealed no significant main effect for age group [$F(1,42) = 2.587$; $p = 0.115$]. Also neither the main effect of prospective memory valence condition [$F(2,84) = 1.657$; $p = 0.197$] nor the interaction reached significance [$F(2,84) = 0.567$; $p = 0.569$].

### Ongoing Task Performance

In a first step, we analyzed correct ongoing task performance including the factors age group (two: younger adults and older adults), valence of the prospective memory session (three: pleasant, neutral, and unpleasant), and valence of the ongoing task stimuli (three: pleasant, neutral, and unpleasant). The ANOVA revealed a significant interaction of the valence of the ongoing task stimuli and age group [$F(2,84) = 3.959$; $p = 0.023$; $\eta_p^2 = 0.086$] and a significant interaction of prospective memory session and valence of the ongoing task stimuli [$F(3.24,136.00) = 6.004$; $p = 0.001$; $\eta_p^2 = 0.125$]. The main effect of prospective memory session approached significance [$F(1.51,63.32) = 3.466$; $p = 0.050$; $\eta_p^2 = 0.076$]. The main effects of age group and valence of the ongoing task stimuli as well as the interaction of prospective memory session and the three-way interaction did not reach significance (all $p > 0.246$).

*Post hoc* comparisons for the interaction of age group by valence of the ongoing task stimuli did not held significant at the follow-up analyses ($p_{adj} > 0.999$). For the interaction of prospective memory session by ongoing task valence, the *post hoc* comparisons showed that performance for pleasant ongoing task trials was slightly higher compared to neutral ongoing task trials ($p_{adj} = 0.025$) in the neutral prospective memory session (for all other comparisons $p_{adj} > 0.096$). Performance of pleasant ongoing task trials was better than for unpleasant ongoing task trials in the pleasant prospective memory session ($p_{adj} = 0.038$; for all other comparisons $p_{adj} > 0.674$). However, there were no differences in the unpleasant prospective memory session between the valence levels of the ongoing task trials (all $p_{adj} > 0.068$).

In a second step, we analyzed the ANOVA of the reaction times for correct ongoing task trials including the factors age group, valence of the prospective memory session, and valence of the ongoing task stimuli. The ANOVA revealed significant main effects of age group [$F(1,42) = 9.416$; $p = 0.004$; $\eta_p^2 = 0.183$] and valence of the ongoing task stimuli [$F(2,84) = 33.441$; $p < 0.001$; $\eta_p^2 = 0.443$] as well as significant interaction of valence of the prospective memory session by valence of the ongoing task stimuli [$F(4,168) = 29.548$; $p < 0.001$; $\eta_p^2 = 0.413$] and a significant three-way interaction of all three factors [$F(4,168) = 4.212$; $p = 0.003$; $\eta_p^2 = 0.091$]. All other main effects and interactions did not turn significant (all $p > 0.309$).

Older adults performed slower than younger adults ($p_{adj} = 0.004$) and participants performed overall faster for neutral ongoing task trials, intermediate for pleasant ongoing task trials, and slowest for unpleasant ongoing task trials (all $p_{adj} < 0.003$). To break down the results of the interactions, we will focus on the three-way interaction by separating the two age groups.

In the unpleasant prospective memory session, younger and older adults showed a similar reaction time pattern. Younger

**TABLE 1** | Behavioral performance rates for younger and older adults.

| | Younger adults | | | Older adults | | |
|---|---|---|---|---|---|---|
| | Valence of the pictures | | | Valence of the pictures | | |
| | **Unpleasant** | **Neutral** | **Pleasant** | **Unpleasant** | **Neutral** | **Pleasant** |
| **OT** | | | | | | |
| Accuracy *(SD)* | | | | | | |
| PM session | | | | | | |
| Unpleasant | 0.94 (0.13) | 0.92 (0.15) | 0.91 (0.15) | 0.93 (0.11) | 0.93 (0.09) | 0.92 (0.08) |
| Neutral | 0.93 (0.08) | 0.93 (0.09) | 0.93 (0.12) | 0.96 (0.02) | 0.96 (0.03) | 0.98 (0.03) |
| Pleasant | 0.96 (0.03) | 0.95 (0.04) | 0.96 (0.04) | 0.94 (0.05) | 0.96 (0.05) | 0.96 (0.05) |
| Reaction time *(SD)* | | | | | | |
| PM session | | | | | | |
| Unpleasant | 769 (184) | 725 (159) | 743 (165) | 932 (184) | 846 (144) | 872 (163) |
| Neutral | 747 (166) | 735 (169) | 734 (163) | 879 (118) | 880 (118) | 851 (114) |
| Pleasant | 760 (164) | 725 (164) | 777 (185) | 868 (120) | 828 (118) | 898 (130) |
| **PM cues** | | | | | | |
| Accuracy *(SD)* | 0.87 (0.15) | 0.86 (0.17) | 0.83 (0.18) | 0.76 (0.30) | 0.86 (0.22) | 0.82 (0.17) |
| Reaction time *(SD)* | 442 (109) | 452 (112) | 454 (104) | 472 (150) | 505 (117) | 520 (142) |
| **Recognition task** | | | | | | |
| Accuracy *(SD)* | | | | | | |
| PM trials | 0.74 (0.21) | 0.70 (0.24) | 0.69 (0.25) | 0.64 (0.28) | 0.72 (0.24) | 0.64 (0.24) |
| OT trials | 0.88 (0.20) | 0.92 (0.18) | 0.90 (0.17) | 0.88 (0.11) | 0.90 (0.09) | 0.92 (0.13) |
| Reaction time *(SD)* | | | | | | |
| PM trials | 942 (129) | 949 (147) | 982 (158) | 1077 (182) | 991 (138) | 992 (268) |
| OT trials | 856 (121) | 845 (106) | 851 (124) | 912 (95) | 878 (101) | 945 (128) |

*OT, ongoing task; PM, prospective memory task; SD, standard deviation; Reaction time in ms.*

adults were fastest for neutral ongoing task trials, intermediate for pleasant ongoing task trials, and slowest for unpleasant ongoing task trials (neutral–pleasant: $p_{adj} = 0.050$; neutral–unpleasant: $p_{adj} = 0.001$; and pleasant–unpleasant: $p_{adj} = 0.026$). Older adults were fastest for the neutral ongoing task trials but reaction times did not differ from pleasant ongoing task trials, and they performed the slowest for the unpleasant ongoing task trials (neutral–pleasant: $p_{adj} = 0.177$; neutral–unpleasant: $p_{adj} = 0.002$; and pleasant–unpleasant: $p_{adj} < 0.001$).

In the neutral prospective memory session, younger adults did not show reaction time differences between the three valence levels of the ongoing task trials (all $p_{adj} > 0.255$). Older adults performed faster for pleasant ongoing task trials than unpleasant trials ($p_{adj} = 0.013$), but there were no differences toward the neutral ongoing task trials (all $p_{adj} > 0.065$).

Finally, in the pleasant prospective memory session, both age groups performed faster for neutral ongoing task trials compared to the emotional trials (all $p_{adj} < 0.001$). Additionally, older adults performed faster on unpleasant trials compared to pleasant trials ($p_{adj} = 0.001$), whereas younger adults did not show that difference ($p_{adj} = 0.108$).

### Recognition Task

For the recognition task, we conducted a mixed ANOVA including the factors age group (two: younger adults and older adults), task type (two: prospective memory cues and ongoing task trials), and valence of the stimuli (three: pleasant, neutral, and unpleasant). The ANOVA for the accuracy rates showed only a significant main effect of task type [$F(1,42) = 33.239$; $p < 0.001$; $\eta_p^2 = 0.442$] but no other effect or interaction turned significant (all $p > 0.134$). Performance rates were better for the ongoing task trials than the prospective memory trials.

We conducted a second ANOVA with the same factors for the reaction times. The ANOVA resulted in a significant main effect of age group [$F(1,41) = 4.376$; $p = 0.043$; $\eta_p^2 = 0.096$] and a significant main effect of task type [$F(1,41) = 38.833$; $p < 0.001$; $\eta_p^2 = 0.486$]; however, no other effect turned significant (all $p > 0.133$). Younger adults performed faster than older adults. Performance rates were faster for ongoing task trials than prospective memory trials.

## Electrophysiological Results

### Encoding Phase

The first PLS analysis (*encoding phase*) involved ERPs elicited by unpleasant, neutral, and pleasant pictures in the encoding phase. **Figure 1** depicts the results of the PLS analysis for the encoding phase. The analysis showed two significant LVs ($p < 0.001$ and $p < 0.035$), which, respectively, accounted for 59.02 and 26.50% of the cross-block covariance. The LV1 captured a contrast between emotional pictures (both unpleasant and pleasant) and neutral pictures, in both younger and older adults (**Figure 1A** depicts the design scores and ERP saliences). The finding replicated the results from Cona et al. (2015a) and extended them to older adults. The LV1 reflected a sustained

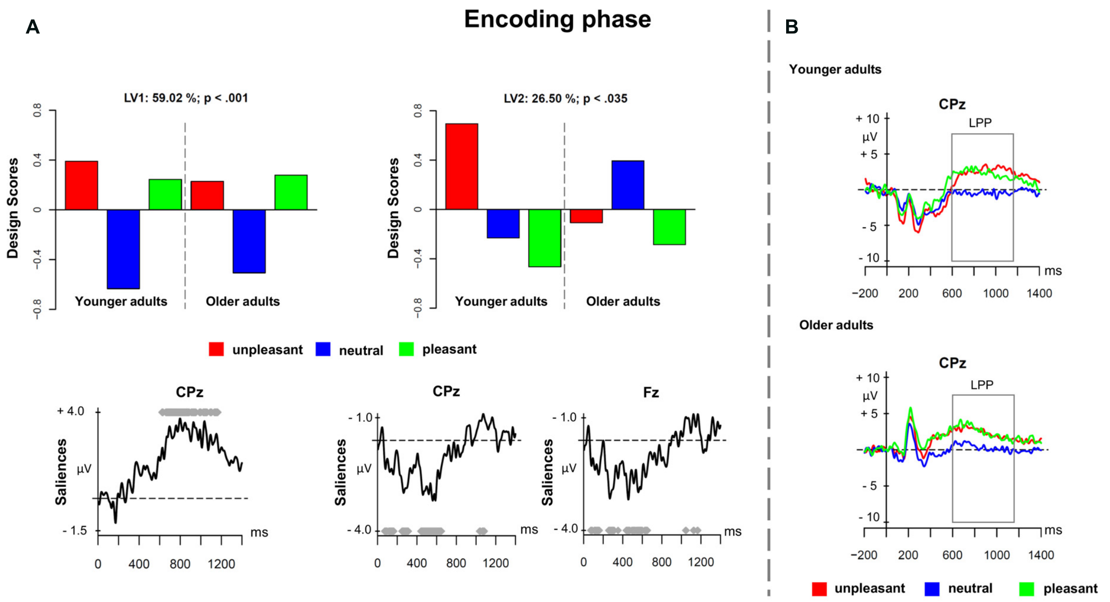

**FIGURE 1 |** Partial least square (PLS) results and grand averages for the encoding phase. **(A)** Design scores and event-related potential (ERP) saliences for the comparison of the three valence conditions of the prospective memory cues separately for younger and older adults. **(B)** Grand-averaged ERPs for younger and older adults at electrode CPz.

positivity associated with emotional stimuli over parietal and centro-parietal electrodes in the time window roughly between 600 and 1200 ms after stimulus onset representing the LPP (**Figure 1B** depicts the ERPs for younger and older adults at electrode CPz). Younger and older adults seemed to recruit more attentional resources for pleasant and unpleasant cues compared to neutral cues expressed in the increased LPP component for emotional material.

The LV2 showed age-related differences in ERPs for the encoding of emotional versus neutral prospective memory cues. **Figure 1A** depicts the design scores and displays age-related differences. In younger adults, the unpleasant prospective memory cues differed substantially compared to both neutral and pleasant cues, suggesting the presence of a negative bias. However, in older adults, there was no such difference present. Regarding the spatial distribution, the modulations associated with the LV2 were widespread over the scalp, involving both earlier and later ERP components. More precisely, emotional stimuli led to enhanced amplitudes in the negative components that occurred in the time windows between 100–180 ms (i.e., N1), 250–350 ms (i.e., N2), and 420–600 ms (i.e., N3). The negative bias – that was expressed only in younger adults – was visible as increased negativity for unpleasant prospective memory cues in the three negative components. This negative modulation could reflect the early posterior negativity (EPN), which is associated with visual processing of emotional stimuli.

## Maintenance Phase

The second PLS analysis (*maintenance phase*) was applied to the ERPs evoked by unpleasant, neutral, and pleasant ongoing task stimuli in the three prospective memory sessions (unpleasant, neutral, and pleasant) in younger and older adults. **Figure 2** shows the results of the PLS analysis for the maintenance phase, and **Figure 3** depicts the ERPs for both age groups and the three different prospective memory sessions.

Three LVs were found to be significant (all *ps* < 0.01). The LV1 accounted for 44.10% of the cross-block covariance and reflected, in younger adults, a difference between monitoring for the presence of unpleasant versus pleasant prospective memory cues. Regardless of the valence of the ongoing stimuli, monitoring for pleasant prospective memory cues led to an increased sustained positivity over frontal and fronto-central regions roughly between 400 and 1000 ms. This frontal and fronto-central slow wave could represent two overlapping components: long-lasting sustained activity associated with strategic monitoring and the LPP. The long-lasting activity that seemed to be associated with strategic monitoring processes might indeed reflect a retrieval mode (Guynn, 2003), which is a process necessary to actively maintain the intention in memory (West, 2011; Cona et al., 2012a,b; Czernochowski et al., 2012). The LPP component could reflect top-down processing and the allocation of attentional resources toward the emotional material, specifically, pleasant material (cf. Hajcak et al., 2006).

The pattern observed for older adults was less clear. The ERP modulations associated with maintaining the pleasant prospective memory cues in older adults were captured by the LV3. For this reason, we decided to present LV3 first before describing the LV2.

As displayed by **Figure 2**, the LV3 accounted for 11.32% of the cross-block covariance and captured, in older adults, a contrast between the pleasant prospective memory session and

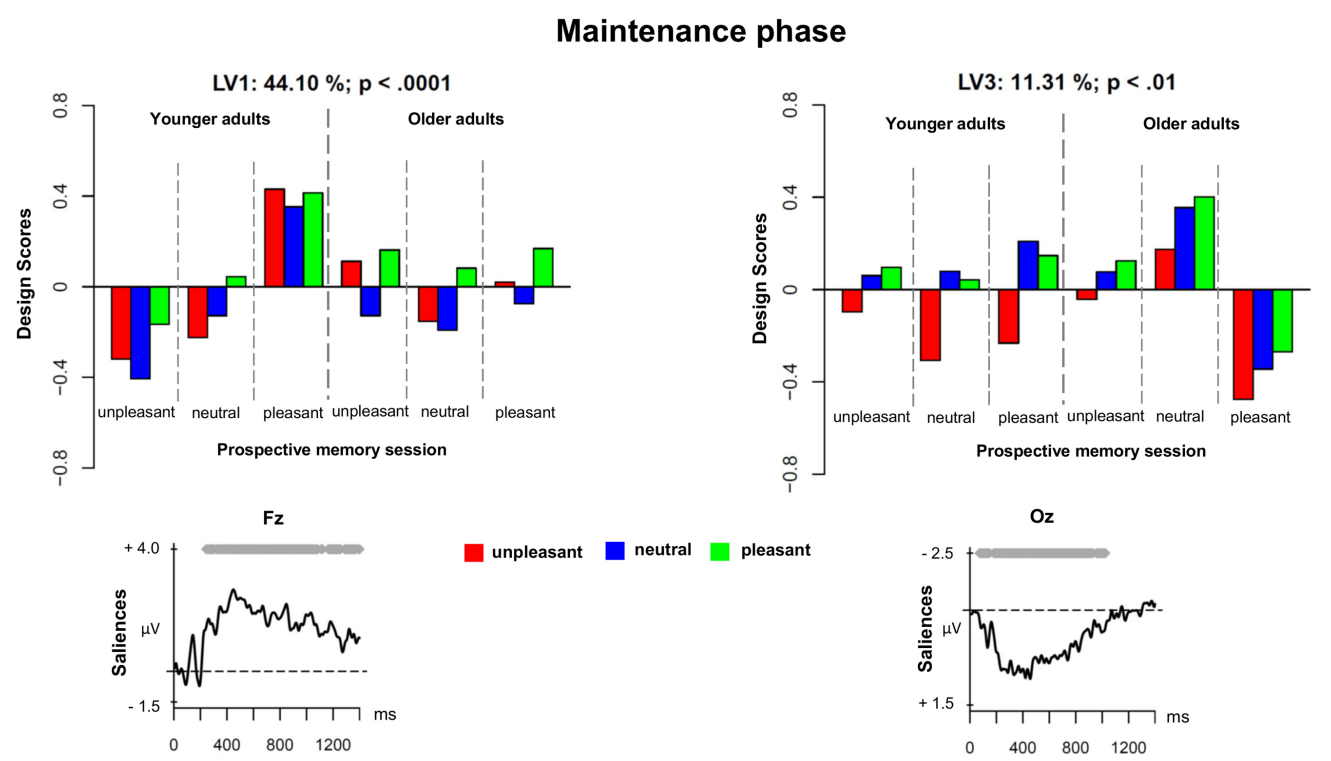

**FIGURE 2 |** Design scores and ERP saliences for the comparison of the three prospective memory sessions and three levels of ongoing task trials during the maintenance phase separately for younger and older adults.

the unpleasant prospective memory session, independently of the valence of the ongoing task stimuli. When comparing the ERP salience maps captured by LV1 and LV3, it was evident that there was a differential effect for maintaining pleasant prospective memory cues in younger compared to older adults. In younger adults, the ERP correlates of this process were expressed in late windows in a small region over frontal and fronto-central sites that likely represented the LPP. In older adults, the maintenance of pleasant prospective memory cues was associated with a very widespread sustained modulation over posterior and occipital sites that started from 150 ms and lasted until 1000 ms (see **Figure 3** for the ERPs in younger and older adults separately). This slow-wave activity in older adults suggests a positivity bias for the maintenance of pleasant prospective memory cues in older adults, which occured already in the early stages of processing as it is evidenced already in the earlier components.

Interestingly, in younger adults, the LV3 captured ERPs that were associated with unpleasant ongoing task stimuli, regardless of the prospective memory session. This corroborates the results evidenced in the analysis of the encoding phase, highlighting a negative bias selectively for younger adults.

We decided to not describe and discuss the LV2 in detail given that the pattern of the design scores is less clear and LV2 is only expressed in a late time window (after 1200 ms). However, with caution, this LV could reflect the presence of a negative bias for younger adults.

## Retrieval Phase

The third PLS analysis (*retrieval phase*) was performed on the ERPs elicited by the prospective memory cues and by the ongoing task stimuli with the same emotional valence of the PM cues in a given session, in younger and older adults. **Figure 4A** depicts the PLS results for the retrieval phase and **Figure 4B** shows the associated ERPs in younger and older adults. This analysis revealed a significant LV1 ($p < 0.0001$) that accounted for 58.13% of the cross-block covariance. LV1 reflected a contrast between prospective memory cues and ongoing task stimuli, revealing that such difference was more expressed in older than younger adults, and especially for pleasant pictures.

The LV1 captured an increased positivity for prospective memory cues, particularly pronounced over frontal regions, in the time window between 400 and 800 ms suggesting a frontal positivity, and a slow-wave negativity at 1000 ms, widely expressed over the scalp. Over parieto-occipital and occipital sites, a transient negativity occurred between 430 and 550 ms that characterized the prospective memory cues and may reflect the N300. These components were more expressed in older than younger adults. The N300 and the frontal positivity are correlates of prospective memory cue detection. The results suggest that older adults showed a positivity bias to detect the pleasant prospective memory cues (N300) and to switch from the ongoing task to the intention (frontal positivity). The late negative slow-wave activity suggests the presence of the parietal positivity

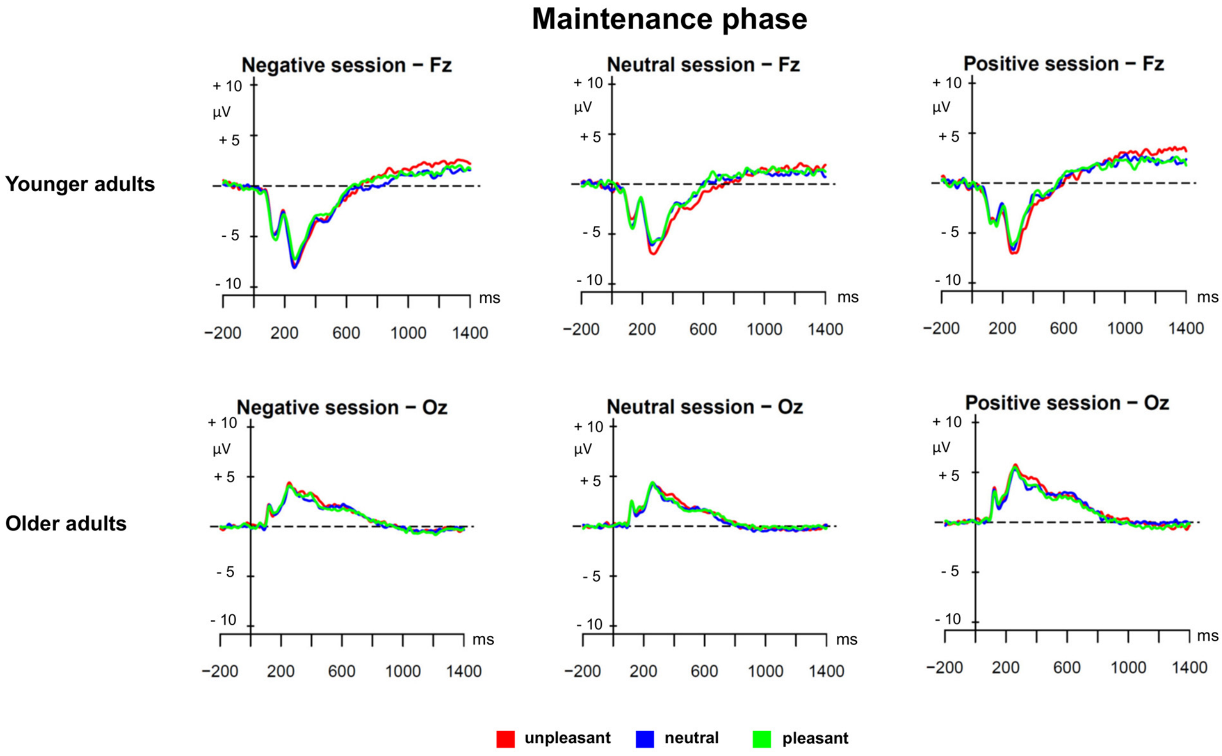

**FIGURE 3 |** Grand averages for the maintenance phase separately for younger and older adults and the three prospective memory sessions.

and could be associated with task set coordination between the intention execution and the ongoing task.

## Recognition Task

The fourth PLS analysis (*recognition task*) included the ERPs elicited by prospective memory cues and ongoing task stimuli in the recognition task, for younger and older adults. **Figure 5** shows the results for the PLS analysis on the recognition task. The analysis showed two significant LVs ($p < 0.001$ and $p < 0.004$) that accounted for 45.38 and 18.06% of the cross-block covariance, respectively. As similarly found in the study by Cona et al. (2015a), LV1 distinguished the unpleasant recognized PM cues from the other conditions (**Figure 5A**). The difference in the magnitude of the design scores suggests that such difference was mainly expressed in younger than older adults. The modulation represented an increased sustained positivity for the unpleasant prospective memory cues in the time window between 500 and 900 ms suggesting a negativity bias in memorizing unpleasant material. This component was widely expressed over the scalp, and might likely be the result of the overlap between the recognition old–new effect and the LPP (**Figure 5B**).

LV2 distinguished the recognized prospective memory cues from the recognized ongoing task stimuli in both age groups (**Figure 5A**). LV2 captured a latency difference in the slow-wave positivity occurring between 500 and 1000 ms over frontal and parietal regions, which might be the result of distinct overlapping components, such as the P3b that might reflect a higher amount of attentional resources allocated for the prospective memory cues, and the parietal old–new effect, that is mainly associated with strategic recognition processes (West and Wymbs, 2004; West, 2011). Prospective memory cues seemed indeed to elicit a delayed sustained positivity compared to the ongoing stimuli, in line with the behavioral results. The differences in the encoding of the two stimuli groups might account for that difference and the sustained activity for the prospective memory stimuli.

# DISCUSSION

The aim of the present study was to investigate the influence of emotional material on prospective memory in younger and older adults. We used an established prospective memory task (Cona et al., 2015a) that manipulated the emotional valence of the prospective memory cues and the ongoing task. Participants had to encode either pleasant, neutral, or unpleasant prospective memory cues before they worked on a picture one-back ongoing task with pleasant, neutral, and unpleasant pictures. Previous studies indicated that older adults might benefit from emotional cues reducing or even eliminating age differences (e.g., Altgassen et al., 2010; Schnitzspahn et al., 2012). Here, it had been suggested that emotional prospective memory cues serve as highly distinct or salient cues which lead to spontaneous retrieval. Spontaneous retrieval is less resource demanding and usually intact in older adults. Alternatively, emotional cues could increase the importance of detecting the cues, and thus, enhance more strategic monitoring, that is resource demanding and decreased

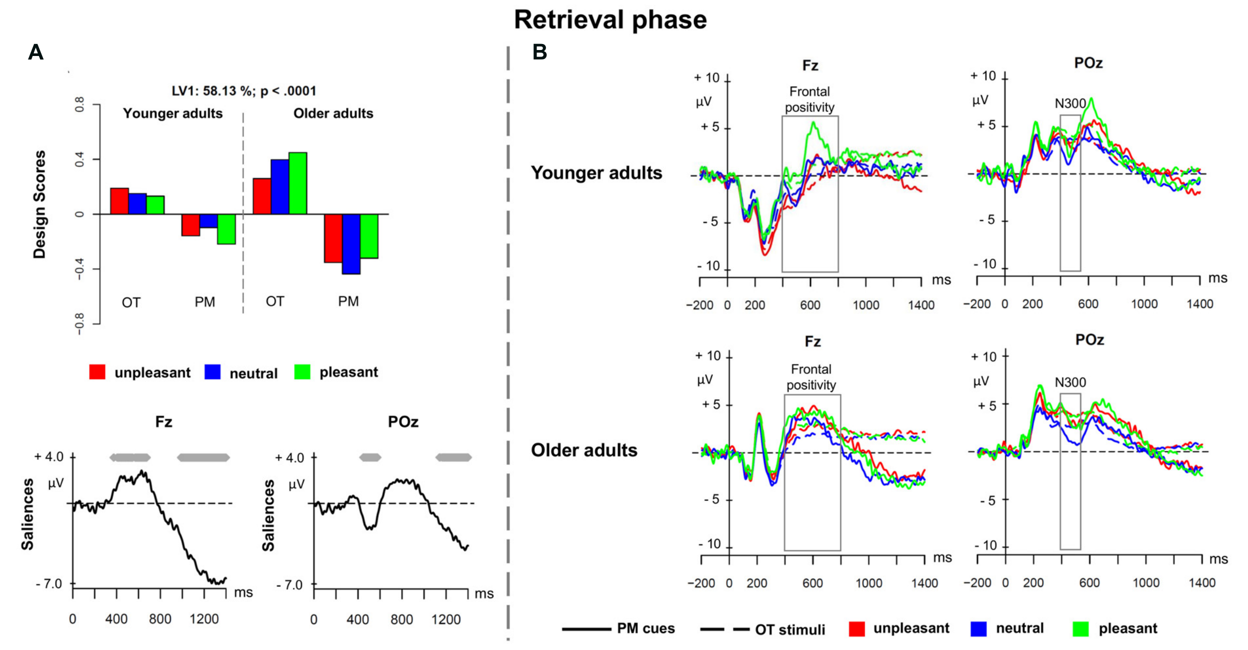

**FIGURE 4 |** Partial least square results and grand averages for the retrieval phase. **(A)** Design scores and ERP saliences for the comparison of the three valence conditions of the prospective memory cues and the corresponding ongoing task trials separately for younger and older adults. **(B)** Grand-averaged ERPs for younger and older adults at electrodes Fz and POz comparing prospective memory cues with ongoing task stimuli at the three valence conditions. PM, prospective memory; OT, ongoing task.

in older adults. To follow up on this debate, we assessed not only behavioral performance but also included electrophysiological measures to uncover the underlying mechanism.

## Behavioral Results

Contrary to our assumption, the behavioral analyses showed no age differences for the prospective memory performance. Younger and older adults performed at similar rates when they had to respond to the prospective memory cues. Furthermore, there were also no performance differences between the three valence conditions. The lack of an age difference was somewhat surprising as it is well established in the literature that prospective memory declines with increasing age (e.g., Ihle et al., 2013). We had assumed that age differences should be small or even eliminated for the emotional conditions, but it was also the case for the neutral condition that resembles a standard prospective memory task. Similar to our results, Cona et al. (2015a) did not find differences between the three valence conditions on prospective memory accuracy in younger adults. They argued that the task was not too demanding for younger adults. Indeed, the task is a so-called focal prospective memory task. Focality is a task property that stimulates either spontaneous retrieval or strategic monitoring depending on the specification (McDaniel and Einstein, 2000). A task is considered as focal, when the detection of prospective memory cue and the ongoing task share the same processes; thus, the retrieval should occur rather spontaneous as the prospective memory cue is processed directly along with the ongoing task. In the present task, participants had to work on a picture one-back task, so they had to process the pictures that also served as prospective memory cues. It is assumed that age differences are reduced under focal conditions (Kliegel et al., 2008b; Ihle et al., 2013).

The findings from the ongoing task revealed more about the influence of the emotional material on performance. Again, we did not find age differences for the ongoing task accuracy. The task itself was not too demanding. It was desirable to use an ongoing task that is equally demanding for both age groups to better compare the underlying mechanisms. For both age groups, performance for pleasant trials was higher than for neutral and unpleasant trials in the neutral and pleasant prospective memory session. The finding indicates a positivity bias that is usually found in older adults. The positivity bias describes the finding that older adults show a processing bias toward positive information (e.g., Mather and Carstensen, 2005). The reaction time data also support this conclusion. In general, older adults showed a slowing in their response times compared to younger adults, which is a widely confirmed finding (e.g., Salthouse, 1996). However, older adults performed faster for pleasant trials than unpleasant or neutral trials in the condition with neutral prospective memory cues, whereas younger adults did not differ between the three valence conditions of the ongoing task. Similar to the results from Cona et al. (2015a), the younger and older adults showed an SSIE (Cohen et al., 2012). Both age groups showed the highest reaction times for unpleasant ongoing task trials when they had to keep in mind unpleasant prospective memory cues. The SSIE indicates that both age groups increased attentional resources for target checking that is a monitoring process where incoming stimuli were evaluated of being a

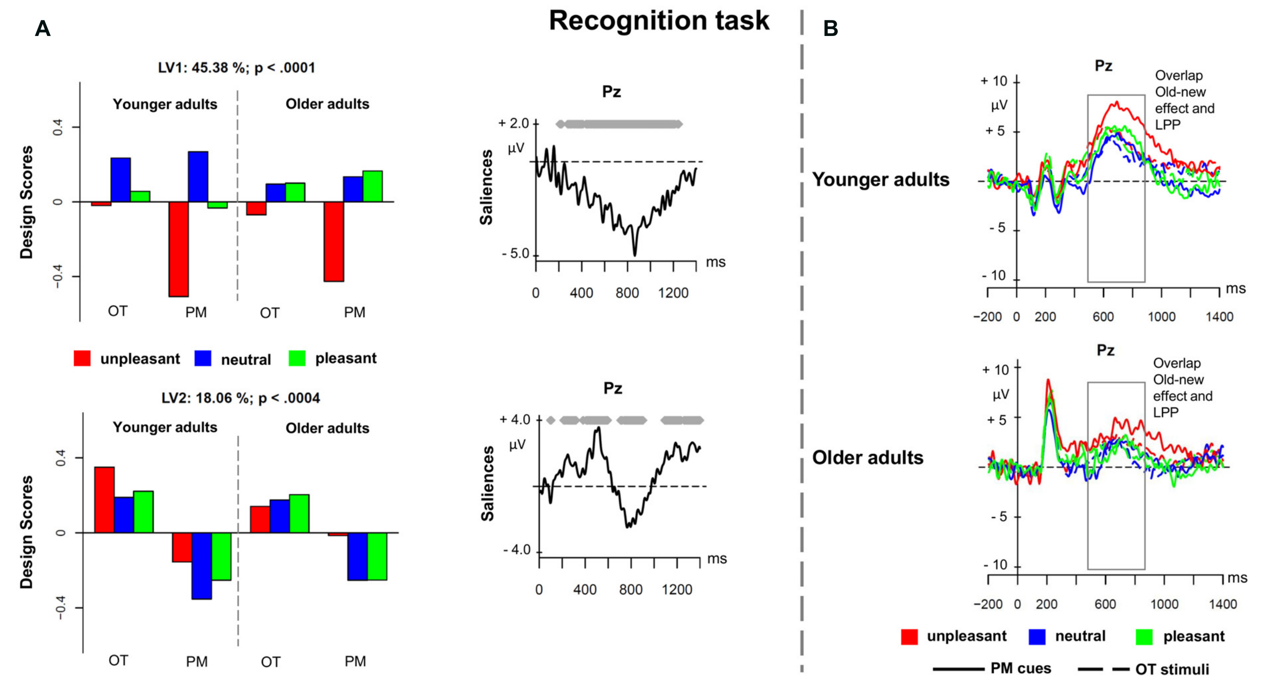

**FIGURE 5 |** Partial least square results and grand averages for the recognition task. **(A)** Design scores and ERP saliences for the comparison of the three valence conditions of the prospective memory cues and the ongoing task trials separately for younger and older adults. **(B)** Grand-averaged ERPs for younger and older adults at electrode Pz comparing prospective memory cues with ongoing task stimuli at the three valence conditions. PM, prospective memory; OT, ongoing task.

prospective memory cue or not (Guynn, 2003). Target checking is an indication for strategic monitoring. Additionally, older adults showed an SSIE effect for pleasant cues and ongoing trials as well, whereas the effect did not occur in younger adults indicating again toward a positivity bias in older adults. In contrast to Cona et al. (2015a), we could not follow up on the findings regarding the recognition task. We only found an advantage for the ongoing task stimuli.

In conclusion, the behavioral findings do not yet allow answering our research question regarding the modulating role of emotional material on prospective remembering. They are partly in line with the beneficial effects reported by Altgassen et al. (2010), who did also not find age differences between younger and older adults in a prospective memory task with emotional cues.

Besides the behavioral measures, we recorded the ERPs to receive a better understanding of the neural modulations that might occur due to the influence of emotional material. The ERP analyses were especially helpful to explore the underlying mechanisms of the different phases of prospective remembering and allowed for differentiated investigation of encoding, maintaining, and retrieving intentions.

## Electrophysiological Results

The first phase of prospective remembering refers to the encoding of the prospective memory cue. Encoding *per se* is usually not assessed as behavioral response; therefore, the ERP results offer important insights. We found evidence for an LPP that was specific to pleasant and unpleasant prospective memory cues but not for neutral cues. The LPP is associated with sustained attention for emotional material indicating that both age groups showed comparable encoding effort for the pleasant and unpleasant cues. Moreover, younger and older adults showed enhanced encoding for the emotional prospective memory cues suggesting that emotional material is processed as a priority not only in younger adults (Dolcos and Cabeza, 2002), but also in older adults.

Interestingly, there was also evidence for age-related differences during encoding. Younger adults showed increased negative activity for unpleasant cues (but not pleasant or neutral cues) in three different time windows widespread over the scalp, whereas older adults did not show differences between the three valence conditions. It could reflect the EPN that is associated with visual processing of stimuli (e.g., Schupp et al., 2003a,b, 2004). The EPN is also sensitive to the arousal of the stimulus material (Olofsson et al., 2008), which might indicate that this negative bias in the younger adults might be linked to the arousing nature of the unpleasant stimuli. This negativity bias in younger adults might reflect an evolutionary bias toward threating stimuli (Öhman and Mineka, 2001).

Regarding the next phase, the maintenance phase, the results showed two interesting findings. In younger adults, we found evidence for increased monitoring for pleasant prospective memory cues independent of the valence of the ongoing task indicated by a frontal-central distributed sustained positivity. Similarly, West (2011) and Cona et al. (2012b) reported sustained positive activity when participants have to hold in mind an intention indicating a retrieval mode (Guynn, 2003). The retrieval mode describes a general state of readiness that the prospective memory cue will arrive. In older adults, the sustained activation associated with monitoring for pleasant cues occurred over posterior and occipital sites. However, it is to note that the EEG has only a poor spatial resolution and we included only 32 electrodes, and therefore, conclusions on the spatial origins of the effects have to be considered with caution. Nevertheless, the finding is in line with our behavioral result, where older adults showed an SSIE for pleasant prospective memory cues and ongoing task trials indicating monitoring for pleasant cues in older adults. Furthermore, we also found an LV specific for unpleasant ongoing trials in younger adults that could reflect the LPP indicating again the negativity bias in younger adults with enhanced monitoring for the unpleasant prospective memory cues.

Interestingly, the findings for the maintenance phase indicate that emotionally valenced cues augment strategic monitoring in both younger and older adults. Contrary to the conclusions by Altgassen et al. (2010), our findings indicate that the detection of emotional cues does not only rely on spontaneous processing but also on more strategic monitoring for the emotional prospective memory cues, which is supported by the allocation of attentional resources toward the emotional cues (Olofsson et al., 2008). The present findings are in line with the theoretical account of cognitive control in aging that postulates two types of cognitive control: proactive control and reactive control (Braver et al., 2001; Braver and West, 2008; Braver, 2012). Intentional behavior can either be driven top-down by proactive control that is a state of anticipation that cognitive control is necessary similar to strategic monitoring; or goal-directed behavior can be driven bottom-up by reactive control that is the activation of cognitive control whenever it is necessary or triggered by external stimuli similar to spontaneous processing. The specificity toward pleasant prospective memory cues might indicate some selective proactive control processes that might be triggered top-down by motivational influences (Braver, 2012).

Regarding the retrieval phase, we found prospective memory specific ERPs that differed from the ongoing task trials. More interestingly, the ERPs were more expressed in older adults, and especially for pleasant prospective memory cues. There was transient negativity in the time window of 430–550 ms, which reflects the N300 and is associated to cue detection. There was also an increased positivity over frontal regions that might reflect the frontal positivity. Finally, there was a later negative slow wave over parieto-occipital sites that might belong to the parietal positivity complex and seems to be related to the coordination between the ongoing task and the prospective memory task (Bisiacchi et al., 2009). Interestingly, these effects were more expressed in the older adults' group than in the younger adults. Previous research on non-emotional material found rather attenuated activity in older adults compared to younger adults (West et al., 2002). Importantly, the effects were mainly captured for pleasant cues indicating the positivity bias in older adults that is widely found for the influence of emotional material on attention and memory (Reed and Carstensen, 2012; Reed et al., 2014). It suggests that at the retrieval phase, there seems to be rather automatic capture of attention toward the pleasant cues that facilitates cue detection and retrieval. The elevated activity in the older adults might be an expression of reactive control in this age group triggered by the pleasant (positively biased) prospective memory cues indicating spontaneous retrieval processes (Altgassen et al., 2010).The advantage for pleasant cues compared to neutral and unpleasant cues in the older adults' group follows up on the finding that neural reactivity toward negative material decreases with increasing age during adulthood (Kisley et al., 2007). The authors investigated the shift from the negativity bias toward the positivity bias in the adulthood lifespan and could show that the negativity bias decreases with increasing age in neural responsivity. The authors found a negative correlation between age and the amplitude of the LPP for unpleasant material but not for neutral and pleasant material. The authors explained their finding with the socioemotional selectivity theory and the proposed shift toward positive information in old adulthood.

Finally, the ERP analysis for the recognition task revealed a negativity bias for the unpleasant prospective memory cues in the younger adults. Although we did not obtain a significant effect, descriptively the behavioral results for the accuracy rates in prospective memory cues tended in the same direction similarly to the results obtained by Cona et al. (2015a). More precisely, this ERP might reflect the recognition old-new effect for prospective memory cues overlapping with the LPP for unpleasant material. Interestingly, the behaviorally delayed response rates for the prospective memory cues were also captured by a delayed sustained positivity.

## Limitations and Outlook

There are some limitations to consider when interpreting the present results. We did not obtain an age effect for the prospective memory performance or the ongoing task performance, which contradicts the literature on age effects in prospective memory. One reason, that was already discussed earlier, might have been the rather easy one-back task as ongoing activity. However, it allowed for having comparable performance rates to investigate age specific effects on the ERP activity. The earlier described decreased activity that is often observed in older adults might also result from increased task demands in the other studies. The performance rates for the prospective memory task, however, suggest that ceiling effects did not drive our results.

The observed spatial differences in ERPs between younger and older adults need further exploration. The EEG is not the appropriate method to investigate spatial sources for the effects although there exists a useful algorithm for source localization (for a review, see Michel et al., 2004). Future studies should also address the role of strategic monitoring during the intention maintenance phase. So far, prospective memory research focused mainly on the retrieval or the encoding phase, mainly because behavioral measures can only be collected for overt behavior. However, using electrophysiological measures, it would be possible to map the neural underpinnings of strategic monitoring during a prospective memory task. Our findings and those by others (West et al., 2011; Cona et al., 2012b) offer first indications for a retrieval mode during the maintenance phase and increased monitoring (e.g., expressed by the sustained positive activity).

## CONCLUSION

Taken together, the present results suggested that prospective memory performance and the underlying neural processing can be modulated by emotional material. Furthermore, by looking at the entire process of prospective remembering including encoding, maintaining, and retrieving of intentions, we could identify differential mechanisms in younger and older adults. More importantly, our results have conceptual implications for the understanding of emotional influences on prospective memory. Our results showed that emotional material fosters strategic monitoring during the maintenance phase and spontaneous processing during the retrieval phase in both age groups. Contradictory to our assumption, monitoring activity was not reduced in older adults. More importantly, the emotional cues seemed to show enhanced processing and a benefit in attention allocation toward the emotional cues. The present findings suggest that emotional cues indeed boost the relevance of the cues, and thus foster attentional monitoring. On the other side, the increased activity during retrieval in older adults supports the notion that emotionally valenced cues increase their distinctiveness, and thus, support the rather spontaneous detection and retrieval (McDaniel and Einstein, 2000; Altgassen et al., 2010). These conclusions are in line with the attention-to-delayed-intention model by Cona et al. (2015b) that provides a theoretical account for the neuroanatomical foundation of prospective remembering including the prefrontal cortex and the mediotemporal lobe and the integration of strategic monitoring and spontaneous retrieval.

Furthermore, our results showed age-related differences in the neural reactivity toward pleasant and unpleasant prospective memory cues. Our findings are in line with the theoretical account of a shift from a negativity bias in younger adults toward a positivity bias in older adults (Carstensen, 2006; Carstensen and DeLiema, 2018). Although our study only investigated cross-sectional data by comparing younger and older adults, the electrophysiological findings suggested a bias in younger adults toward the unpleasant pictures and a preference for the pleasant images in older adults.

In sum, our findings suggest evidence for both assumptions on how emotional material might influence prospective remembering in older adults and even overcoming age differences. However, the role of top-down and bottom-up processing differs with respect to the specific phase of prospective remembering and the emotional valence of the prospective memory cues.

## ETHICS STATEMENT

This study was carried out in accordance with the recommendations of ethical guidelines of the Ethics Committee of the Faculty of Psychology and Educational Sciences of the University of Geneva. All subjects gave written informed consent in accordance with the Declaration of Helsinki. The protocol was approved by the Ethics Committee of the Faculty of Psychology and Educational Sciences of the University of Geneva.

## AUTHOR CONTRIBUTIONS

AH, MK, PB, and GC designed the study. AH and MK collected the data. AH analyzed the behavioral data. GC analyzed the electrophysiological data with the help of AH. AH and GC wrote the paper with edits from MK and PB.

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REVIEW
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# The Influence of Different Kinds of Incentives on Decision-Making and Cognitive Control in Adolescent Development: A Review of Behavioral and Neuroscientific Studies

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A number of recent hypothetical models on adolescent development take a dual-systems perspective and propose an imbalance in the maturation of neural systems underlying reward-driven and control-related behavior. In particular, such models suggest that the relative dominance of the early emerging subcortical reward system over the later emerging prefrontal-guided control system leads to higher risk-taking and sensation-seeking behavior in mid-adolescents. Here, we will review recent empirical evidence from behavioral and neuroscientific studies examining interactions between these systems and showing that empirical evidence in support for the view of a higher sensitivity to rewards in mid-adolescents is rather mixed. One possible explanation for this may be the use of different kinds and amounts of incentives across studies. We will therefore include developmental studies comparing the differential influence of primary and secondary incentives, as well as those investigating within the class of secondary incentives the effects of monetary, cognitive, or social incentives. We hypothesized that the value of receiving sweets or sours, winning or losing small or large amounts of money, and being accepted or rejected from a peer group may also changes across development, and thereby might modulate age differences in decision-making and cognitive control. Our review revealed that although developmental studies directly comparing different kinds of incentives are rather scarce, results of various studies rather consistently showed only minor age differences in the impact of incentives on the behavioral level. In tendency, adolescents were more sensitive to higher amounts of incentives and larger uncertainty of receiving them, as well as to social incentives such as the presence of peers observing them. Electrophysiological studies showed that processing efficiency was enhanced during anticipation of incentives and receiving them, irrespective of incentive type. Again, we found no strong evidence for interactions with age across studies. Finally, functional brain imaging studies revealed evidence for overlapping brain regions activated during processing of primary and secondary incentives, as well as social and non-social incentives. Adolescents recruited similar reward-related and control-related brain regions as adults did, but to a different degree. Implications for future research will be discussed.

**Keywords: adolescence, incentive type, decision-making, cognitive control, social-emotional system**

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## INTRODUCTION

The development throughout adolescence has received an immense scientific interest in the past decades. Researchers from various disciplines have investigated the typical and atypical development in this period of the lifespan to describe and understand biological, social-emotional, cognitive control, and neurological changes. As a transition phase between childhood and adulthood, adolescence has been considered as a sensitive period with heightened vulnerability and demands for adjustment in behavior (Steinberg, 2005; Crone and Dahl, 2012) and sociocultural processing (e.g., Blakemore and Mills, 2014). A number of significant developmental tasks have to be mastered, such as becoming independent from parents, dealing with dramatic hormonal and physical changes, finding a peer group and close interpersonal relationships, and regulating emotions and feelings. If adolescents fail to solve such developmental tasks, their higher vulnerability may result in major problems of behavioral regulation expressed in delinquent behavior, abnormal substance use, such as binge drinking and drug use, and risky behavior, such as reckless driving, as well as in emotional dysfunctions, such as developing depressions and eating disorders. Scientists and also politicians became sensitive to these problems, as adolescents have a four time higher risk of death as a consequence of accidents, injuries, or suicide than children or adults (cf. Eaton et al., 2008).

Evidence from developmental neuroscience about the interplay between emotional/motivational and cognitive development and brain maturation has strongly inspired new ideas and hypothetical models about changes in brain structure and function and their relation to behavior throughout adolescence. To date, quite a number of comprehensive and excellent reviews addressing this interplay, already exist in the literature (Yurgelun-Todd, 2007; Casey et al., 2008; Steinberg, 2008; Geier and Luna, 2009; Luna et al., 2010; Somerville and Casey, 2010; Somerville et al., 2010; Richards et al., 2013; Crone, 2014; Shulman et al., 2016; for a critical comment, see Van den Bos and Eppinger, 2016). Therefore, we will only briefly summarize the most prominent theoretical conceptions and then highlight the potential advantages of applying neuroscientific methods for providing empirical support of differential functions of incentives (rewards and punishments) on decision-making and cognitive control behavior. In particular, we will focus on the questions whether different kinds and amounts of incentives are processed similarly, have a similar impact on control behavior, and have the same function and importance throughout adolescence. Therefore, we will summarize recent evidence on the influence of primary incentives (e.g., food, liquids, etc.) and secondary incentives (e.g., monetary, cognitive, and social) on decision-making and cognitive control functioning. Given that empirical findings of higher risk taking and reward sensitivity in adolescents seem rather mixed, we have the working hypothesis that the type of incentive may explain the inconsistent findings in the literature. To date, it is relatively unknown whether the subjective value of incentives will change in the transition from childhood to adulthood, and if so, how this might influence current theoretical models and interpretation of research findings. Because our main interest is on developmental changes in processing incentives, we will include only studies investigating a relatively large age range around adolescence and studies comparing at least two age groups, thereby one group of children or adolescents.

## THEORETICAL VIEWS ON THE INTERPLAY BETWEEN THE DEVELOPMENT OF SOCIAL-EMOTIONAL AND COGNITIVE CONTROL PROCESSING

Researchers from the field of developmental cognitive neuroscience have suggested that a differential maturation of two brain systems associated with socio-emotional and cognitive control processes can explain the higher reward sensitivity, impulsivity, and risk-taking behavior in adolescence. These so-called dual-system models propose that the social-emotional system including the striatum, medial and orbital prefrontal cortices matures earlier than the cognitive control system including the lateral prefrontal, lateral parietal, and anterior cingulate cortices. According to these models, risk-taking behavior is primarily increased in mid-adolescence as the socio-emotional system is highly activated by incentive-related information whereas the cognitive control system is not yet efficiently developed to regulate this bottom-up driven behavior (e.g., Casey et al., 2008; Steinberg, 2008; Luna and Wright, 2016). Although these models vary in their specific assumptions about the developmental course in these two brain systems, they all agree on a differential maturation of these two brain systems as a source of higher impulsivity, sensation seeking, and risky decision-making during adolescence (for a detailed review, Shulman et al., 2016). The triadic model is the only one that posits three interacting subsystems (Ernst and Fudge, 2009; Ernst, 2014). This model builds upon dual-system models but assumes a third brain system (mainly the amygdala) recruited for processing the intensity of emotions and avoidance behavior.

Clear empirical support in favor for the one or the other model is currently lacking. Most studies did not measure indicators reflecting the socio-emotional and cognitive control brain systems, as well as risky decision-making in common across a wider age range, which makes it difficult or impossible to test the theoretical assumptions of different dual-system models against each other. Moreover, the existing empirical evidence on whether incentives either enhance or hamper decision-making and cognitive control functioning and more so for adolescents than for both children and adults is rather inconsistent. Several reasons might explain these inconsistencies. First, studies vary a lot in the investigated age ranges and most studies only included two age groups to examine age differences (i.e., non-linear age trends cannot be determined). Second, studies also vary in the type of tasks and experimental paradigms applied to measure cognitive control processes in decision-making situations (Richards et al., 2013). Third, the impact of incentives has been investigated with different methods, ranging from questionnaires and behavioral data to neuroscientific methods [mostly, functional magnetic resonance imaging (fMRI) and electroencephalogram (EEG)]. The major advantage of neuroscientific methods here is that the influence of incentives can be observed in different phases of goal-directed behavior, such as during the anticipation/preparation, the decision/response selection, and finally during the feedback/evaluation phase. Indeed, there is already evidence that the same type of incentive can result in a hypoactivation or hyperactivation of the same brain system (e.g., the striatum) in adolescents relative to adults, depending on the processing phase (incentive anticipation or response selection; e.g., Geier and Luna, 2009). Hence, the differential functions of incentives for controlling and regulating behavior may also contribute to the inconsistent findings in the literature and need to be considered as well (cf. Richards et al., 2013). Fourth, one aspect that has been largely neglected is the role of the type and amount of incentives. Receiving 5 cents, a sweet, or a smile can have a different subjective value for individuals and the relative preference for specific incentives may change during developmental transitions. Here, we aim to review recent evidence from neuroscientific studies to answer the question of whether similar or different mechanisms and brain systems are at work when different kinds of incentives motivate behavior.

## DIFFERENTIAL FUNCTIONS OF INCENTIVES ON DECISION-MAKING AND COGNITIVE CONTROL BEHAVIOR

How goal-directed behavior is motivated is differently conceptualized across research fields in psychology (for a review, see Braver et al., 2014). For the purpose of this review, we will use the term incentive or incentive value as it is used in the reinforcement learning and cognitive neuroscience literature. Stimuli leading to a larger probability that a specific behavior will be shown more often in the future, and leading to more engagement of individuals toward approaching and consuming them, are positive reinforcers or rewards. In contrast, stimuli leading to a larger probability that a specific behavior will be shown less in the future, and leading toward avoiding them, are negative reinforcers or punishments. Primary incentives are innate, such as food, liquids, or sex, and are often used to modify behavior in animals, while secondary incentives are learned, such as monetary, cognitive, or social ones. Both primary and secondary incentives can vary in their amount, magnitude, probability of occurrence, delay, and so on. Whereas the delay of rewards is relatively well examined in infant research, researchers only recently have started to systematically investigate the effects of the amount, magnitude, and probability of incentives on the development of goal-directed behavior and decision-making (Defoe et al., 2015).

Interestingly, recent advances in cognitive neuroscience have identified different neuronal structures that are associated with incentive value coding in separate phases of goal-directed and choice behavior (for a review, Ruff and Fehr, 2014). Dopamineric neurons in the ventral tegmental area and substantia nigra are assumed to code the anticipation of rewards. The discrepancy between an anticipated value and the received outcome value during learning is also encoded in dopamineric neurons and this prediction error signal is used to update the anticipated value of stimuli to optimally learn and adapt the behavior to actual task demands. Changes in the neuronal activity of the orbitofrontal cortex (OFC) have been observed during receipt or consumption of rewards, while the anterior cingulate cortex (ACC), anterior insula and the amygdala are also activated during experiencing pain and receiving punishment. Finally, the ventromedial prefrontal cortex (vmPFC) is recruited during the decision process when anticipated values and response options need to be integrated (for details, see Ruff and Fehr, 2014). Although the types of cognitive processes and associated brain structures will vary along different experimental paradigms and task demands, we will distinguish between phases of anticipating incentives during preparation or response selection and receiving or consuming incentives during the feedback phase. This will help us to identify differential effects of the same incentives as well as similar effects of different incentives in these phases.

In sum, we will report and summarize results from developmental studies that have investigated the impact of primary and secondary incentives on decision-making (e.g., gambling tasks), on cognitive control (e.g., go-nogo tasks or anti-saccade tasks), and on learning from feedback (e.g., reinforcement learning tasks). Our aim is to examine (a) whether different kinds of incentives may have a common or a different function in different stages of motivated behavior, (b) whether the effects are age-invariant or not, and (c) whether similar brain networks are involved in incentive processing across age. Therefore, we include the main findings from behavioral, EEG, and fMRI studies that are briefly summarized in **Tables 1–3**, respectively, along with information about age ranges, type of task and incentive, and processing stage (only in **Tables 2**, **3**). Note that we include only developmental studies in these tables that at least compared two age groups or investigated a broader age range during adolescence.

## HOW DO DIFFERENT INCENTIVES INFLUENCE DECISION-MAKING AND COGNITIVE CONTROL?

### Primary Incentives

Primary incentives have mainly been applied in animal research to motivate behavioral changes and learning (cf. Schultz et al., 1997). In contrast, rather few developmental studies have investigated the impact of primary incentives on goal-directed behavior and decision-making. In comparison to secondary incentives, primary incentives can be delivered immediately, and therefore may be more valuable, motivating, and salient in children than in adolescents or adults (cf. Luking et al., 2014).

We found three studies that have examined the influence of primary rewards on decision-making (Hayden and Platt, 2009; Galván and McGlennen, 2013; Luking et al., 2014). For instance, Luking et al. (2014) were interested in whether receiving or losing candies modulates behavioral choices. Children and young adults were more likely to repeat the same choice after receiving a candy than after losing one, known as “win-stay—lose-shift”

**TABLE 1 |** Overview of behavioral studies.

| Authors | Age groups (age range in years) | Task | Incentive type | Main results |
|---|---|---|---|---|
| Galván and McGlennen, 2013 | - Adolescents (13–17)<br>- Young adults (23–35) | Passive reward-delivery task | Primary (water, sucrose, salty or no liquid in neutral option) | - No age differences in reaction to water, sucrose, salty and neutral liquid<br>- Higher positive ratings to sucrose than salty liquids in adolescents than adults on a liquid rating scale |
| Luking et al., 2014 | - Children (7–11)<br>- Young adults (22–26) | Gambling task (card guessing game) | Primary (high and low gains, 4 or 2 pieces; high and low losses, 2 or 1 pieces) | - No age differences in win-stay lose-shift strategy<br>- Children reported more overall positive feelings during the task than adults in a post-scan questionnaire |
| Grose-Fifer et al., 2014 | - Adolescents (13–17)<br>- Young adults (23–35) | Gambling task (card guessing game, reward probability 50%) | Monetary (high and low gains, 32–40 Cents; high and low losses, 6–11 Cents) | Both age groups selected high-monetary incentive cards more often than low-monetary incentive cards |
| May et al., 2004 | Children and adolescents (8–18) | Gambling task (card guessing game) | Monetary (neutral trials, no reward; gain trials, 1 Dollar; loss trials, 50 Cents) | No age differences in win-stay lose-shift strategy |
| Van Duijvenvoorde et al., 2014 | - Adolescents (10–16)<br>- Young adults (18–25) | Gambling task (slot machine task, reward probability 33 and 66%) | Monetary (passed trials, no reward; gain and loss trials, ±10 Cents) | Tendency for risky decisions was not related to age, pubertal development, or reward sensitivity |
| Ernst et al., 2005 | - Adolescents (9–17)<br>- Young adults (20–40) | Gambling task (Wheel of Fortune, reward probability 50%) | Monetary (high and low gains, 4 Dollar or 50 Cents; or reward omission) | - Both age groups more satisfied with high than low gains<br>- Adolescents reported more positive feelings than adults in gain trials in a post-scan questionnaire on incentive delivery |
| Bjork et al., 2010 | - Adolescents (12–17)<br>- Adults (22–42) | Monetary Incentive Delay (MID) Task | Monetary (neutral trials, no reward/ loss; high and low gain and loss trials, 50 Cents or 5 Dollar) | Faster responding and higher accuracy with increasing incentives irrespectively of the valence, but no age differences therein |
| Bjork et al., 2004 | - Adolescents (12–17)<br>- Adults (22–28) | Monetary Incentive Delay (MID) Task | Monetary (neutral trials, no reward/loss; high and low gain and loss trials, 20 Cents, 1 Dollar or 5 Dollar) | No effect of reward magnitude or age group on accuracy or reaction times |
| Galván et al., 2006 | - Children (7–11)<br>- Adolescents (13–17)<br>- Young adults (23–29) | Two-choice reaction time task (reward probability 100%) | Monetary (low, medium, and high number of monetary coins) | Faster reaction times to high than medium and low rewards and this effect is most pronounced in adolescents |
| Cohen et al., 2010 | - Children (8–12)<br>- Adolescents (14–19)<br>- Aduts (25–30) | Probabilistic learning task (83% predictable and random condition) | Monetary (no-reward vs. high and low gain trials, 25 or 5 Cents) | Faster responding to large than small incentives only for the adolescent group |
| Unger et al., 2014 | - Children (10–11)<br>- Mid adolescents (13–14)<br>- Late adolescents (15–17) | Reinforcement learning task (100% valid feedback) | Monetary (no-incentive vs. gain and loss trials, 37 Cents) | - Faster responding and better accuracy on win and loss trials for all age groups<br>- Faster learning for older participants but no age differences in interaction with incentives |

*(Continued)*

**TABLE 1 |** Continued

| **Authors** | **Age groups (age range in years)** | **Task** | **Incentive type** | **Main results** |
|---|---|---|---|---|
| Santesso et al., 2011 | - Adolescents (16–17)<br>- Young adults (18–29) | Gambling task (60:40% win-loss ratio) | Monetary (high and low gains and losses, 195–205 Cents or 45–55 Cents) | - Adolescents and adults do not differ in reward and punishment sensitivity in personality scales and post-experimental questionnaires<br>- Slower response times when two low or high cards were presented compared to one low and one high card |
| Van Leijenhorst et al., 2006 | - Early adolescents (9–12)<br>- Young adults (18–26) | Gambling task (cake task, high and low risk trials) | Cognitive (gain and loss trials; 1 point) | - Both age groups made better predictions under low-risk than high-risk trials and this performance difference was most pronounced in young adolescents |
| Teslovich et al., 2014 | - Adolescents (11–20)<br>- Adults (22–30) | Random Dot Motion Task | Cognitive (high and low gain trials, 5 or 1 points) | Slower responding for large rewards in the group of adolescents relative to adults, who showed slower responding to small rewards |
| Paulsen et al., 2015 | Children and adolescents (10–22) | Inhibitory control (antisaccade task) | Cognitive (no-reward vs. gain and loss trials, 5 points) | - No differences in reaction times between neutral, gain or loss condition<br>- No age differences in incentive processing |
| Padmanabhan et al., 2011 | - Children (8–13)<br>- Adolescents (14–17)<br>- Adults (18–25) | Inhibitory control (antisaccade task) | Cognitive (no incentive vs. potential gain of points) | Adolescents improved inhibitory control with gains to the adults' performance level |
| Geier and Luna, 2012 | - Adolescents (13–17)<br>- Adults (18–29) | Inhibitory control (antisaccade task) | Cognitive (neutral vs. gain and loss trials, 1–5 points) | No age interaction on loss trials but adolescents made more errors on gain trials |
| Hämmerer et al., 2010 | - Children (9–11)<br>- Adolescents (13–14)<br>- Young adults (20–30)<br>- Older adults (65–75) | Probabilistic learning task (65, 75, or 85% positive feedback probability) | Cognitive (gain and loss of feedback points, 10 points) | - Higher variability in decision-making after loss than gain feedback over all age groups<br>- Adolescents and young adults needed less trials to learn correct responses from trial feedback, showed less variability in decision-making and learned more from gains than from losses as compared to younger and older age groups |
| Chein et al., 2011 | - Adolescents (14–18)<br>- Young adults (19–22)<br>- Adults (24–29) | Risk-taking task (Stoplight task) | Social-induced (alone and peer condition: two friends) | Adolescents but not older age-groups exhibited more risk-decisions when being observed by peers |
| Jones et al., 2014 | - Children (8–12)<br>- Adolescents (13–17)<br>- Young adults (18–25) | Social reinforcement learning task (33, 66, and 100% positive feedback probability) | Social-induced (positive and no positive social feedback) | - Independent of age, rare probability of positive feedback led to more false answers than both continuous or frequent positive feedback<br>- Adolescents demonstrated a lower positive learning rate than children and adults<br>- Participants with a higher positive learning rate were more sensitive to feedback probabilities |

**TABLE 2 |** Overview of EEG findings.

| Authors | Age groups (age range in years) | Task | Incentive type | Phases | Main results |
|---|---|---|---|---|---|
| Crowley et al., 2013 | - Children (10–12)<br>- Early adolescents (13–14)<br>- Late adolescents (15–17) | Gambling task (Balloon task, reward probability 50%) | Monetary (no-reward vs. gain trials, 10 Cents) | Receiving incentives | - Larger FRN amplitude to neutral than gain trials<br>- Larger FRN amplitude for males than females<br>- Larger FRN for 10–12 and 13–14 year-olds than 15–17 year-olds irrespective of gains and losses<br>- Longer FRN latency for gain than neutral trials<br>- Longer FRN latency for males than females on gain trials<br>- Reduced latency from 10–12 to 15–17 year-olds irrespective of gains and losses |
| Gonzalez-Gadea et al., 2016 | Adolescents (8–15) | Gambling task (high and low advantageous and disadvantageous decks) | Monetary (high and low gains, 2–4 Dollar; and losses, 1–14 Dollar) | Receiving incentives | - Larger FRN amplitude to losses than gains |
| Grose-Fifer et al., 2014 | - Adolescents (13–17)<br>- Young adults (23–35) | Gambling task (Card guessing game, reward probability 50%) | Monetary (high and low gains, 32–40 Cents; high and low losses, 6–11 Cents) | Receiving incentives | - Larger FRN amplitude for losses than gains<br>- Larger FRN amplitude for low than high gains in males<br>- FRN ratio (low gains vs. losses) smaller in adolescent males<br>- Longer FRN latency to losses than gains<br>- Longer FRN latency to high than low outcomes<br>- Longer FRN latency to high gains and losses than to low gains and losses in adolescent males |
| Santesso et al., 2011 | - Adolescents (16–17)<br>- Young adults (18–29) | Gambling task (60 and 40% win-loss ratio) | Monetary (high and low gains and losses, 195-205 Cents and 45–55 Cents) | Receiving incentives | - Larger FRN amplitude for losses than gains<br>- Larger FRN amplitude for low than high gains<br>- FRN amplitude to gains and losses larger for individuals with high score on sensitivity to punishment scales in a personality questionnaire |
| Unger et al., 2014 | - Children (10–11)<br>- Mid adolescents (13–14)<br>- Late adolescents (15–17) | Reinforcement learning task (100% valid feedback) | Monetary (no-incentive vs. gain and loss trials, 37 Cents) | Receiving incentives | - Larger ERN/Ne amplitude for younger and older adolescents than children<br>- Larger ERN/Ne and Pe in incorrect than correct trials<br>- Reduced Pe in late adolescents compared to younger age groups<br>- Larger Pe in gain than neutral and loss trials<br>- No interaction of age and incentive condition in the ERN/Ne amplitude or Pe amplitude |
| Lukie et al., 2014 | - Children (8–13)<br>- Adolescents (14–17)<br>- Young adults (18–23) | Gambling task (virtual maze, reward probability 50%) | Cognitive (reward and non-reward trials in form of fruits) | Receiving incentives | - No age differences in reward positivity<br>- Longer latency for children in reward positivity |

*(Continued)*

**TABLE 2** | Continued

| Authors | Age groups (age range in years) | Task | Incentive type | Phases | Main results |
|---|---|---|---|---|---|
| Hämmerer et al., 2010 | - Children (9–11)<br>- Adolescents (13–14)<br>- Young adults (20–30)<br>- Older adults (65–75) | Probabilistic learning task (65, 75, or 85% positive feedback probability) | Cognitive (gain and loss of feedback points, 10 points) | Receiving incentives | - Children showed largest overall FRN of all age groups<br>- Children and older adults showed smaller differences between FRN after gains and FRN after losses<br>- Younger adults showed larger enhancement of FRN after losses than children |

*FRN, Feedback-related negativity; ERN/Ne, Error-related Negativity; Pe, Error Positivity.*

strategy. In a post-experimental questionnaire, children reported more overall positive feelings during the task, suggesting a higher subjective value of sweet incentives for children than for adults. A similar finding has been reported by Galván and McGlennen (2013), who compared the effects of appetitive (i.e., sugary) and aversive (i.e., salty) liquids between adolescents and young adults. Both groups reported positive feelings toward appetitive (i.e., sugary) and negative feelings to aversive (i.e., salty) liquids, and this difference was even more pronounced for adolescents than for adults. Hence, both studies support the view that primary incentives are particularly salient to children and adolescents when compared to adults. A third study investigated only younger adults but considered individual differences in risk taking which is often higher in adolescents (Hayden and Platt, 2009). This study directly compared primary and secondary incentives (sugary liquid vs. money) within subjects. The results indicated that although there were individual differences in either preferring or avoiding risks, these were independent of the kinds of incentives given.

Neuroscientific methods like fMRI are suitable to investigate whether age differences in brain activity occur during the processing of primary incentives, i.e., during anticipating or consuming those (Geier and Luna, 2009; Galván and McGlennen, 2013; Luking et al., 2014). For instance, Galván and McGlennen (2013) found no age differences during the anticipation of positive and negative primary incentives in the ventral striatum (VS), OFC, insula, and inferior frontal gyrus. In contrast, during consumption, they found larger activations in the VS in adolescents than young adults, and this activation was positively correlated with increasingly positive ratings for appetitive sugary liquids in adolescents, but not in adults. However, substantial developmental differences in reward delivery have been detected particularly for aversive primary incentives and the omission of rewards. Here, adolescents relative to adults showed exaggerated striatal responses to the delivery of aversive salty liquids (Galván and McGlennen, 2013), and children had a larger activation in the dorsal/posterior insula after candy losses than adults (Luking et al., 2014).

Taken together, primary incentives seem particularly salient in childhood and adolescence as revealed by self-reports, but had no influence on the behavioral choices itself. On the neural level, adolescents relative to adults showed an increased sensitivity in the VS only during consummatory, but not during anticipatory incentive processing. This pattern of results may support a bias in decision-making in adolescents in a way that behavior is less motivated by potentially rewarding activities but is more tuned toward consumption of risk-related rewards, such as alcoholic drinks, drugs, and future choices (Bjork et al., 2010). More importantly, when carefully controlling for the separation between incentive anticipation and delivery as well as for applying child-friendly incentives to equate motivation between age groups, adolescents tend to be highly sensitive to the loss of incentives, suggesting that the striatum codes susceptibility to punishment regimes in adolescence.

## Secondary Incentives

Secondary reinforcers are learned by definition and can be characterized as monetary, cognitive, or social (Montague and Berns, 2002). In the following, we will first review empirical studies examining the effects of monetary incentives, before we turn to cognitive and social ones. Within each section, we will first report behavioral findings (see **Table 1**), and then the neuronal signatures of incentive processing during different stages as measured with even-related potentials (ERPs) and fMRI (see **Tables 2**, **3**).

### Monetary Incentives

Most of the developmental studies to date applied monetary incentives to investigate age-related differences in incentive processing (cf. Bjork et al., 2004, 2010; Galván et al., 2006; Crowley et al., 2013; Gonzalez-Gadea et al., 2016). Although monetary incentives are easily applicable, studies markedly differ (a) in reward magnitude, ranging from a few cents to several euros per trial, (b) in whether monetary feedback is provided in a trial-based or block-wise manner, and (c) in whether wins and losses are presented with equal probability or loss aversion is considered (Santesso et al., 2011; Kujawa et al., 2014). These differences modify the relative "risk" within the decision-making process that subjects may discount on each trial and need to be considered for comparison across different studies. A further major problem for developmental studies is to compare a fixed amount of money across age groups, as receiving, for instance, 50 cents has a different meaning for children and late-adolescents.

**TABLE 3 |** Overview of fMRI findings.

| Authors | Age groups | Task | Incentive type | Phases | Main results |
|---|---|---|---|---|---|
| Galván and McGlennen, 2013 | - Adolescents (13–17)<br>- Young adults (23–35) | Passive reward-delivery task | Primary (water, sucrose, salty, or no liquid in neutral option) | - Anticipating incentives<br>- Receiving incentives | - No age and condition interactions in the OFC, IFG, insula and caudate<br>- Stronger activation to sugary liquids in adolescents than young adults in the VS<br>- Adolescents show exaggerated striatal activity to aversive salty liquids relative to young adults |
| Luking et al., 2014 | - Children (7–11)<br>- Young adults (22–26) | Gambling task (card guessing game) | Primary (high and low gains, 4 or 2 pieces; high and low losses, 2 or 1 pieces) | Receiving incentives | - Stronger activation in the dorsal/posterior insula after losses in children than in adults<br>- Stronger activation in the anterior insula after losses in adults than in children |
| May et al., 2004 | - Children and adolescents (8–18) | Gambling task (card guessing game) | Monetary (neutral trials, no reward; gain trials, 1 Dollar; loss trials, 50 Cents) | Receiving incentives | - Larger and later peak activations in the striatum and OFC to gains than losses<br>- No age or gender differences in these activations |
| Van Leijenhorst et al., 2010 | - Children (10–12)<br>- Adolescents (14–15)<br>- Young adults (18–23) | Gambling task (slot machine task, reward probability 50 %) | Monetary (neutral and gain trials; 5 Cents) | - Anticipating incentives<br>- Receiving incentives | - Children and adolescents showed larger activation of the anterior insula to potential gain cues / to neutral cues which were more similar to gain cues<br>- Larger striatal activity to reward delivery in adolescents<br>- Young adults showed larger OFC activation to omission of incentives |
| Van Duijvenvoorde et al., 2014 | - Adolescents (10–16)<br>- Young adults (18–25) | Gambling task (slot machine task, reward probability 33 and 66%) | Monetary (passed trials, no reward; gain and loss trials, ±10 Cents) | Receiving incentives | - Larger medial PFC and VS activations to gains than losses<br>- Activation in medial PFC and VS was related to the tendency to choose the risky option<br>- No age differences in these activations<br>- Individual differences in reward sensitivity were related to activation of VS during development |
| Ernst et al., 2005 | - Adolescents (9–17)<br>- Young adults (20–40) | Gambling task (wheel of fortune, reward probability 50%) | Monetary (high and low gains, 4 Dollar or 50 Cents; or reward omission) | Receiving incentives | - Larger nucleus accumbens and bilateral amgydala activation for gain than loss trials<br>- Larger nucleus accumbens activation in adolescents than young adults during reward omission<br>- Larger amygdala activity to incentive omission in young adults than adolescents<br>- Negative emotion correlated with amygdala response to losses in young adults, positive emotions correlated with nucleus accumbens activity in adolescents |
| Cohen et al., 2010 | - Children (8–12)<br>- Adolescents (14–19)<br>- Adults (25–30) | Probabilistic learning task (83% predictable and random condition) | Monetary (no-reward vs. high and low gain trials, 25 or 5 Cents) | - Anticipating incentives<br>- Receiving incentives | - Greater striatal activation with increasing age<br>- Hypersensitive response to unpredicted rewards in striatum and angular gyrus in adolescents as compared to children and adults<br>- Medial PFC was sensitive to reward magnitude, showing a linear increase in sensitivity with increasing age |

*(Continued)*

**TABLE 3 |** Continued

| **Authors** | **Age groups** | **Task** | **Incentive type** | **Phases** | **Main results** |
|---|---|---|---|---|---|
| Bjork et al., 2010 | - Adolescents (12–17)<br>- Adults (22–42) | Monetary Incentive Delay (MID) Task | Monetary (neutral trials, no reward/loss; high and low gain and loss trials, 50 Cents or 5 Dollar) | - Anticipating incentives<br>- Receiving incentives | - Reduced activation in the nucleus accumbens for gain than neutral trials in adolescents relative to adults<br>- No age differences in brain activations |
| Bjork et al., 2004 | - Adolescents (12–17)<br>- Adults (22–28) | Monetary Incentive Delay (MID) Task | Monetary (neutral trials, no reward/ loss; high and low gain and loss trials, 20 Cents, 1 Dollar or 5 Dollar) | - Anticipating incentives<br>- Receiving incentives | - Reduced activation in the VS and amygdala for gain than neutral trials in adolescents relative to adults<br>- No age differences in brain activations |
| Galván et al., 2006 | - Children (7–11)<br>- Adolescents (13–17)<br>- Young adults (23–29) | Two-choice reaction time task (reward probability 100%) | Monetary (low, medium, and high number of monetary coins) | Both anticipating and receiving incentives | - Stronger activation in the nucleus accumbens and lateral OFC with increasing incentives<br>- Adolescents showed larger activation in reward-related brain regions relative to children and young adults |
| Van Leijenhorst et al., 2006 | - Early adolescents (9–12)<br>- Young adults (18–26) | Gambling task (cake task, high and low risk trials) | Cognitive (gain and loss trials; 1 point) | - Anticipating incentives<br>- Receiving incentives | - Higher activation in the OFC and DLPFC for high- than low-risk trials, but no age differences<br>- Larger ACC activation in adolescents on high- than low- risk trials relative to young adults<br>- Both age groups showed a larger activation for receiving negative than positive incentives in the VLPFC<br>- Stronger activation in the OFC for negative vs. positive feedback in early adolescents relative to adults |
| Teslovich et al., 2014 | - Adolescents (11–20)<br>- Adults (22–30) | Random Dot Motion Task | Cognitive (high and low gain trials; 5 or 1 points) | Receiving incentives | - Larger VS activation for larger than smaller incentives for both age groups<br>- Stronger activation in the DLPFC and IPS for adolescents relative to adults when incentives are large |
| Paulsen et al., 2015 | - Adolescents (10–22) | Inhibitory control (antisaccade task) | Cognitive (no-reward vs. gain and loss trials, 5 points) | Receiving incentives | - No age differences in VS activation<br>- Striatal activation was associated with better inhibitory control in neutral trials<br>- Activation in the VS on no-incentive trials was associated with better inhibitory control, especially in adolescents < 17 years, whereas these activations dampened performance for adolescents > 17 years<br>- Negative correlation between age and activation of the amygdala in loss trials |
| Padmanabhan et al., 2011 | - Children (8–13)<br>- Adolescents (14–17)<br>- Adults (18–25) | Inhibitory control (antisaccade task) | Cognitive (no incentive vs. potential gain of points) | Receiving incentives | - Adolescent-specific enhanced striatal activity, associated with reward processing, and enhanced activity in areas responsible for inhibitory control during reward trials |

*(Continued)*

**TABLE 3 |** Continued

| Authors | Age groups | Task | Incentive type | Phases | Main results |
|---|---|---|---|---|---|
| Chein et al., 2011 | - Adolescents (14–18)<br>- Young adults (19–22)<br>- Adults (24–29) | Risk-taking task (Stoplight Task) | Social-induced (alone and peer condition: two friends) | Anticipating incentives | - Stronger activation of reward-related brain areas (VS, OFC) during risky decision making in adolescents when peers were watching<br>- Independent of social context, adults engaged lateral PFC more strongly than adolescents<br>- Activity in VS and OFC was associated with risky-decision making in adolescents only |
| Smith et al., 2015 | - Adolescents (14–19)<br>- Adults (24–32) | Decision making (guessing task without risk) | Social-induced (alone and peer condition: two friends) | Receiving incentives | - Stronger activation in the VS in adolescents during decision making when peers were watching |
| Gunther Moor et al., 2010 | - Pre-pubertal children (8–10)<br>- Early adolescents (12–14)<br>- Older adolescents (16–17)<br>- Young adults (19–25) | Feedback processing (social judgment task) | Social-induced (feedback whether a person would like them or not) | - Anticipating incentives<br>- Receiving incentives | - Stronger activation of ventromedial PFC and striatum during the expectation to be liked in older adolescents and adults<br>- Similar activation in ventromedial PFC and striatum in all age groups when expectation to be liked was followed by social acceptance feedback<br>- Linear increase in activation with age in striatum, subcallosal cortex, paracingulate cortex, lateral PFC and OFC when expectation not to be liked was followed by negative social feedback |
| Jones et al., 2014 | - Children (8–12)<br>- Adolescents (13–17)<br>- Young adults (18–25) | Social reinforcement learning task (33, 66, and 100% positive feedback probability) | Social-induced (positive and no positive social feedback) | Receiving incentives | - Anterior to mid insula activation was correlated with the positive prediction error in adolescents<br>- Adolescents engaged putamen and supplementary motor area more than children or adults in response to positive reinforcement<br>- VS and medial PFC equally engaged across age |

#### *Behavioral findings*

Studies that have used gambling tasks to examine the impact of monetary incentives on age differences in decision-making often found that choice behavior was age-invariant to the magnitude of monetary incentives (Grose-Fifer et al., 2014) and of risk (Van Duijvenvoorde et al., 2014). For instance, Grose-Fifer et al. (2014) applied a card-gambling task in which monetary wins and losses were either small or large (for details, see **Table 1**). On each trial, adolescents and adults were to choose either a high- or a low-monetary incentive card. Both age groups did not differ in choice behavior and selected high-monetary incentive cards more often than low-monetary incentive cards. Likewise, Van Duijvenvoorde et al. (2014) used a slot-machine task and compared adolescents and adults in risk taking by manipulating the chance to win (66 vs. 33%) or to lose 10 cents. Again, both age groups did not differ in their choices to play and by this in risk taking (Van Duijvenvoorde et al., 2014). However, monetary incentives were probably too low to induce risky decisions in the later study. May et al. (2004) investigated age differences in a two-choice card guessing game in which children and adolescents had to guess whether the hidden number of an upcoming card was greater or less than five. Correct guesses resulted in a gain of one Dollar and incorrect guesses in a loss of 0.5 Dollar, relative to a neutral condition. This ratio was selected to control for loss-aversion in human decision-making (May et al., 2004). Results showed that age did not account for the amount of variability of choosing the same response after a previous reward (i.e., win-stay strategy) or the opposite response after a previous loss (i.e., lose-shift strategy), suggesting that children and adolescents do not differ in choice-behavior when loss-aversion is considered.

In two studies by Bjork et al. (2004, 2010), the effects of magnitude of the monetary incentives was measured by a modified Monetary Incentive Delay (MID) task in which different cues indicated monetary incentives and risks (e.g., win or lose 0, 0.5, 1, or 5$). While the first study did not reveal an effect of incentive magnitude on task performance (Bjork et al., 2004), in the second study adolescents and adults showed faster responding to target stimuli as incentive magnitude increased on both gain and loss trials and again, there were no age differences in these effects (Bjork et al., 2010).

A similar finding has been reported in a study of Unger et al. (2014) who investigated how monetary incentives change performance in a learning task. Results indicated better performance in the two incentivized conditions, that is, children, mid-adolescents, and late adolescents responded faster and more accurately on gain and loss trials relative to the neutral condition (for details, see **Table 1**). Again, there were no age differences in performance benefits when incentives were provided during learning. However, Galván et al. (2006) applied a learning task in which children, adolescents, and adults had to respond as quickly as possible to a cue that was associated with either a low, medium, or large incentive value. Although all age groups responded faster to large incentives, the RT-difference between incentive values was largest in the group of adolescents. Similarly, Cohen et al. (2010) found that only adolescents responded faster to large than small incentives as compared to children and adults in a probabilistic learning task.

Considering individual differences, personality scales as well as post-experimental questionnaires further revealed that adolescents and adults do not differ in reward and punishment sensitivity (Santesso et al., 2011), as well as in positive feelings related to large compared to small monetary incentives (Ernst, 2014). However, adolescents reported more positive feelings than adults during winning money, but not during reward omission (Ernst et al., 2005). The latter result has been explained by the larger motivational salience of monetary incentives in adolescence than adulthood (e.g., Ernst, 2014).

In sum, the behavioral data mostly show that children, adolescents, and adults do not differ in choice behavior and risk-taking, as all age groups are more likely to select high than low monetary reward trials in gambling tasks. All age groups also respond faster on high than low incentive trials, achieve higher accuracy on incentive trials than on neutral trials, and there were no age differences in win-stay and lose-shift strategies in learning tasks. There is some evidence that adolescents respond faster to large than small monetary incentives, and that they report more positive feelings after receiving monetary incentives than adults do.

### *EEG findings*

Most ERP-studies so far have focused on the processing of incentive delivery. A number of studies applied gambling tasks and measured feedback processing, as indexed by the amplitude of the feedback-related negativity (FRN). Researchers found a larger FRN for loss or neutral than for gain trials (Santesso et al., 2011; Crowley et al., 2013; Grose-Fifer et al., 2014; Kujawa et al., 2015; Gonzalez-Gadea et al., 2016) as well as for small than large monetary gains (Santesso et al., 2011), with only small age differences therein. However, differences in FRN amplitudes to monetary incentives may be modulated by individual differences in emotionality, punishment sensitivity, and gender (Crowley et al., 2013; Kujawa et al., 2015). For instance, Santesso et al. (2011) found larger FRN amplitudes to both gains and losses for those individuals that reported higher levels of punishment sensitivity, also irrespective of age. With regard to gender differences, Grose-Fifer et al. (2014) reported that adolescent males showed larger FRN amplitudes to small than large wins, less FRN-differentiation between low gains and losses, as well as delayed FRN latencies to high losses as compared to females. Furthermore, FRN amplitudes in females (adolescents and young adults) were only modulated by the valence (i.e., larger for losses than for gains), suggesting that females may represent incentives only in the two categories positive and negative. In contrast, males seem more sensitive to the value of incentives, and thereby more prone to risk-taking. As most studies did not report age differences, these findings need to be replicated before strong conclusions can be drawn.

Another study focused on the investigation of error processing, as indexed by the error-related negativity (ERN/Ne) and error positivity (Pe), during response execution, when monetary incentives were anticipated. Applying a reinforcement learning task, Unger et al. (2014) showed a larger ERN/Ne for younger (13–14 years) and older adolescents (15–17 years) than for children (10–11 years) but no modulation of the ERN/Ne by monetary incentives, suggesting that adolescents were better able to represent correct and incorrect responses during learning, irrespective of anticipating positive and negative monetary incentives. The Pe, that is often interpreted as subjective evaluation of responses, was also larger for erroneous than correct responses. Moreover, it was also larger for monetary gains than losses and no-incentives, and was reduced for older adolescents relative to the other two age groups. Again, these effects were not modulated by the incentive manipulation. Hence, although the Pe was sensitive to the value of incentives as well as to age, the two factors did not interact with each other.

To summarize, neuronal correlates associated with coding prediction errors clearly indicate that the magnitude and valence of monetary incentives impact processing of feedback delivery, as reflected in a larger FRN to losses than wins and to small than large wins (at least in males), as well as error evaluation, as reflected in a larger Pe to wins than losses. In contrast, error processing (as reflected in the ERN/Ne) during anticipation of monetary incentives was insensitive to the magnitude and valence of monetary incentives. However, although these neuronal correlates are age-sensitive, no interactions of age with the value of monetary incentives were obtained.

### *fMRI findings*

Most of the neuroimaging studies also have investigated processing of monetary incentives with variants of gambling tasks. For instance, May et al. (2004) used a card guessing game to investigate children and adolescents between 8 and 18 years when receiving either a positive incentive (i.e., possibility to win 1 Dollar) or a negative incentive (i.e., risk to lose 0.5 Dollar). They found similar brain activations in the striatum and lateral and medial OFC to the delivery of rewards as compared to previous results in adults. Interestingly, the possibility of receiving positive monetary incentives led to larger and later peak activations in the aforementioned brain regions than that of negative incentives, in line with the view that the striatum and OFC are involved in anticipating and encoding the value of incentives. However, no gender and age differences were obtained in this effect. It should be noted that the positive incentive was twice as much as the negative one. Hence, differences in incentive magnitude might have driven the latter effect (May et al., 2004). Nevertheless, Van Duijvenvoorde et al. (2014) found a similar result in adolescents and adults using a so-called slot-machine task. In this study, neuronal responses to feedback delivery after decisions to take a gamble showed larger activation in bilateral VS and medial PFC for gains than losses. In this study, both gains and losses were equivalent (i.e., winning or losing 10 cents). In line with the previous study, they also found no evidence for age differences in reward-related brain activations.

Cohen et al. (2010) examined feedback processing during the delivery of incentives in children, adolescents, and adults in a reinforcement learning task with large (25 cents) and small (5 cents) monetary incentives for correct responses. This condition was contrasted with a non-incentive condition for incorrect responses. In contrast to the findings from the gambling studies reported above, they found that adolescents had a hypersensitive response to unpredicted rewards in the striatum and the angular gyrus as compared to children and adults. Additionally, a region in the medial PFC was sensitive to reward magnitude, but here, a linear increase in sensitivity was found with increasing age. Galván et al. (2006) also found age differences in incentive processing between children, adolescents, and adults in a learning task in which responses to three types of cues were rewarded with high, medium, and large incentives. Across the whole trial, they found an increased activation in the nucleus accumbens and lateral OFC with larger incentive values. In contrast to the aforementioned studies, adolescents showed enhanced incentive-related activity in the nucleus accumbens relative to both children and adults, whereas larger lateral OFC activity was found in children as compared to the two older age groups. These results suggests a different developmental maturation of incentive-related brain regions, as subcortical structures, such as the nucleus accumbens, seem to become disproportionally activated as compared to the later maturing lateral OFC, supporting top-down cognitive control. The difference between studies might be due to different incentive schedules, as the study by Galván et al. (2006) applied a 100% reward probability schedule whereas the previous study did not.

Other studies not only investigated incentive delivery, but also the anticipation and omission of incentives in order to answer the question of whether increased risk-taking in adolescence results from an overestimation of anticipated incentives, from a higher responsiveness to receiving incentives, or both. To this end, Van Leijenhorst et al. (2010) applied the slot-machine task in early and mid-adolescents and young adults. In the incentive anticipation phase, both groups of adolescents showed larger activation in the anterior insula on trials signaling potential gains, but this effect was absent in the group of young adults. In the outcome phase, the two adolescent groups, but not the young adults, also showed larger activations in the striatum during trials signaling incentive delivery. This finding was corroborated by a quadratic age trend of the VS to rewards. In contrast, young adults showed larger activation of the OFC on trials, signaling incentive omission. These findings support the view that middle adolescence is characterized by overactive incentive-related brain regions, especially during reward delivery. Conversely, OFC activations in young adults to the omission of reward may signal the need for increased attention and adjustment of behavior following negative outcomes that is reduced in adolescents (Van Leijenhorst et al., 2010).

In a similar study, Ernst et al. (2005) investigated brain activations specifically to the omission of incentives (i.e., possibility to win either 4 or 0.5 Dollar or nothing) in a wheel-of-fortune task. For both adolescents and young adults, they found larger brain activations for the delivery than the omission of incentives in the bilateral amygdala and the nucleus accumbens. Whereas reductions in neuronal activations to the omission of rewards were encoded in the amygdala in adults, adolescents showed the same activation difference in the nucleus accumbens. Hence, adolescents and adults seem to differ more reliably in response to negative (i.e., omission) than positive monetary incentives. The weaker involvement of the amygdala in response to the omission of incentives may reflect a lower sensitivity to potential harm and less avoidance of negative situations in adolescents, accompanied by a more active reward-related system as reflected by nucleus accumbens activity. This pattern in turn might explain the higher propensity for risk and novelty seeking in adolescents.

Concerning the anticipation and delivery of monetary rewards during cognitive control, the studies by Bjork et al. (2004, 2010) point to a different pattern of age-related differences. In both studies, they applied a MID task in which five different cues indicated monetary incentives and risks (for details, see **Table 3**). During incentive anticipation, Bjork et al. (2004, 2010) reported reduced nucleus accumbens, VS, and amygdala recruitment by monetary gains relative to no gains in adolescents as compared to adults. In contrast to the previous studies, age differences in incentive-related brain regions were not obtained during the delivery of rewards. Hence, the results suggest that when incentives are bound to individual performance instead of choice behavior, and are measured in separate stages during anticipation and consummation, differential activation patterns in reward-related and control-related brain regions are observed in adolescents (Bjork et al., 2004; for a similar result using a longitudinal design, see Lamm et al., 2014).

Apart from age differences in neuronal correlates of reward anticipation, delivery, and omission, both the study by Van Duijvenvoorde et al. (2014) and Ernst et al. (2005) emphasized the role of individual differences in personality traits and affective states during gambling. In the former study, activations of the VS and medial PFC for play decisions were related to individual differences in scores on the BAS sub-scale Fun-Seeking: Subjects, who were more willing to approach potentially rewarding events in daily-life, showed a larger activation to incentives in the VS and medial PFC (Van Duijvenvoorde et al., 2014). In the latter study, Ernst et al. (2005) showed reduced amygdala responses to omission of incentives to be correlated with self-reported negative affect in adults, whereas adolescents showed correlations between nucleus accumbens activity and positive affect.

Taken together, results on age differences in brain activations in reward-related and control-related regions are mixed, and vary with the magnitude and probability of monetary incentives as well as with the type of task and stage of processing. When incentive values are high and the uncertainty of receiving them is rather low, an imbalance between the highly activated reward region and low activated control regions may lead to more impulsive and risky decision-making in adolescence.

## Cognitive Incentives

Regarding cognitive incentives, one can differentiate between written feedback concerning performance accuracy on the preceding trial (e.g., Kim et al., 2014) and visual feedback indicating points for correct responses that are counted during performing the task and can be exchanged for monetary compensation at the end of the task (e.g., Paulsen et al., 2015). Also, some studies employ abstract feedback symbols (i.e., smiley, circles, or shapes, cf. Bjork et al., 2004; Kujawa et al., 2015) or category members (i.e., fruits, cf. Lukie et al., 2014) whose (often monetary) value is learned beforehand. These types of incentives are used to reduce the potential impact of age differences in the perceived value of, for instance, monetary incentives, that otherwise could lead to age differences in motivated behavior (e.g., Teslovich et al., 2014).

### *Behavioral findings*

Van Leijenhorst et al. (2006) applied a gambling task called "cake task" involving high- and low-risk trials. Early adolescents and young adults had to predict choices of the computer and received either one point for a correct prediction that was in accordance with the computer's (random) choice or a loss of one point for an incorrect prediction. Early adolescents and adults made better predictions under low-risk conditions. Under high-risk conditions, early adolescents were in tendency more prone to risk-taking than adults, as they made more incorrect predictions than adults. However, the high-risk condition in that study might also have induced larger response conflict due to higher perceptual demands. Therefore, it is difficult to conclude whether children were indeed more sensitive to risk taking under high-risk conditions (Van Leijenhorst et al., 2006).

As gambling tasks *per se* do not give rise to age-related differences in task performance (Lukie et al., 2014), other studies investigated the role of cognitive incentives in simple and more complex tasks requiring cognitive control. For instance, using a simple perceptual RT task, Teslovich et al. (2014) found that adolescents were in particular sensitive to high positive cognitive incentives. They showed slower response times when large rewards could be lost, while young adults showed a speeded responding under this condition. Hence, age differences occur with larger magnitude of positive incentives (which acquire a negative value when large rewards are lost). Groom et al. (2010) investigated whether cognitive incentives would increase inhibitory performance in adolescents by varying not only the amount but also the valence of cognitive incentives (see **Table 1**). The high incentive condition enhanced inhibitory control performance, irrespective of the valence of incentives. Thus, positive and negative cognitive incentives, when strictly comparable in task design, are equally appropriate to foster performance in adolescence. Padmanabhan et al. (2011) also found that children and adolescents showed improvements to adults' performance levels in inhibitory control when potential incentives could be received (Padmanabhan et al., 2011). In contrast, Paulsen et al. (2015) applied an anti-saccade task to measure inhibitory control and investigated the impact of positive and negative cognitive incentives (i.e., gain or loss of 5 points). Their results indicated no effect of incentives on task performance, irrespective of age. Moreover, Geier and Luna (2012) even found negative effects of abstract reward cues (indicating trials with potential wins or losses of points, or neutral trials) on inhibitory control. In this anti-saccade study, adolescents committed more errors on gain trials than adults but not on loss trials. Thus, whether cognitive incentives influence inhibitory control may also depend on the type of response or the demands on inhibitory control.

The effect of cognitive incentives has also been investigated in reinforcement learning tasks (Hämmerer et al., 2010), in which participants performed a probabilistic two-choice learning task resulting in gains and losses of feedback points after each trial. Here, in contrast to children and older adults, adolescents and young adults learned faster from feedback and showed less switching of choices, and this difference was more pronounced after a positive than after a negative cognitive incentive. However, the switching of choices was more frequent after a negative incentive in all age groups.

Together, the behavioral results reveal that cognitive incentives can facilitate inhibitory control in adolescent, but not in children, depending on the type of inhibitory task. While behavioral adjustment after negative cognitive incentives is found across all age groups, adolescents' performance in decision-making is driven by response conflict on high-risk tasks (e.g., not receiving a large positive incentive). The latter effect suggests that losses involve emotional processing that is target to profound maturational changes during adolescence (Hämmerer et al., 2010; Paulsen et al., 2015).

### *EEG findings*

Only rather few studies have investigated the neuronal signatures of incentive anticipation and delivery. For instance, the study by Groom et al. (2010) compared ERP correlates during response selection during a go-nogo task in which positive and negative cognitive incentives (gaining vs. losing points vs. neutral condition) were compared between blocks, so that the effects of incentives on task preparation cannot be investigated. Adolescents showed a larger N2-amplitude in positive than negative incentive and neutral blocks, indicating an early attentional process toward processing the positive valence of cues. However, this effect did not interact with demands on inhibitory control, that is, the positive valence effect was not different between no-go and go trials. They also showed a larger P3 amplitude in incentive blocks than in neutral blocks, suggesting a higher processing effort on motivated salient conditions. Again, this effect did not interact with inhibitory control demands (for a similar finding in young adults, see Schmitt et al., 2015).

A larger number of studies has focused on error- and feedback-related components (the ERN/Ne and FRN; for a review on developmental changes in these components, see

Ferdinand and Kray, 2014) in order to investigate the impact of cognitive incentives on learning and monitoring processes. One study reported larger amplitudes of the ERN/Ne and Pe for errors than correct responses during an inhibitory control task in adolescents (Groom et al., 2013). However, there was no effect of incentive value (i.e., differences between high or low positive or negative cognitive incentives) on ERN/Ne and Pe. In a similar vein, Lukie et al. (2014) found no age differences in processing different cognitive incentives (i.e., symbolic gains and losses) on amplitudes of the FRN. However, the study was a pure gambling task and therefore one cannot assess the impact of reward feedback on ERP measures of cognitive control and reinforcement learning. To investigate this issue, Hämmerer et al. (2010) applied an incentivized probabilistic learning task in more fine-grained age groups. They found that although having the largest FRN amplitudes overall, children showed smaller differences between FRN amplitudes after gains and losses relative to adolescents and young adults. This pattern remained stable even after controlling for baseline FRN size and for changes in the FRN after gain feedback in each age group. The findings suggest that children are less able to yield a differentiated classification of favorable and less favorable outcomes for task-specific goals, as indicated by FRN ratio scores, and to use cognitive feedback for adapting to task-specific goals (for a similar result, see Ferdinand et al., 2016).

#### *fMRI findings*

Brain imaging studies on developmental changes during anticipating and receiving cognitive incentives have revealed large activation overlap in brain networks between early adolescents and adults (Van Leijenhorst et al., 2006). In particular, Van Leijenhorst and colleagues examined age differences in brain activations during the decision-making process itself and processing feedback between low- and high-risk conditions in selected regions of interest. During decision-making, they found higher activations in the OFC and DLPFC for high- than low-risk conditions but no age effects in this difference, suggesting similar recruitment of brain regions known to be involved in anticipation of incentives and representation of risk options in early adolescents and adults. However, adolescents mainly differed from adults in higher activations of the ACC on high- than low-risk trials, suggesting that they perceived either more conflict or needed to engage more heavily in performance monitoring during high-risk choices. This finding was in line with the behavioral results, showing more incorrect decisions in early adolescents during higher uncertainty for correct predictions (Van Leijenhorst et al., 2006).

The study by Van Leijenhorst et al. (2006) also assessed age differences in receiving cognitive incentives (i.e., during feedback processing). They found that both age groups showed a larger activation for receiving negative than positive feedback in the VLPFC, known to be recruited during punishment. Moreover, early adolescents showed a larger activation in the right lateral OFC for negative than positive cognitive incentives, irrespective of the risk level, while for young adults this difference in brain activation was less pronounced. The age difference was due to differences in brain activations on negative feedback trials, suggesting that early adolescents were more sensitive to negative than positive feedback. This region is associated with coding the magnitude of both positive and negative outcomes and with implementing behavioral adjustments after negative feedback (Tsuchida et al., 2010). However, the study did not manipulate the magnitude of incentives as, for instance, the study by Teslovich et al. (2014). They compared receiving a small (1 point) and a large (5 point) positive incentive between adolescents and adults in three regions of interest, in the VS, IFC, and DLPFC. The results indicated a larger activation in the VS for larger than smaller positive incentives, but no age differences in this effect. In contrast, adolescents showed larger activations in the IPS and DLPFC for larger than smaller rewards. The increased activation of the fronto-pariatal network for higher incentives in adolescents has been interpreted as a bias in response selection in order to slow down responding until enough evidence is accumulated for a correct decision. Unfortunately, this latter study did not separate anticipation and delivery of incentives, and did not manipulate the magnitude of negative incentives so that the results of both studies are difficult to compare.

Padmanabhan et al. (2011) examined the effects of rewards on inhibitory control in an anti-saccade task. They investigated children, adolescents, and adults and compared conditions with an abstract cue indicating a potential win (that was later converted into a monetary bonus) and with an abstract cue that served as a neutral trial. They found an adolescent-specific enhancement in VS activity, and in areas responsible for inhibitory control during reward trials. Paulsen et al. (2015) investigated the contribution of age and inhibitory control performance on fronto-striatal activations in the anti-saccade task in 10–22 year-olds during positive and negative cognitive incentives (gaining vs. losing points vs. neutral). Although striatal activation during the decision-making process on neutral trials was associated with overall better inhibitory control, younger and older subjects did not differ in striatal activation during positive incentive conditions. However, inhibitory control performance in adolescents younger than 17 years benefitted from fronto-striatal activation during neutral trials, whereas these activations hampered anti-saccade performance in adolescents from 17 years on. Interestingly, age was negatively correlated with activation in the amygdala during loss trials only, suggesting that the amygdala of younger adolescents was more sensitive to losses. The results suggest a transition phase of fronto-striatal recruitment in adolescence, in which fronto-striatal regions benefit cognitive control performance and in which emotional processing in the amygdala mediates bottom-up processing during inhibitory control in younger adults (Paulsen et al., 2015).

Together, although ERP and fMRI methods are well suitable to examine whether (cognitive) incentives influence decision-making and cognitive control behavior in different stages, the existing studies have rarely made use of it. From EEG studies, we have learned that during the decision-making processing (anticipation of incentives) both children and adults show enhanced attention and processing effort under motivated conditions as compared to neutral ones, indexed by larger N2 and P3 amplitudes. Children and adults are also similarly sensitive to risky decisions, as they show similar changes in brain activation in prefrontal regions (OFC, DLFPC) when positive incentives are less likely. Here they differ only in higher ACC activation, signaling higher conflict processing in such situations. During response selection and receiving feedback, it seems that children are less able to differentiate between positive and negative cognitive incentives as reflected in smaller FRN difference scores than in adolescents and adults. Both adolescents and adults are sensitive to negative cognitive incentives, indicated by a larger recruitment of the VLPFC on negative than on positive incentive trials. In contrast, adolescents show a larger recruitment of cognitive control networks, and a lower amygdala activation in response to losses.

## Social Incentives

Given that the processing of social information underlies dramatic developmental changes over the course of adolescence, and that the social context might be the most salient factor influencing the behavior of youth (Crone and Dahl, 2012), it is somewhat surprising that most developmental studies so far have focused on the impact of cognitive and monetary incentives on decision-making and goal-directed behavior. In recent years, some researchers suggested that adolescents may be specifically sensitive to perceiving, processing, and responding to social information (e.g., Blakemore and Mills, 2014). In particular, adolescents spend a greater amount of time with peers (Csikszentmihalyi and Larson, 1984) and are increasingly preoccupied with peer opinions (Brown, 1990) and acceptance (Parkhurst and Hopmeyer, 1998). The influence of positive and negative social incentives can be measured in different ways, for instance, by inducing social acceptance/inclusion or social rejection/exclusion from a peer group (e.g., induced with the Cyberball paradigm). Moreover, already the presence of peers or its simulation (e.g., by a chatroom) is sufficient to create a social context that affects decision-making and goal-directed behavior, known as the peer-effect (e.g., Gardner and Steinberg, 2005).

### *Behavioral findings*

A number of studies, applying experimental decision-making tasks, have already shown that the presence of peers leads to higher risk taking in adolescents than in adults (Gardner and Steinberg, 2005; Chein et al., 2011; O'Brien et al., 2011; for a review, Albert et al., 2013; Weigard et al., 2014). For instance, researchers have used the so-called Stoplight task, a driving game in which participants advance through several intersections to reach a goal as fast as possible (e.g., Chein et al., 2011). They compared adolescents and two groups of adults in their risky decisions (driving across the stoplight and risking a crash) under conditions in which they performed the simulated driving task either alone or under observation of peers. Only adolescents took more risky decisions under the peer observation compared to the alone condition, while this peer effect was not present in the two groups of adults (Chein et al., 2011). The peer effect can also be obtained by the simulated presence of peers in late adolescents (e.g., Weigard et al., 2014). Interestingly, the peer effect disappeared when a slightly older adult is included into the peer group (Silva et al., 2016), in the presence of the mother (Telzer et al., 2015), and in the presence of an unknown adult (Guassi Moreira and Telzer, 2016), suggesting that this effect is highly sensible to the social context. However, one may argue that the Stoplight task is a rather specific risk-taking setting so that the peer effect cannot be generalized to other risk-taking tasks. Two recent studies have used the Balloon Analogue Risk Task (BART; Lejuez et al., 2002) or an adapted version of it in which a simulated balloon can be inflated via a balloon pump (button press). Each pump signifies a small win that can be accumulated within a trial. After each pump, participants have the choice to either save the money, or to inflate the balloon further, taking the risk for the balloon to burst and to lose the already accumulated money. Indeed, both studies were not able to replicate the peer effect when measuring risk taking by the overall number of inflated balloons (Reynolds et al., 2014; Kessler et al., 2017).

The direct reaction of peers, such as including or excluding an individual into the peer group, may be a stronger incentive for adolescents than the sole presence of a peer. Feelings of exclusion and inclusion from a group often have been induced with the so-called Cyberball paradigm (for details, see Williams et al., 2000). It has been shown that the Cyberball task induces distress (Masten et al., 2009; Bolling et al., 2011; Sebastian et al., 2011), threat (Abrams et al., 2011; Sebastian et al., 2011; Van Noordt et al., 2015), and worse mood (Gunther Moor et al., 2012). Evidence for the effects of inclusion/exclusion from a peer group on decision-making and cognitive control are rather scarce so far. Peake et al. (2013) showed that adolescents revealed a tendency for increased GO-decisions in the Stoplight task after being excluded in a preceding Cyberball game. Adolescents with greater susceptibility to peer influence also displayed larger increases in risky decisions after being socially excluded by peers (Peake et al., 2013).

Recently, Jones et al. (2014) investigated whether children, adolescents, and adults learned an association between the probability of receiving positive feedback and a particular peer (feedback stimulus). Unbeknownst to the participants, the probability of receiving a positive incentive from the three peers was experimentally manipulated, with one peer providing incentives rarely (33% of trials), the other frequently (66% of trials), and the last peer on all trials (continuous). Independent of age, rare probability of positive feedback led to a higher error rate than the other two peer conditions. Learning from positive feedback showed a quadratic age trend, with adolescents demonstrating a lower positive learning rate than children and adults. Thus, while children as well as adults reacted faster to peers that were associated with more frequent positive feedback, adolescents seemed to be motivated equally by all positive social incentives.

The reported quadratic age effect has not been found in other learning tasks (Van den Bos et al., 2012; Christakou et al., 2013). Therefore, either adolescents did not learn to discriminate between the peers associated with different amounts of positive social feedback, or the reinforcement learning predictions did not represent the adolescents' behavior. Accordingly, their learning rate profile could be associated with a general higher sensibility for receiving peer approval (Collins and and Steinberg, 2007).

In sum, social-induced feedback, like acceptance and rejection by peers, but also their mere presence, has an impact on adolescent decision-making. When observed by peers, whether they were present during testing and close friends, or simulated and unknown, adolescents show heightened propensities for risky decisions and immediate rewards. However, only the minority of studies compared different age groups and no study included longitudinal data, making it difficult to account for developmental differences in the influence of social incentives on decision-making and cognitive control behavior over the course of adolescence.

### *EEG findings*

Only a handful of ERP studies have investigated the influence of social incentives on electrophysiological markers of decision-making and cognitive control in developmental samples. These studies have revealed several important findings. First, they have shown that the mere presence of peers can influence the significance of (negative) feedback as reflected in the size of the FRN. However, peer presence does not uniformly lead to weakened processing of negative as compared to positive, rewarding feedback, but also depends on the specific situational context (Segalowitz et al., 2011; Kessler et al., 2017). Second, social rejection feedback elicits early (as indexed by the FRN) and later (as indexed by the P3b) feedback processing similar to the FRN after cognitive or monetary feedback with the later processes also depending on peer relationship (Kujawa et al., 2014; Gonzalez-Gadea et al., 2016; Kuo et al., 2017). And third, social exclusion as examined in the Cyberball game elicits larger slow-wave activity (Crowley et al., 2010; White et al., 2012) as well as enhanced medial frontal theta oscillations (Van Noordt et al., 2015), both related to the distress this exclusion causes. However, none of these studies actually examined developmental effects by comparing different age groups or analyzing correlations with age.

### *fMRI findings*

fMRI findings on decision-making corroborate the above reported behavioral results by demonstrating adolescent-specific neuronal activations when making risky decisions under conditions of peer observation. The study by Chein et al. (2011) found that 14–18 year-olds had significantly stronger activation of reward-related brain areas, like the VS and OFC, during the execution of risky decisions in the Stoplight task when their peers were watching them. Additionally, activity in these brain regions was associated with risky decision-making as indicated by significantly increased activity for GO relative to STOP trials. In contrast, adults showed no such difference as a function of social context. Moreover, they found that adults engaged several lateral PFC areas more strongly than adolescents, indicating enhanced recruitment of cognitive control. This activation pattern, however, was independent of social context, meaning that an immature cognitive control system in adolescents cannot account for peer influences during risky decision-making. Thus, these findings are conceptually in line with the idea of an enhanced reward-seeking motivation in mid-adolescents.

Similarly, Smith et al. (2015) examined adolescents and adults in a card guessing task that included rewarded and non-rewarded trials. Additionally, social context was manipulated by having participants complete the task both alone and while being observed by peers. When observed by peers, adolescents exhibited greater VS activation than adults, but no age-related differences were found when the task was completed alone. These findings suggest that during adolescence, peer presence influences recruitment of reward-related regions in a reward-processing task even when this task involves no risk taking at all.

Concerning the processing of social acceptance and rejection feedback, Gunther Moor et al. (2010) examined children, early adolescents, older adolescents, and young adults in a social judgement task. They presented photographs of peers and asked their participants to predict whether they would be liked by this person. This was followed by feedback ("yes" vs. "no") indicating whether the person actually liked them or not. Their results showed that the expectation to be liked was accompanied by activation of the ventromedial PFC (a region known to be involved in processing of self-relevant information) and the striatum. This activation was similar in older adolescents and adults, but less pronounced in children and early adolescents. Furthermore, when the expectation to be liked was followed by social acceptance feedback, the ventromedial PFC and the striatum were similarly responsive across all age groups. In contrast, when the expectation to not be liked was followed by negative feedback, the striatum, subcallosal cortex, paracingulate cortex, later PDF and OFC showed linear increases in activation with increasing age. Because this activation was also positively correlated to the resistance to peer influence, the authors interpret this finding as adults being better in regulating the negative feelings that are linked to social rejection. These results are not consistent with the notion of an enhancement of social feedback processing in adolescence. However, they highlight the importance of positive social feedback in general, because already children at the age of 8–10 years were rather sensitive to acceptance feedback.

In contrast, a very similar study by Jones et al. (2014) demonstrated an enhanced sensitivity to unexpected social acceptance feedback in adolescents as compared to children and adults. The authors compared the effects of social reinforcement (receiving a note vs. receiving no note) by peers that differed in the amount of positive reinforcement they gave (rare to frequent). The results showed that especially in adolescents, the anterior to mid insula response was correlated with the positive prediction error (receiving a note from a peer that gave positive reinforcement only rarely). This finding may indicate an enhanced salience of positive social reinforcement during adolescence. Additionally, adolescents activated regions responsible for response planning (putamen and supplementary motor area) more than children and adults when they received positive social reinforcement, which suggests that peer approval may motivate adolescents toward action. VS and medial PFC were equally engaged across age, which could reflect that the perceived value of peers based on their reinforcement history was equivalent for children, adolescents, and adults. These findings suggest that fundamental reinforcement learning mechanisms support social reinforcement learning from late childhood to adulthood. In contrast, the heightened activity in the insular cortex and regions within response planning circuitry of adolescents may suggest an affective-motivational sensitivity toward any peer approval.

Together, the reported fMRI data reveal that risky decisions seem to be rewarding for adolescents because they lead to activation in reward-related neuronal circuitry. Additionally, peer presence enhances the recruitment of these reward-related brain areas and can also dampen activity in a fronto-parietal network responsible for performance in cognitive tasks. As opposed to the studies on peer presence, the results of the few studies examining social acceptance and rejection feedback are less consistent and clearly further research is needed comparing several age groups or even groups differing in pubertal status.

### Direct Comparisons of Secondary Incentives

Only a small number of studies so far have directly compared the impact of different kinds of incentives on decision-making and goal-directed behavior in adolescence and the underlying neuronal circuitry. These studies are primarily motivated by the claim that different types of incentives share the same neuronal basis, supporting the idea of a "common neural currency" of rewards, and investigating atypical processing of rewards in clinical subsamples that will be not reported here (e.g., Autism Spectrum Disorder, Internet-addicts). We found one study that directly compared primary and secondary incentives that is reported in section Primary Incentives, so that we will focus here on comparisons between secondary incentives. We will also not include studies investigating only adults (e.g., Izuma et al., 2008; Flores et al., 2015), clinical subsamples (e.g., Lin et al., 2012; Kim et al., 2014; Gonzalez-Gadea et al., 2016), or one age group (Op de Macks et al., 2017).

In an attempt to compare social and monetary feedback, Ethridge et al. (2017) tested differential neural responses to social and monetary incentives in young-adolescents and emerging adults. Social feedback was induced through acceptance and rejection feedback while participants engaged in the so-called Doors task (Proudfit, 2014). Positive and negative feedback in the social condition was indicated by a green "thumbs up" for acceptance or by a red "thumbs down" for rejection. In the monetary condition, a green arrow pointing up indicated a win of $0.50 and a red arrow pointing down indicated a loss of $0.25. In addition, adults were informed that they could win up to $10, whereas young-adolescents were informed that they could win only up to $5, while all participants were given in fact $5 following the monetary decision-making task. During feedback presentation, the author reported an enhanced reward positivity for social acceptance and winning money as compared to social and monetary negative feedback. The results revealed that the young adolescents showed this effect on both types of incentives, thus did not differentiate between them. In contrast, the adults showed a larger positivity to monetary than social positive incentives, suggesting at first glance developmental changes in the relative importance of incentive cues. However, the findings are difficult to interpret as adults could win twice as much as adolescents which can also explain the differences between the age groups.

## DISCUSSION

The overarching aim of this review was to provide an overview on the impact of different kinds of incentives, in particular, monetary, cognitive, and socials ones, on age differences in decision-making and cognitive control tasks. We were specifically interested in answering the following questions: (1) Do we find age differences in how different kinds of incentives motivate behavior in these tasks; (2) if so, do these age differences primarily occur during anticipation or consuming/receiving incentives; (3) is there evidence for common or distinct neuronal activations across incentives, as well as for age differences in recruiting incentive-related brain regions.

### Do Different Kinds of Incentives Motivate Behavior Differently During Adolescence?

Considering the overall findings at the behavioral level, most of the studies did not find age differences in the impact of different kinds of incentives on decision-making and cognitive control. Although primary incentives are more salient in childhood and adolescence than in adults (based on subjective self-reports), they did not modulate age differences in behavioral choices itself. Monetary as well as cognitive incentives led to better task performance in most studies, but again there were no age-differential effects in these benefits or on behavioral adjustments. Again, adolescents differed from other age groups in self-reported positive feelings about gaining money and there was only few evidence that adolescents were more prone to receiving or not receiving larger monetary incentives. If at all, it seems that social incentives have an age-differential effect on adolescents' decision-making in terms of taking higher risks in the presence, acceptance or rejections of peers. However, only rather few studies compared different age groups and it remains unclear whether the peer effect is restricted to very specific task settings. These findings suggest that different kinds of incentives did not differ in their impact on age differences in decision-making and cognitive control behavior. Only one recent developmental study directly compared monetary and social incentives and found that adults were more responsive to monetary than social ones, while no such difference was obtained for young adolescents. However, given the small number of developmental studies so far, future research directly comparing the differential functions of incentives throughout adolescent development is clearly warranted.

### Do Different Kinds of Incentives Influence Neuronal Mechanisms During Anticipating and Receiving Incentives Differently in Adolescents?

Although an ERP approach is well suitable to examine cognitive and neuronal mechanisms separately in stages of anticipating and receiving incentives, only rather few developmental studies have made use of it to determine age differences in decision-making and cognitive control. Studies investigating the impact of monetary incentives mostly used reinforcement learning tasks and clearly found that both the magnitude and valence of incentives influence feedback processing, in contrast to the anticipation of incentives (here error processing). There is scarce evidence for gender by age interactions on processing monetary incentives but these findings need to be replicated before strong conclusions can be drawn. Studies investigating the impact of cognitive incentives focused on the examination of receiving incentives and again found no evidence supporting the view that adolescents process cognitive incentives differently from adults. Only children were less able to differentiate between positive and negative cognitive incentives as compared to adolescents, due to their immature cognitive control system.

### Age Differences in the Recruitment of Incentive-Related Brain Regions During Anticipating and Receiving Incentives

In adults, there are first reviews and meta-analytic studies pointing to an overlapping processing network for different types of incentives including the ventral medial PFC, OFC, medial PFC, ACC, the posterior cingulate cortex (PCC), the inferior parietal lobule and some regions of the lateral PFC in decision-making (e.g., Liu et al., 2011; Sescousse et al., 2013). Such overlap in recruitment of incentive-related brain regions was found when comparing the processing of primary and secondary incentives (e.g., Lieberman and Eisenberger, 2009; Bartra et al., 2013; see Sescousse et al., 2013, for a review), as well as when comparing social and non-social decision-making (for reviews, Amodio and Frith, 2006; Ruff and Fehr, 2014; see also Saxe and Haushofer, 2008).

To determine age-related differences between adolescents and adults in recruiting incentive-related processing, Silverman et al. (2015) recently reported results of a meta-analysis including 26 fMRI studies. Although they found overlapping brain activation in the incentive-related network, including major nodes such as the ventral and dorsal striatum, insula and the PCC, suggesting that adolescents activate a similar incentive-related network as adults do, adolescents showed a greater likelihood for activation in a number of these regions. However, they also reported age differences in activating brain regions during anticipation and consumption/receipt of rewards. Adolescents showed a larger activation in the insula, amygdala, and putamen during anticipation and larger amygdala activation during receiving feedback, suggesting a higher sensitivity to salient stimuli. When comparing positive to negative incentives, adolescents showed larger activation in the accumbens, PCC, and OFC. Relative to adults, adolescents showed a reduced activation for negative incentives in the amygdala, OFC, and ACC (Silverman et al., 2015).

Concerning the different types of incentives, as reviewed here, it has been shown that adolescents were particularly sensitive to consuming or not receiving primary incentives as reflected in increased activation in the VS relative to adults. A much larger number of studies investigated the impact of monetary incentives and yielded very mixed results: Age differences in brain activations in reward-related and control-related regions were rather inconsistently found depending on the type of task and stage of processing. Generally, it seems that adolescents were sensitive to a "hot" context, that is, when incentive values are high and the probability of receiving them is rather low, an imbalance between the highly activated reward region and low activated control regions may lead to more impulsive and risky decision-making in adolescence. Moreover, receiving negative cognitive incentives led to higher recruitment of control brain regions as well as to a lower amygdala activation, signaling lower sensitivity to potential negative outcomes in adolescents.

## CONCLUSIONS AND OUTLOOK

Most of the developmental studies included in this review compared only two age groups or investigated a restricted age range in a cross-sectional research design. These limitations make it impossible to evaluate current neurobiological developmental models against each other. Comparing different types of incentives and their impact on age differences in decision-making and cognitive control revealed that the effects were quite similar on the behavioral level and mostly age differences were not observable. These findings seem to conflict with the current theoretical models as well as with the research findings on the neuronal level that often showed higher recruitment of control-related brain regions in adults and higher activation in reward-related brain regions in adolescents. Future research thus needs to better integrate and relate the results of different data levels. We also recommend that future research in this field should make more use of neuroscientific methods in order to directly compare differential functions of primary and secondary incentives in different stages of processing (i.e., preparation, response selection, outcome evaluation). This will help us to determine the relative importance of different kinds of incentives on cognitive and neuronal mechanisms. However, the review of findings also revealed that if monetary incentives were rather high, decision options were unknown, or in a social context (presence of peers), adolescents indeed behaved differently compared to adults (and children), at least in particular tasks. Hence, one challenge for future studies will be to further specify in well-controlled studies, which contextual factors are critical for inducing an imbalance between reward and control networks in adolescents, and to also consider the role of individual differences in the subjective valuation of different kinds of incentives across age.

## AUTHOR CONTRIBUTIONS

All authors contributed to the writing of the review. JK wrote the Introduction and Discussion part. HS summarized research findings on cognitive and monetary incentives. CL summarized the behavioral findings of social incentives and NF the neuroscientific findings of social incentives. All authors provided feedback to the other parts. Tables were created by HS, CL, and NF.

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REVIEW
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# Motivational Influences on Performance Monitoring and Cognitive Control Across the Adult Lifespan

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Cognitive control refers to the ability to regulate cognitive processing according to the tasks at hand, especially when these are demanding. It includes maintaining and updating relevant information in working memory, inhibiting irrelevant information, and flexibly switching between tasks. Performance monitoring denotes the processing of feedback from the environment and the detection of errors or other unexpected events and signals when cognitive control needs to be exerted. These two aspects of behavioral adaptation critically rely on the integrity of the frontal lobes, which are known to show pronounced age-related performance decrements. By contrast, there is evidence that processing of rewards remains relatively intact across the adult lifespan. Hence, motivation may play an important role in modulating or even counteracting age-related changes in cognitive control functions. To answer this question, neuroscientific data can be particularly useful to uncover potential underlying mechanisms beyond behavioral outcome. The aims of this article are twofold: First, to review and systematize the extant literature on how motivational incentives can modulate performance monitoring and cognitive control in young and older adults. Second, to demonstrate that important pieces of empirical data are currently missing for the evaluation of this central question, specifically in old age. Hence, we would like to stimulate further research uncovering potential mechanisms underlying motivation-cognition interactions in young and in particular in older adults and investigating whether or not those can help to ameliorate age-related impairments.

**Keywords: cognitive control, performance monitoring, adult lifespan, incentives, motivation**

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## INTRODUCTION

It is well known that many cognitive functions, mainly those from the domain of fluid intelligence, decline with increasing age (Baltes, 1997; Baltes et al., 1999). By contrast, there is evidence that affective and motivational information processing remains relatively intact across the adult lifespan. Neuroscientific research has corroborated these findings by revealing diverging trajectories of cognitive and affective neural substrates, with cognitive prefrontal circuits being more strongly affected by aging than affective ones (for reviews, see Eppinger et al., 2011; Mata et al., 2011; Mather, 2012). Recent research has also demonstrated that motivational influences can modulate cognitive functioning and enhance performance in diverse cognitive tasks (for a review, see Braver et al., 2014), for instance that rewards can improve memory performance (Wittmann et al., 2005; Adcock et al., 2006; Halsband et al., 2012). This interaction of motivation and cognition is particularly relevant for aging research as it may provide an opportunity to ameliorate age-related impairments.

The goal of this article is to review and systematize recent research examining the influence of motivational incentives on performance monitoring and cognitive control across the adult lifespan. Performance monitoring denotes the processing of environmental feedback, the detection and processing of errors and of unexpected events. It is an important prerequisite for the flexible adaptation of behavior to varying situational demands because it signals when our behavior was inadequate or did not lead to the expected goal. It is also a precondition for the implementation of cognitive control because it signals when (more) cognitive control is needed. Cognitive control is the ability to guide one's own behavior and cognitive processes in a goal-directed way. It is a multidimensional construct comprising several core components, including the ability to select relevant information, to keep it active in working memory and protect it against irrelevant information (Miyake et al., 2000; Hofmann et al., 2012; Miyake and Friedman, 2012; Grange and Houghton, 2014).

These fundamental cognitive functions constitute the basis for more complex abilities like adaptive behavior, rational decision making, or self-regulation (Hofmann et al., 2012). They also rely heavily on prefrontal cortex (PFC) functioning and are highly susceptible to age-related decline (e.g., West, 1996; Braver and Barch, 2002; Miller and Cohen, 2001; Paxton et al., 2008). Hence, it is an important question whether motivation can modulate age-related decline in these abilities. In this article, we will first address the question of how the processing of motivational incentives changes across the adult lifespan (see section "Processing of Rewards"). We will then review the literature on motivational influences on performance monitoring (see section "Motivational Influences on Performance Monitoring") and cognitive control (see section "Motivational Influences on Cognitive Control"). These sections show that age-related differences of motivational impact on these two aspects of cognition are scarcely examined up-to-date (for an overview, see **Tables 1**, **2**). Thus, we will briefly summarize research findings in young adults and focus on older participants whenever possible. Finally, we will discuss the extant empirical findings on motivation–cognition interactions in the light of aging models on cognitive control functioning (see section "Potential Mechanisms of Motivation on Performance Monitoring and Cognitive Control in Old Age") and discuss caveats and limitations that this line of research is confronted with, in particular the lack of systematic evaluations of cognition-motivation interactions in older adults (see section "Open Issues, Caveats, and Future Directions").

## PROCESSING OF REWARDS

A fundamental question is whether the processing of rewards and punishments changes across the adult lifespan. If younger and older adults process these incentives differently, this fundamental difference may have important implications for how and whether incentives can exert their influence over other cognitive processes.

From a theoretical perspective, there is reason to believe that rewards and punishments change their motivational value over the lifespan. For instance, the socio-emotional selectivity theory (Mather and Carstensen, 2005; Reed and Carstensen, 2012) assumes that there is an emphasis on emotional satisfaction and well-being in old age when future time horizons are restricted and that this is the reason for an age-related positivity shift, i.e., the preferred processing of positive information. This effect has been found mainly in the domains of attention (Mather and Carstensen, 2005; Isaacowitz et al., 2006) and memory (Kennedy et al., 2004; Grady et al., 2007). For instance, when shown positive, negative, and neutral pictures, older adults recall more positive pictures and fewer negative pictures than younger adults (Charles et al., 2003). However, it remains unclear to what extent the positivity-effect generalizes to other domains of cognitive functioning. The same argument can be put forward concerning the model of selection, optimization and compensation by Baltes and colleagues (e.g., Baltes and Baltes, 1990; Ebner et al., 2006). Similar to the socio-emotional selectivity theory, this model assumes that positive and negative motivational information differentially affect cognition in older adults. However, it proposes that the prevention of losses is more relevant to older adults than the receipt of gains (for a similar view, see Brandtstädter, 2009). Because age-related differences in reward processing *per se* are not the main focus of this article, in the following we will present only a short summary on the main findings of this research area and direct the interested reader to the respective literature (for reviews, see Eppinger et al., 2011; Mata et al., 2011).

### Reward Anticipation and Delivery

Existing functional magnetic resonance imaging (fMRI) studies have examined the activation of reward networks during the anticipation and the delivery of rewards by means of incentive delay tasks. In young adults, these studies have consistently found that anticipation and delivery of rewards and punishments activate parts of the ventral striatum (bilateral caudate nucleus and bilateral putamen), the insula, the dorsal midbrain, and the orbitofrontal cortex (e.g., Delgado et al., 2000, 2003; Knutson et al., 2000; Breiter et al., 2001; Nieuwenhuis et al., 2005; Elliott et al., 2008; Rolls and Grabenhorst, 2008; for a review, see Delgado, 2007). This line of research has also shown that reward-network responses during anticipation and outcome processing show relatively little age-related change. For example, Samanez-Larkin et al. (2007) examined anticipation of gains and losses in a monetary incentive delay task. They found that older adults demonstrated preserved gain anticipation in the ventral striatum and the insula (for similar results, see Rademacher et al., 2014; Spaniol et al., 2015), but also a reduced activation in the nucleus caudatus and the insula during loss anticipation as compared to younger adults. This latter finding was also consistent with older adults' self-report indicating that they experienced reduced negative affect (Samanez-Larkin et al., 2007). Cox et al. (2008) focused on the delivery of monetary rewards and punishments in a card-guessing task. They found that older adults showed the same activation foci and temporal dynamics during reward and punishment delivery as younger adults. Interestingly, both studies hint at the possibility of a positivity bias in old age, consistent with the socio-emotional selectivity theory (Mather and Carstensen, 2005; Reed and Carstensen, 2012). While Samanez-Larkin et al. (2007) found that older adults may be less sensitive to loss cues than younger adults, Cox et al. (2008) found a trend for older adults to show a decreased response to punishments. However, more research is needed to corroborate these rather subtle effects.

### Reward Prediction Errors

In contrast to reward processing *per se*, older adults show decreased functioning in processing reward prediction errors, i.e., the difference between expected and actual rewards (for a review, see Mata et al., 2011). This is most evident during reinforcement learning, where learning is induced by rewards or punishments that indicate whether an event has been better or worse than predicted. For instance, Eppinger et al. (2013) examined younger and older participants in a reinforcement learning task with a reward (win vs. no-win) and a punishment (loss vs. no-loss) condition using fMRI. They found that older adults showed less learning in combination with reduced activity in the ventromedial PFC in the reward condition but not in the punishment condition. Moreover, they found a reduced sensitivity to reward prediction errors in the ventral striatum in older adults (Eppinger et al., 2013; for similar results, see Schott et al., 2007; Mell et al., 2009; Samanez-Larkin et al., 2014).

Reward prediction errors have also been examined by means of event-related potentials (ERPs) and several components have been associated with their detection (for reviews, see Folstein and Van Petten, 2008; Gehring et al., 2012). Most important in the present context is the feedback-related negativity (FRN), which is thought to originate (at least in part) from the anterior cingulate cortex (Miltner et al., 1997; Ferdinand and Opitz, 2014). It is usually measured over fronto-central brain areas after participants receive unexpected feedback or rewards/punishments (e.g., Gehring and Willoughby, 2002; Holroyd and Coles, 2002; Ferdinand et al., 2012). In line with the above fMRI findings, ERP studies have demonstrated that older adults generally show reduced feedback negativities (e.g., Mathalon et al., 2003; Mathewson et al., 2005; Hämmerer et al., 2010; Bellebaum et al., 2011) as compared to younger adults. According to Nieuwenhuis et al. (2002), this is the result of a weakened reinforcement learning signal from the dopamine system to the mediofrontal cortex, specifically the anterior cingulate.

As a consequence of the above findings, it has been suggested that the sensitivity to rewards and previously learned reward associations remain intact over the adult lifespan, whereas a network of neural systems that supports novel reward learning changes with age (e.g., Samanez-Larkin et al., 2014). Specifically, an age-related reduction in structural connectivity between the striatum and the PFC has been found (Samanez-Larkin et al., 2012). This reduction in connectivity may influence the dynamic updating of reward predictions and thus explain the age-related impairments in reward prediction error processing (Eppinger et al., 2011). This line of argumentation is also corroborated by ERP studies showing that age differences in the FRN are reduced when the task's difficulty level is adaptive (e.g., Eppinger et al., 2008; Ferdinand and Kray, 2013). This implies that neither reward processing nor prediction error processing *per se* is impaired in old age, but that the decreased availability of processing resources leads to the observed age effects in reward prediction error processing.

## MOTIVATIONAL INFLUENCES ON PERFORMANCE MONITORING

Performance monitoring includes the detection and processing of errors and external feedback as well as the detection of other unexpected events in our environment. It is a crucial prerequisite to flexibly adjust our behavior to different situational demands, because it signals when behavior has not resulted in the desired outcome. By this, it is an important marker indicating that heightened cognitive control is necessary. There are several theories about how performance monitoring contributes to behavioral changes (for an overview, see Alexander and Brown, 2010). What is common to most of them is that we make predictions about the outcome of events and compare them to the actual outcome. When this comparison results in a mismatch, the brain generates a (reward) prediction error signal, which is then used to adjust our behavior and update our expectancies for the future. Hence, a core component of performance monitoring is the generation of a (reward) prediction error.

Performance monitoring involves a cognitive as well as an affective component, which are probably inseparably interwoven in daily life. For instance, receiving negative feedback from another person regarding our behavior is rarely just purely informative, but also has an emotional impact. Therefore, a separation of performance monitoring and motivational influences on performance monitoring is difficult. This is also reflected in recent research where oftentimes no differentiation is made between "abstract performance feedback" and "reward or punishment feedback." Instead, it is assumed that even abstract performance feedback has a rewarding or punishing effect and thus has a motivational impact. Conversely, it is oftentimes implicitly assumed that monetary gains can be used as positive feedback and losses as negative feedback without affecting the basic monitoring processes (cf. Holroyd and Coles, 2002). For this reason, the effect of motivational influences on error and feedback processing has typically been examined by manipulating the amount of the reward that can be won or lost. Other manipulations include comparing different types of rewarding feedback and inducing a motivational mindset by presenting a win or loss cue prior to the task at hand. These three types of motivational manipulations will be reviewed in the following (see **Table 1**).

**TABLE 1 |** Behavioral and neuroscientific studies examining age differences in performance monitoring.

| Study | Method | Age groups | Motivational influence | Paradigm | Main results |
|---|---|---|---|---|---|
| Gorlick et al., 2013 | Behavioral | 18–35 and 60–82 years | Cognitive feedback (point gain vs. point loss) vs. social feedback (happy vs. angry faces) | Rule learning and set shifting via feedback | Experiment 1 (face feedback):<br>• Minimal load on cognitive control: happy-face feedback attenuated age-related deficits in initial rule learning and angry-face feedback led to age-related deficits in initial rule learning and set shifting<br>• High load on cognitive control: angry-face feedback attenuated age-related deficits in initial rule learning and set shifting whereas happy-face feedback led to age-related deficits in initial rule learning and set shifting<br>Experiment 2 (point feedback):<br>• Age-related deficits in initial rule learning and set shifting under low and high cognitive load for point-gain and point-loss conditions |
| Kardos et al., 2016a | ERPs | 21–28 and 62–72 years | Points accumulated during experiment are added to participation fee | Balloon Analog Risk Task | • In young, reward positivity increased as function of reward contingencies with largest amplitude for rewarding feedback followed by the decision to stop<br>• Older adults characterized by hesitation and more deliberative decision making, reward positivity did not reflect the effect of reward structure |
| Kardos et al., 2016b | ERPs | 18–32 and 62–72 years | Two amounts of monetary gains/losses | Gambling task | • Riskier choices after negative feedback<br>• In young adults, FRN was indicator of goodness of outcome (loss or gain), P3 showed a complex picture of feedback evaluation with selective sensitivity to large amount of gains<br>• In older adults, outcome valence had no effect on FRN, P3 was insensitive of the complex outcome properties |
| Nashiro et al., 2011 | Behavioral | Exp 1:<br>18–25 and 62–83 years<br>Exp 2:<br>18–24 and 69–93 years<br>Exp 3:<br>18–26 years | Angry and happy faces as feedback vs. more or less points | Learning and set shifting task | • Older adults made more errors than younger adults in the angry face feedback condition, but no age differences in happy face feedback condition |

## Reward Magnitude

In fMRI studies, evidence has accumulated showing that activity in the striatum varies as a linear function of reward magnitude. For example, Bjork et al. (2010) found that the ventral striatum was sensitive to the amount of monetary gains in young adults during the anticipation and the receipt of gains and losses in a monetary incentive delay task (see also Bjork et al., 2004; Izuma et al., 2008). Similarly, Delgado et al. (2003) found that in young participants the dorsal striatum, more specifically the nucleus caudate in the left hemisphere of the brain, was sensitive to both magnitude and valence: the highest activations were found for high rewards, followed by small rewards. Small punishments elicited even less activation of the nucleus caudate and the lowest activations were associated with large punishments.

In studies using ERPs, however, the results are far less consistent. Some studies found that the fast detection process as indexed by the FRN is not modulated by the size of gains or losses in young adults (Holroyd et al., 2004; Sato et al., 2005). Others found that the FRN in response to negative feedback was larger the larger the amount of money that could have been gained (Bellebaum et al., 2010) or that it was only sensitive to the magnitude of wins, but not losses (Zottoli and Grose-Fifer, 2012; Lole et al., 2013; Grose-Fifer et al., 2014). One explanation for these mixed findings could be related to the gender of the participants: the effects of reward magnitude on FRN in mixed-gender samples might be driven primarily by males, because two of the above studies found a larger FRN to small as compared to large wins for young adult males only (Zottoli and Grose-Fifer, 2012; Grose-Fifer et al., 2014). This might indicate that large wins are especially salient for young adult males, a sample that is known to be highly risk seeking and reward driven. Another explanation for the inconsistent findings might be due to the fact that most of the above studies that did not find a sensitivity of the FRN to reward magnitude did not control for subjects' expectancies. However, expectancies are of critical importance because a prediction error is the deviation of an actual outcome from an expected one (cf. Bellebaum et al., 2010). In line with this view, Hajcak et al. (2007) found a gradual increase in FRN amplitude with increasing prediction error when participants' expectancies were taken into account. Taken together, this implies that the FRN is not sensitive to reward magnitude *per se*, but to the size of the prediction error. This might or might not coincide with reward magnitude, depending on the study design. In contrast to the FRN, reward magnitude has been found to influence a later ERP component, the P300. The P300 is a large positive deflection following the FRN that is probably associated with working memory updating after unexpected task-relevant events (e.g., Polich, 2007) and which reflects a slower and more elaborate feedback evaluation process than the FRN (e.g., Ferdinand and Kray, 2013). Sato et al. (2005) found that P300 amplitude increased with reward magnitude, irrespective of valence (for a similar result, see Grose-Fifer et al., 2014; Kardos et al., 2016b).

Studies examining this question in older adults are scarce. Kardos et al. (2016b) examined younger and older adults in a two-choice gambling task with two amounts of monetary stakes. Their results in the sample of young adults closely resemble those by Sato et al. (2005) reported above, by demonstrating that the FRN reflected the goodness of the outcome in a binary fashion (loss vs. gain), while the P3 showed a complex picture of feedback evaluation with selective sensitivity to large gains. In contrast, in older adults outcome valence had no effect on FRN amplitude and the P300 was insensitive to outcome magnitude. Thus, it may be the case that due to limited processing resources, older adults strategically focus on the most important aspects of a feedback stimulus (cf. Ferdinand and Kray, 2013). Thus, adding more information to the feedback stimulus (magnitude information in addition to valence information) may not be the optimal way to vary reward magnitude in older adults (see also Herbert et al., 2011). In a similar vein, Kardos et al. (2016a) examined risk taking behavior in younger and older adults using the Balloon Analog Risk Task in which each pump on a virtual balloon increased the probability of a balloon burst but also increased the chance to earn a larger reward. Again, the positivity after reward feedback increased as a function of reward contingencies with the largest positivity after reward feedback followed by the decision to stop inflating the balloon. This graded ERP response was not found in older adults. Also, older adults showed more hesitation and more deliberative decision making. Thus, the lack of differentiation in the ERP response to rewarding feedback might be related to more uncertainty and variability in decision making under risky circumstances.

Taken together, there is clear evidence from neuroscientific studies that younger adults process reward magnitude. It also modulates performance monitoring, although it is not yet clear which specific monitoring mechanisms are affected most. The few cross-sectional studies show a markedly different result pattern for older adults which seem to be insensitive to reward magnitude.

## Incentive Cues

A second possibility for examining motivation-cognition interactions in performance monitoring is to present a win or loss cue prior to the task at hand and thus induce a motivational mindset. This might be the most promising approach to examine the effect of incentives on performance monitoring because the same cognitive task can be examined in distinct motivational conditions (gain or loss mindset) and compared to a neutral condition without incentives. Hajcak et al. (2005b), for instance, examined error monitoring in a flanker task in young adults. Each trial was preceded by a cue indicating the value of the trial (5 or 100 points that were converted to money at the end of the experiment). While performance did not differ between the two trial types, the size of the error negativity (ERN/Ne; Falkenstein et al., 1990; Gehring et al., 1993), an ERP component signaling the detection of a committed error and the need for behavioral adaptation, was substantially larger in high-value trials (Hajcak et al., 2005a). Pailing and Segalowitz (2004) examined error monitoring in a letter discrimination task with young adults and compared conditions in which potential rewards could be gained with a no reward condition. In contrast to Hajcak et al. (2005a), they found that monetary incentives had a motivational effect on behavior and led to better task performance, although this was not reflected in a modulation of the ERN. However, the authors assumed that this could be due to a ceiling effect because their participants were highly motivated in all study conditions. To reconcile these seemingly contradictory findings, one could speculate that the two studies above differed in terms of task difficulty. Motivational incentives presumably can only impact performance when there is sufficient room for improvement. When participants are already performing at floor or at ceiling because either the task is too hard or too easy, incentives might still have an effect on the salience of an error as reflected in the ERN but not on performance (see also section "Open Issues, Caveats, and Future Directions"). As for feedback processing, Threadgill and Gable (2016) presented cues indicating a potential monetary reward or a neutral cue at the start of each trial in a flanker task. They found that in young adults, a reward cue in comparison to a neutral cue sped up performance and led to a larger reward positivity, an ERP component in the time window of the FRN reflecting processing of positive outcomes. Similarly, Flores et al. (2015) compared feedback processing in a monetary and a social incentive delay task and found a larger FRN and P300 in trials with potential rewards (monetary and social) as compared with no potential rewards (see also section "Different types of rewards").

Taken together, cues signaling potential rewards seem to be effective motivational incentives for young adults and enhance error and feedback processing when there is room to improve performance. To our knowledge, there are no similar studies examining the effect of motivational incentive cues on performance monitoring in old age. However, because performance monitoring is a prerequisite for behavioral adaptation which is impaired in older adults (see section "Reward Prediction Errors"), it would be crucial to know how it could be supported or even improved.

## Different Types of Rewards

Another approach to investigate motivational influences on performance monitoring is to compare the effects of different types of reward feedback. In the context of performance monitoring, the most commonly used types of feedback are abstract performance feedback, e.g., symbols informing participants whether their response has been correct/incorrect, and monetary feedback, i.e., amounts of money won/lost. Other types of feedback are scarcely investigated. However, different types of rewards can have a different subjective value and therefore have different motivational impact. Which reward is perceived as most motivating could also change across the lifespan. For instance, preserved cognitive functioning plays a key role in old age (Baltes and Baltes, 1990; Brandtstädter, 2009). Hence, one could speculate that performance feedback, especially in a social context, might be more effective in older adults than monetary rewards, and also one prominent reason for older adults to participate in experimental studies (see also section "Open Issues, Caveats, and Future Directions").

In line with this idea, some studies have used social stimuli as feedback, like social acceptance or rejection (Davey et al., 2011; Kujawa et al., 2014) or emotional faces (Zhang et al., 2012; Vrticka et al., 2014). In rare cases, primary reinforcers like candy or soft drinks have been used (Luking and Barch, 2013). However, these studies did not include a direct comparison between different types of rewarding feedback, so a potential additional motivational influence of reward feedback as compared to performance feedback cannot be investigated.

Only a handful of studies have explicitly contrasted the effect of different types of rewarding feedback in the same paradigm. Hurlemann et al. (2010) compared abstract performance feedback (green vs. red lights) with social feedback (smiling vs. angry faces) in a behavioral item-category learning paradigm with young adult males in their twenties. They found better performance in conditions with social feedback. Gorlick et al. (2013) examined younger and older adults in a rule learning task with cognitive (point-gain vs. point-loss) and social (happy vs. angry faces) feedback. They did not find performance differences in the two conditions in younger adults. However, although older adults showed age-related impairments in learning, those were substantially smaller in the condition with social feedback. This effect showed complex interactions with feedback valence (positive vs. negative) and working memory demands: in conditions of low working memory demands, age-effects were reduced by positive but enlarged by negative social feedback. Thus, while older adults profited from positive social feedback, negative social feedback had deteriorating effects. For high working memory load, the opposite pattern emerged. Notably, this effect was not found for cognitive feedback, emphasizing a special role of social feedback in old age (see also Nashiro et al., 2011).

Importantly, although these behavioral studies use paradigms that are commonly used in the area of performance monitoring, one can only speculate which specific cognitive processes are affected by the incentives in these tasks. Here, neuroscientific measures can be extremely helpful. To this effect, Hajcak et al. (2005b) used ERPs to examine error monitoring in a flanker task with university students in a social evaluation and a control condition. Although no performance difference was found between the two conditions, in the social evaluation condition the ERN after committed errors was substantially larger, i.e., the monitoring system was much more sensitive. As for feedback processing, Dekkers et al. (2015) conducted a social-judgment and an age-judgment task with young women. In the social-judgment task, participants had to judge whether they expected a person to like them or not. In the age-judgment task they were to judge whether the person was their age or not. Afterwards they received feedback about their judgment (yes/no). While there was no effect of task condition on the FRN, a greater P3 was found in the social-judgment compared with the age-judgment task. So one could speculate that in addition to the type of incentive (social vs. performance feedback), the nature of the incentive, i.e., whether it is of a more sustained (being observed for a period of time) or transient (feedback) nature, might influence which phase of performance monitoring is affected.

Flores et al. (2015) investigated young adults in a monetary incentive delay (MID) and a social incentive delay (SID) task while recording ERPs. In these tasks, an abstract incentive cue was shown, representing either no incentive, a monetary, or a social incentive that could be obtained for correct performance in the following trial. After having performed on the trial, monetary (blank coin, 10 or 20 cent coins) or social feedback (blank faces, faces with a slight or big smile) was presented. During incentive cue presentation, they found an enhanced attentional allocation (as reflected in the N1) and higher motivational salience (P2 and P3) to all cues signaling a potential reward. Additionally, there was a differential influence of the type of incentive: while social incentives affected processing in a very early time interval (larger N1), monetary incentives influenced later and more elaborate processing stages (larger P3). In the feedback processing phase, a larger FRN and P3 was found for all types of rewarding feedback. Moreover, monetary feedback resulted in a larger P2 and FRN than social feedback, reflecting a heightened motivational salience of monetary feedback (Flores et al., 2015). This is in line with a study by van den Berg et al. (2012), who found heightened motivational salience to monetary rewards as compared to abstract performance feedback indexed by a larger FRN and P3, and a study by Lin et al. (2012), who found faster learning in a monetary than a social reward condition in younger adults. Together, these studies clearly show that monetary and social reward feedback lead to enhanced performance monitoring and better learning and that younger adults seem to favor monetary over social rewards. Importantly, whether this greater sensitivity for monetary rewards is a specific effect found in younger adults and whether the same pattern of results would have been observed for potential losses is still an open question and beyond the scope of the reported studies.

Functional magnetic resonance imaging studies provide evidence that there are common as well as distinct brain areas involved in processing different types of rewards. Together, the existing data speak in favor of an anterior–posterior gradient in the orbitofrontal cortex, with primary reinforcers activating more posterior areas and more complex or abstract reinforcers activating more anterior regions (Izuma et al., 2008; Daniel and Pollmann, 2010; Lin et al., 2012; for meta-analysis, see Clithero and Rangel, 2014). However, the studies also show that there are shared brain structures responsible for the calculation of a subjective value, which allow to judge and compare different kinds of rewards or feedback on a common scale. These regions include the ventromedial PFC, posterior cingulate cortex, and striatum (Peters and Büchel, 2010; for a review, see Ruff and Fehr, 2014). To our knowledge, there are no similar fMRI or ERP studies comparing the processing of different types of rewards in older adults.

### Interim Conclusion

To conclude, the above studies demonstrate that motivational factors consistently enhance performance monitoring and improve performance in young adults. Neuroscientific studies examining age-related differences in this domain are rare and longitudinal data are missing completely, so it remains an open issue whether or under which circumstances motivational factors can enhance performance monitoring in older adults and diminish age-related impairments. Still, some preliminary conclusions can be drawn from the existing studies. First, adding additional information to the feedback stimulus seems to be an inappropriate way to examine motivational influences in older adults. This may be due to limited processing resources, which force older adults to focus on the most relevant properties of a feedback stimulus (cf. Herbert et al., 2011; Ferdinand and Kray, 2013). Thus, to examine whether reward magnitude influences monitoring processes in older adults, future studies need to find a way to either lower processing demands in general (e.g., by giving older adults more time to process feedback or by using very simple tasks) or to use feedback stimuli in which reward magnitude is incorporated in a more intuitive way (e.g., by using slightly vs. strongly smiling/frowning faces that can be processed holistically). Second, the existing studies indicate that under specific circumstances – when sufficient processing resources are available – positive incentives can ameliorate age-related performance deficits, while negative incentives can have deteriorating effects in older adults. However, this tentative conclusion is mainly based on the results of one behavioral study (Gorlick et al., 2013), which needs to be corroborated by convergent behavioral evidence from related paradigms and also by neuroscientific studies that can shed light on the cognitive mechanisms underlying this behavioral effect. Third, the studies reviewed above also hint at the idea that different types of incentives might be differentially motivating across the life span. While young adults seem highly susceptible to monetary rewards (Lin et al., 2012; van den Berg et al., 2012; Flores et al., 2015), social feedback seems especially effective in older adults (Gorlick et al., 2013). Nevertheless, studies comparing several kinds of incentives in both young and older adults and in the same paradigm are still missing.

## MOTIVATIONAL INFLUENCES ON COGNITIVE CONTROL

Cognitive control refers to the ability to regulate cognitive processes according to current task demands. This is particularly relevant when the task requires frequent updating of relevant information in working memory and protection against incoming irrelevant information (Miyake et al., 2000; Hofmann et al., 2012; Miyake and Friedman, 2012; Grange and Houghton, 2014). While performance monitoring allows us to identify situations in which additional control is necessary, the recruitment of additional task-specific cognitive resources is typically referred to as cognitive control *per se*. In line with the vulnerability of the PFC to aging, many empirical studies to date have identified pronounced age-associated deficits in tasks requiring cognitive control, specifically as task demands increase (for reviews, see Fabiani, 2012; Kray and Ferdinand, 2014). Hence, it is particularly relevant to examine whether motivational interventions could help to mitigate these age-related deficits in cognitive control.

The term *cognitive* control itself implies an inherent contrast to affective processing, raising the question whether and how motivation can influence purely cognitive mental operations. The precise nature of cognitive control is difficult to define, as it regulates the balance between many cognitive sub-processes necessary to successfully perform a task, the changing demands of the environment which may suddenly require immediate attention, and each individual's overarching long-term goals such as the desire to perform well. In fact, enhanced control processes are often conceived as a filter blending out potentially distracting information and enabling us to focus exclusively on task-relevant details. However, the balance between long-term goals, the specific set of requirements of each task, and changing situational demands cannot be reached with a static filtering mechanism alone. Hence, in order to specify mechanisms of cognitive control, the environmental context and characteristics of the individual solving the task need to be taken into account. As participants vary in terms of task-relevant abilities, the amount of cognitive control that needs to be – and can be – mustered successfully is different for each participant and also between age groups. Moreover, many tasks can be approached successfully with more than one strategy, hence sometimes several types of qualitatively different cognitive control mechanisms can be feasible (see also Section "Potential Mechanisms of Motivation on Performance Monitoring and Cognitive Control in Old Age"). Finally, the recruitment of additional control processes is effortful and cannot be maintained for long periods of time, otherwise it would be optimal to keep cognitive control up-regulated for the duration of the task (Braver et al., 2007). More recent evidence suggests that participants differ in terms of how much effort they are willing to invest (Jimura et al., 2010) and choose the appropriate strategy maximizing not necessarily task performance, but rather a compromise between the maximum performance and effort invested. Hence, the regulation of cognitive control is not only influenced by task characteristics and intellectual abilities, but also by current motivational states (Chiew and Braver, 2011). Notably, strategies or types of cognitive control mechanisms used to approach a task can also differ as a function of age. For instance, older adults typically adopt a conservative response criterion emphasizing accuracy at the expense of speed regardless of task characteristics (e.g., Czernochowski et al., 2010). Hence,

**TABLE 2 |** Behavioral and neuroscientific studies examining age differences in cognitive control.

| Study | Method | Age groups | Motivational influence | Paradigm | Main results |
|---|---|---|---|---|---|
| Di Rosa et al., 2015 | Behavioral | 20–35 and 48–81 years (and Parkinson patients: 49–85 years) | Monetary rewards (+0.15€) for fast correct responses in a reward block and punishments (−0.15€) for slow and/or incorrect responses in a punishment block | Simon task | • For young adults, smaller Simon effects for blocks with potential losses than rewards<br>• No systematic behavioral differences between reward and loss conditions for older adults<br>• Young adults shifted to a more conservative response tendency in the loss condition, whereas older adults adopted a more conservative response criterion for the reward condition. |
| Drueke et al., 2012 | Behavioral | 23.9 and 70.5 years | Groups with block-wise performance feedback (mean RT) vs. without feedback | Flanker task | • In younger adults, performance feedback led to faster RTs and smaller RT congruency effects at the expense of increased error rates<br>• In older adults, feedback led to higher error rates, but had no effect on RT |
| Drueke et al., 2015 | fMRI | 20–38 and 62–77 years | Trial-wise performance feedback (happy, sad or neutral smileys) | Flanker task | • Younger and older adults showed comparable reward-related activation<br>• Positive feedback elicited the strongest striatal and amygdala activation and slightly faster reaction times in older and younger adults |
| Schmitt et al., 2015 | ERPs | 19–28 and 69–78 years | Monetary incentives (gains, losses, or neutral) | Modified AX-CPT | • Age-invariant enhanced processing of gain and loss as compared to neutral cues<br>• Younger adults were particularly susceptible to potential losses as indexed by improved context maintenance (larger CNV) prior to the probe and increased conflict detection (N450) and resolution (sustained positivity) during response selection after loss cues<br>• Older adults showed enhanced cognitive control during task preparation (larger cue-locked P3b) and during response preparation and execution (prolonged probe-locked P3b) after gain and loss cues |
| Schmitt et al., 2017 | ERPs | 65–76 and 69–78 years | Monetary incentives (gains, losses, or neutral) | Modified AX-CPT | • When incentives are presented in a block-wise manner, older adults initially process cues signaling potential losses more strongly, but invest more cognitive resources in preparatory processes like context updating in conditions with potential gains |
| Spaniol et al., 2015 | fMRI | 20–33 and 60–78 years | Monetary incentives (Win $5, Win $0, Lose $5, and Lose $0) | Monetary incentive delay (MID) task | • Two significant latent variables representing distinct incentive-related activation patterns:<br>(1) Robust activation of the reward network, not modulated by age<br>(2) Peaking 10 s after cue onset, reduced deactivation of default-network regions and increased activation of prefrontal cognitive-control regions in older adults |
| Wild-Wall et al., 2009 | ERPs | 23.7 and 57.5 years | Verbal performance feedback (correct/incorrect) | Motor timing task | • Both age groups more accurate following positive compared to negative feedback<br>• Only young adults improved following negative performance feedback, older adults more likely to commit another error following an error feedback<br>• Only for young adults, differences in FRN amplitudes between error and correct feedback correspond to the percentage of correct responses<br>• Reduced differentiation of FRN amplitudes between correct and incorrect trials for older adults |
| Williams et al., 2017 | Behavioral | 18–34 and 60–82 years | Gains and losses | Attention network test (ANT) | • Both types of rewards improved overall performance (dividing RT by accuracy) across groups, but both effects were more pronounced for younger adults<br>• Rewards not only reduced overall RTs, but also considerably increased interference effects in terms of accuracy (modified speed/accuracy tradeoff rather than enhanced cognitive control) |

age may be an important factor determining which cognitive control mechanisms will be employed (Braver et al., 2007).

In the following, we will review empirical evidence on whether and how motivation can moderate the amount or type of cognitive control recruited in service of task performance (see **Table 2**). Note that some of the studies reported in this section examine performance monitoring, however, with a specific focus on how it may lead to enhanced cognitive control. In Section "Performance Feedback as Incentive," we will examine how subsequent task performance and cognitive control are affected by performance feedback, which is often used in a non-systematic fashion in a general attempt to improve performance. Section "Processing of Reward Feedback" will summarize how experimentally introduced rewards or losses act as incentives for engaging in effortful cognitive control, whereas Section "Dissociating Specific Processing Stages With Incentive or Task-Preparation Cues" will focus on the role of different incentives cues and how they might differentially influence cognitive control.

## Performance Feedback as Incentive

One way to motivationally influence performance is to give general performance feedback. Often a summary of performance in the previous block is provided before participants can take a brief pause from the task and have the opportunity to reflect on it. In fact, many studies in which motivation is not studied experimentally rely on such an informal way to remind participants that there is room for improvement, sometimes by providing other participants' outcome as a social reference or by emphasizing either response speed or accuracy. However, this type of feedback does not always lead to the expected improvements in performance, but can also have detrimental effects, especially for older adults. For instance, Drueke et al. (2012) provided block-wise feedback to young and older participants. Performance feedback was given to half of the participants in each age group, based on response times during a flanker task. For the young, feedback led to faster reaction times (RT) at the expense of reduced accuracy. Notably, the feedback-induced focus on response speed also affected control processes: RT congruency effects (i.e., the difference between incongruent and congruent trials) were reduced for the feedback group compared to their peers who did not receive performance feedback, suggesting enhanced processing of relevant stimuli and/or more successful inhibition of irrelevant stimuli. By contrast, older adults' performance speed was not modulated by performance feedback, but the feedback group of older adults still committed more errors (Drueke et al., 2012), suggesting that older adults failed to modulate their task approach successfully. Although this initial study exclusively relied on behavioral data, one could speculate that the older adults in the feedback group misallocated attentional resources otherwise available for successful task performance. However, it remains unclear how cognitive control mechanisms are modulated by this block-wise intervention resuming the performance level of many trials.

In general, performance feedback should be most informative for future response selection when given on a trial-by-trial basis. According to the conflict monitoring account (Botvinick et al., 2001), negative performance feedback in particular provides potentially useful information, signaling the need to revise the current response strategy and to recruit additional cognitive control processes. However, even negative performance feedback given after each response does not necessarily promote cognitive control processes. For instance, in an fMRI version of their flanker task, Drueke et al. (2015) provided performance feedback to young and older participants on a trial-by-trial basis. In addition, performance remained unevaluated in one third of all trials. For both age groups, subsequent RTs were faster after positive compared to neutral feedback, whereas negative feedback did not modulate performance. Imaging data revealed that task-relevant areas and those related to reward processing were active to a similar extent in both age groups, whereas older adults also activated additional brain regions (Drueke et al., 2015). This pattern of unspecific over-activation or de-differentiation of brain activity is often observed in older adults, and usually taken as evidence for an – not necessarily successful – attempt to compensate age-related deficits (for a review, see Reuter-Lorenz and Lustig, 2005). Similarly, in an ERP study, young and older adults were asked to produce precisely timed motor responses and received verbal feedback (correct/incorrect) after each response (Wild-Wall et al., 2009). Only young adults successfully implemented negative performance feedback to promote subsequent performance, whereas older adults were much more likely to commit another error following an error feedback (conditional probability $p = 0.67$) compared to following a correct response feedback ($p = 0.33$). The authors attributed this particular difficulty in regulating response speed to age-associated deficits in the dopamine system responsible for precise motor timing. In line with the results reported above, both age groups were more accurate in producing a precisely timed motor response following positive compared to negative feedback (Wild-Wall et al., 2009). Electrophysiological data collected during this task can provide useful information on the mechanisms underlying feedback processing and potential cognitive control processes. For young adults, differences in FRN amplitudes between error and correct feedback corresponded to the percentage of correct responses, suggesting that feedback information was used to adjust the timing of subsequent responses, although negative feedback did not contain information on whether the response was given too slow or too fast. Notably, no such association was observed in older adults, who also showed a reduced differentiation of FRN amplitudes between correct and incorrect trials, implying a high level of conflict across conditions. These results suggest that older adults had difficulties to differentiate conditions in which enhanced cognitive control was necessary (Wild-Wall et al., 2009).

Notably, in the studies reviewed above, the presence or absence of cognitive control mechanisms is inferred indirectly by analyzing how performance in subsequent trials is modulated as a consequence of negative or positive external feedback regarding response speed. Together, these findings imply that only younger adults successfully re-vise their current task approach and manage to improve their performance in subsequent trials. It remains unclear why older adults do not succeed in improving their performance following negative feedback: In line with the evidence reviewed in Section "Motivational Influences on Performance Monitoring," electrophysiological data suggest that feedback processing as a signal to initiate cognitive control processes remains relatively intact in old age, as long as task demands are not too high. However, older adults often show heightened conflict processing even for correct trials (cf. Nessler et al., 2007; Czernochowski et al., 2010). In line with these less differentiated conflict signals, older adults may have difficulty to resolve the experienced conflict by recruiting additional control processes, in particular when response conflict is accumulating over several trials. Moreover, attempts to recruit additional control processes may be less successful in older adults.

In addition, intrinsic and long-term motivational age differences participants bring to the lab are likely to affect how performance feedback is being processed and whether or not participants will be willing and able to recruit additional cognitive control processes. Positive feedback – signaling that the current task approach is suitable and should be continued, potentially with enhanced effort – may be more instrumental in optimizing task performance than negative feedback and has similar consequences for young and older adults. Conversely, negative performance feedback can tie attentional resources and distract participants in subsequent trials, specifically individuals who are highly motivated to perform well but do not have much room for improvement. For instance, when feedback is based predominantly on speed of processing, older adults may find themselves unable to respond faster. In this scenario, negative performance feedback is presumably also particularly salient for older adults who like to be re-assured that their performance level is still age-appropriate (cf. Baltes and Baltes, 1990; Ebner et al., 2006; Brandtstädter, 2009). Hence, older adults can be particularly sensitive to negative feedback, which can have negative rather than beneficial effects. As a result, in the studies reviewed above, only young adults were sometimes able to successfully recruit cognitive control following negative performance feedback.

## Processing of Reward Feedback

A more direct way to examine the influence of motivation is to provide rewards for (rapid and) correct task performance, often consistently across many trials (i.e., block-wise modulation). While this approach will not capture potential trial-by-trial fluctuations of cognitive control, some strategic adjustments may rather be reflected in tonic activity. Taking advantage of this approach, Locke and Braver (2008) were the first to compare young adults performing the AX-CPT task in blocks associated with either monetary rewards or losses compared to baseline performance. In this paradigm, participants are asked to respond to a target X whenever it is preceded by a specific cue A and to withhold a response in all other cue-target combinations (AY, BX, and BY and sometimes also No-Go trials, which occur in around 10% of trials each). In line with enhanced advance preparation, young participants were considerably faster to respond on the frequent AX trials during the reward block compared to either baseline or monetary loss condition. However, this condition was also associated with a selective increase in AY errors, suggesting that faster RTs on the majority of trials were achieved at the expense of increased errors in this rare trial type. Imaging data identified sustained activity in a network of right-lateralized regions including lateral PFC, right parietal and dorsal medio-frontal cortex, presumably reflecting context maintenance underlying this behavioral reward effect. Conversely, for the monetary loss condition, AX errors increased despite slow RTs, but NoGo errors were substantially reduced, suggesting that participants adopted a more cautious response criterion (Locke and Braver, 2008; see also Chiew and Braver, 2014). Notably, increased reliance on advance preparation is only observed when rewards are provided contingent on correct performance, whereas performance was not modulated for a group of young adults who received rewards randomly as *a gift* and hence unrelated to performance (Fröber and Dreisbach, 2016, see also Fröber and Dreisbach, 2014). Thus, enhanced cognitive control is only recruited in service of optimizing performance when superior performance is instrumental to gain rewards.

To summarize, rewards consistently modulate young adults' behavior when provided contingent on individual performance. Positive incentives promote fast responses presumably via advance preparation, albeit sometimes at the expense of increased errors rates in rare task conditions requiring response inhibition. In these reward conditions, neuroimaging studies have identified a network of sustained activity predominantly in lateral prefrontal brain regions consistent with task maintenance. Introducing penalty incentives does not activate these areas and tends to have weaker impact on performance, associated with slower responses and a more conservative response criterion.

To our knowledge, only three studies so far explicitly studied rewards in the context of aging in cognitive control paradigms. Di Rosa et al. (2015) compared sequential blocks of monetary rewards or losses (0.15€) between young and older participants. During a Simon paradigm, a bonus was awarded for fast and correct responses, whereas slow or incorrect responses were associated with losses. For young adults, Simon effects (i.e., differences in accuracy for incongruent vs. congruent trials) were smaller for blocks with potential losses than rewards, suggesting more efficient processing for the loss condition. For older adults, behavioral differences between reward and loss conditions were less systematic. In addition, young adults shifted to a more conservative response tendency in the loss condition, whereas older adults adopted did so in the reward condition. These opposing patterns imply that rewards and losses had a qualitatively different impact in each age group (Di Rosa et al., 2015). In a task combining flanker and attentional cueing, Williams et al. (2017) provided incentives on randomly intermixed trials. Young and older participants could either gain or avoid loosing $.10 from a pre-experimental balance of $30 (between-participant comparisons). A combined performance index was used to compare the age groups, indicating that both types of rewards improved overall performance across groups, but both effects were more pronounced for younger adults (Williams et al., 2017). However, as increasingly fast and accurate responses were rewarded/not penalized in this paradigm, rewards not only reduced overall RTs, but also considerably increased interference effects in terms of accuracy. This pattern of results suggests that incentives encouraged participants to prioritize speed at the expense of overall accuracy rather than to enhance cognitive control. Using functional imaging, Spaniol et al. (2015) compared how young and older adults evaluate monetary incentive cues ($5 vs. $0) signaling how much money could be gained or lost in the subsequent trial. Performance in a target detection task was equated between age groups by adjusting the target duration based on each individual's performance in the previous trial. Still, cumulative earnings were higher for young adults, who modulated their performance as a function of incentives much more than did older adults. Conversely, associated fMRI data revealed age-invariant activity in the reward circuitry. However, in line with the behavioral earnings, only young adults de-activated the default network for the gain/loss condition more than for the $0 condition. Despite the age-invariant reward-activation, the reverse pattern (i.e., increased task preparation for the non-incentive conditions) was observed in older adults, suggesting difficulties in modulating preparation as a function of changing task incentives (Spaniol et al., 2015).

To summarize, tentative evidence available so far suggests that behavioral age differences in cognitive control persist when monetary rewards or losses are added to the informational content of performance feedback. Older adults appear to scarcely modify their behavior based on rewards. Conversely, young adults incorporate reward contingencies more flexibly, in particular when emphasis is placed on response speed. Hence, young adults might revise their current strategy, but not necessarily recruit additional control processes successfully (e.g., when a focus on response speed is associated with reduced accuracy). As a result, the precise impact of incentives often depends on which aspect of behavioral performance is examined. Notably, the scarce extant data point to an incentive-based shift in task strategy for the young, but not in older adults. Imaging data complement this picture with unspecific or de-differentiated brain activation patterns during advance preparation (cf. Czernochowski, 2011). However, the precise mechanisms how motivation can modulate cognitive control and whether age mediates these reward effects remain unclear.

## Dissociating Specific Processing Stages With Incentive or Task-Preparation Cues

Instead of providing rewarding feedback in randomized trials or blocks of trials, incentives can also be associated with selective aspects of a complex task. For instance, when one of two tasks during a task-switching paradigm is consistently associated with a bonus, RTs in young adults decrease for the bonus task, and specifically for trials requiring enhanced control due to a switch between tasks. Remarkably, performance for the bonus task also improved for the majority of trials in which no bonus was delivered, and overall task performance improved as an unpredicted side effect, implying that enhanced motivation for one task may not be easy to modulate in a transient manner (Kleinsorge and Rinkenauer, 2012, Exp 1, cf. Section 4.2). Krebs et al. (2013) showed similar effects for young adults in a Stroop task with a fixed association between two out of four colors and potential monetary gains or losses ($.10). Moreover, they found that rewards modulated early fronto-central and occipital ERP components (like the N200 and P300), in line with enhanced attentional processing of reward-related target information and enhanced behavioral performance. Also, conflict-related ERP components (like the $N_{inc}$ and LPC) were observed considerably earlier, suggesting that reward prospects modulate the temporal dynamics of conflict processing (Krebs et al., 2013). Thus, a fixed association between rewarded tasks or stimuli results in enhanced processing for reward-related stimuli, presumably affecting early attentional stages of stimulus evaluation as well as conflict-processing. However, no data on older adults and potential age differences in selectively rewarding certain task aspects are currently available.

Different processing stages can also be dissociated using high-resolution pupillometry. For instance, Chiew and Braver (2013) provided incentives during the AX-CPT on a trial-by-trial basis in a potential reward block as compared to a block without incentives to young participants. Pupil dilation effects were observed prior to the probe during context cue maintenance, along with more efficient performance on AX trials and an increased error rate on AY trials, suggesting that participants considerably relied on advance preparation. In addition to these transient effects, sustained pupil dilation effects were observed during the entire potential reward block, indicating that reward incentives increased the use of cognitive control on a trial-wise as well as block-wise fashion (Chiew and Braver, 2013).

In the vast majority of studies reviewed so far, participants were provided with cues signaling an incentive for the upcoming trial, allowing for task-unspecific advance preparation. Another approach is to provide participants with advance information about the upcoming task, enabling them to prepare more specifically. For instance, Chiew and Braver (2016) compared the effects of reward cues with cues indicating whether the upcoming flanker trial would consist of congruent, neutral, or incongruent stimuli and used drops of apple juice as primary reinforcer in thirsty young participants. Only when reward cues were associated with task-informative cues, cognitive control was enhanced as evident in reduced interference costs.

To the best of our knowledge, only two studies to date examined how incentives specifically modulate temporally distinct cognitive control processes in older adults. In a study by Schmitt et al. (2015), young and older participants performed a version of the AX-CPT including the trial-wise presentation of incentive cues announcing potential monetary gains, losses, or neutral outcomes depending on performance. ERPs revealed enhanced processing of gain and loss compared to neutral cues that was age-invariant. Additionally, younger adults were particularly susceptible to potential losses as indexed by improved preparatory context maintenance (larger CNV) prior to probe presentation as well as increased conflict detection (N450) and resolution (sustained positivity) during response selection whenever incorrect responding would have led to a loss. Conversely, older adults showed enhanced control processes during task preparation (larger cue-locked P3b) and during response preparation and execution (prolonged probe-locked P3b) after gain and loss cues (Schmitt et al., 2015). In a follow-up study, Schmitt et al. (2017) demonstrated that a trial-wise presentation of incentive cues in older adults results in different effects than a block-wise presentation, presumably due to stronger demands on processing resources. When incentives were presented in a block-wise manner, older adults initially processed cues signaling potential losses more strongly, but later during the AX-CPT invested more cognitive resources in preparatory processes like context updating in conditions with potential gains. Hence, how positive and negative incentive cues influence cognitive control in older adults depends on the demands of cue processing.

## Interim Conclusion

In a more or less systematic attempt to modulate cognitive control, various ways of providing performance feedback have been used, and some of the reported inconsistencies can be attributed to subtle differences in the type or timing of this feedback. Two conclusions can be derived from these studies: performance feedback has larger impacts on young than older adults, and positive feedback improves performance more consistently than negative feedback. Conversely, the extent to which negative feedback is instrumental in improving performance depends on the exact paradigm and available processing resources, hence older adults' performance may suffer rather than benefit from performance feedback. Cognitive accounts have tried to explain this phenomenon with unsuccessful attempts to up-regulate control processes and less differentiated conflict signals accumulating over several trials. Alternatively, age differences in long-time motivations like the desire to perform well or anxiety related to age-related performance decrements could be responsible for the failure to benefit from negative performance feedback, which would both render negative performance feedback particular salient for older adults. As a result, attentional resources would be taken away from pursuing the task at hand. The scarce available evidence suggests that adding monetary rewards or losses to informational performance feedback does not change this general pattern of results. Indeed, behavioral age differences in cognitive control might even increase as young adults incorporate reward contingencies more flexibly and might enhance cognitive control based on reward prospect, whereas older adults barely modify their behavior based on motivational incentives (Williams et al., 2017), or change their response pattern with respect to speed-accuracy tradeoffs to the opposite direction compared to young adults (Di Rosa et al., 2015).

Critically, cognitive control mechanisms are typically inferred indirectly by analyzing how performance in subsequent trials is modulated as a consequence of feedback. In order to determine how differential control processes may be targeted by incentives, more specific task manipulations are necessary. One promising way is to provide advance cues to specifically assess the effects of incentives or to allow for task-specific preparation. During incentive cue processing, the extant data consistently point to an incentive-based shift in task strategy consistent with enhanced preparation for reward-trials in the young. With respect to aging, evidence is scarce: only one fMRI study examined reward cue processing in older adults. Despite age-invariant activity in the reward circuitry, older adults increased task preparation for the non-incentive conditions and thus earned fewer rewards compared to the young who showed the opposite pattern (Spaniol et al., 2015). Similarly, two recent ERP studies provide evidence that older adults modulate early preparatory cognitive processes and late response-selection stages based on reward or loss incentive cues, however, rely on different processes compared to young adults (Schmitt et al., 2015, 2017). Notably, timing is critical for efficient use of both incentive and task-specific cues, and enhanced cognitive control is only observed when sufficient time is available to process incentive cues and hence allow advance preparation (Chiew and Braver, 2016). Notably, older adults often require additional time to prepare for an upcoming task, and age differences in recruiting cognitive control are smaller for long as compared to shorter preparatory intervals (cf. Czernochowski, 2011).

Taken together, age differences are often accentuated rather than diminished when providing performance feedback or monetary rewards in an attempt to enhance motivation. Only under specific circumstances, control processes appear to be effectively enhanced by motivational interventions in older adults, for instance when positive feedback is provided based on performance aspects with sufficient room to improve, or when early advance cues provide the opportunity to make up for less efficient processing in old age. However, the precise mechanisms underlying successful motivational interventions currently remain open.

# POTENTIAL MECHANISMS OF MOTIVATION ON PERFORMANCE MONITORING AND COGNITIVE CONTROL IN OLD AGE

In order to fully understand cognitive processing in old age, it is critical to take into account neurobiological factors associated with aging and potentially underlying observed changes in cognition. Despite an immense variability of cognitive functions observed in old age (Fabiani, 2012) and the potential role of compensation and functional re-organization to mitigate existing neurological deficits (e.g., Stern, 2002; Reuter-Lorenz and Lustig, 2005; Czernochowski et al., 2008), two neurobiological factors have been consistently implicated in cognitive aging: in terms of brain structures, negative consequences of aging are particularly pronounced in the PFC (for reviews, see Raz, 2000; Samson and Barnes, 2013), and specifically the dorsolateral PFC (e.g., MacPherson et al., 2002), implying that at least some deficits in cognitive control operations relying on these brain areas are characteristic for older individuals. In terms of neurotransmitter systems, aging affects predominantly dopaminergic pathways, also responsible for motivation and reward processing (for reviews, see Bäckman et al., 2000). In line with the pivotal role of dopamine for reward processing, pharmacological increases in dopamine levels further enhance the differentiation between rewarded and non-rewarded conditions in young adults relative to placebo (e.g., Weis et al., 2012), implying that reduced levels of dopamine might directly underlie at least some of the observed age differences reviewed above. However, large inter-individual variability and distinct optimal dopamine levels depending on the precise nature of each cognitive control task complicate the study of the precise dose-dependent effects of dopamine (Cools and D'Esposito, 2011).

One very influential neurobiological model of aging and its impact on cognitive control that might be able to incorporate the influence of motivation on cognition proposes that disruptions in dopaminergic neurotransmission can be understood as a common underlying mechanism for a variety of age-associated deficits across multiple cognitive domains (Braver and Barch, 2002). According to this model, the dorsolateral PFC and dopaminergic projections to this region are held to serve three distinct functions: (1) active maintenance of context representations in working memory, (2) biasing of local representations to prioritize currently relevant information according to this context, and (3) a gating mechanism subserved by phasic releases of dopamine to allow newly relevant information to be used for updating context information when appropriate. Dopaminergic projections to the dorsolateral PFC are believed to regulate the balance between stable context representations, necessary to inhibit currently irrelevant information in the pursuit of goal-directed behavior, and the flexibility to update context information according to new demands or task instructions. Of particular relevance for the question of how motivation might affect cognition, the phasic release of dopamine may trigger the updating of context information by signaling reward-predictive information to be represented as context. When these dopaminergic pathways are disturbed in the aging process, older adults will experience difficulty in the active representation of context in working memory, causing cognitive deficits across various cognitive domains. Notably, context updating associated with the phasic release of dopamine appears most vulnerable to aging, and deficits in this particular aspect of cognitive functioning are observed already relatively early in the aging process. Conversely, the tonic release of dopamine has been implicated in the active maintenance of context information and seems susceptible to more advanced age only. Ultimately, these changes negatively impact various aspects of cognitive control, which relies on an active representation of current task rules and goals (Braver and Barch, 2002). Hence, it is of utmost importance to know how these age deficits can be ameliorated. The above literature review demonstrated that using rewards to influence performance monitoring and cognitive control might be a promising way to do this. However, empirical research to date has only begun to elucidate the precise circumstances in which enhanced motivation will have the desired effects.

## The Dual Mechanisms of Control (DMC) Framework

As mentioned above, the conflict monitoring account (Botvinick et al., 2001) proposes that the detection of response conflict, provided externally by negative performance feedback or internally by realizing that we just committed an error, can trigger the recruitment of additional control resources to promote future task performance. This mechanism can prevent further response conflict in subsequent trials until control resources are no longer deemed necessary and hence are down-regulated again. Extending this model by introducing an alternative to this so-called *reactive control*, the DMC framework (Braver et al., 2007; Braver, 2012) posits that additional control processes can be activated proactively when upcoming response conflict can be expected, for instance when participants are required to maintain a task context during sustained attention tasks. Hence, *proactive control* is a more stable and temporally sustained process resulting in both fast and accurate responses, as conflict does not need to be detected and resolved. As proactive control in particular is not feasible in situations of unexpected response conflict and requires considerable attentional resources to be maintained over time, participants switch to a more reactive control-mode when necessary. The reactive control process, in turn, is subject to considerable trial-by-trial variability, and particularly useful in a self-paced task when responses can be withheld as response conflict builds up due to simultaneous activation of response tendencies until the appropriate response selection can be employed to allow for slow, but accurate responding. Hence, both control processes can be used flexibly according to task demands and attentional resources and are subject to continuous fluctuations. Therefore, the DMC framework has important implications for the role of motivation in moderating cognitive control. In recent years, empirical evidence for the DMC has dissociated proactive vs. reactive control modes and its putative underlying neuronal substrates using fMRI (e.g., Locke and Braver, 2008), ERPs (e.g., Czernochowski, 2014; Arbula et al., 2016) or high-resolution pupillometry (Chiew and Braver, 2013). However, it is often not sufficient to allow for advance preparation when trying to elicit proactive control, even when there is room for improvement in individual task performance. Notably, prior work has consistently demonstrated that young adults are particularly likely to activate the demanding proactive control mode promoting advanced preparation when motivation is enhanced via performance-contingent reward incentives.

In the context of aging research, the DMC model is particularly intriguing as older individuals have specific deficits in context processing as a result of neurodegenerative decline in the prefrontal dopamine system (cf. Braver et al., 2001), as detailed above. By comparing fMRI activity during the AX-CPT paradigm, Paxton et al. (2008) provided empirical support for a dissociable time course of control processes in young and older participants when no incentives or external performance feedback were provided. In line with a proactive control strategy and the results reviewed above, right dorsolateral PFC activity was observed during the cue-target interval for young adults. By contrast, older adults only activated this area after target onset, suggesting a shift to a reactive control strategy (Paxton et al., 2008). This initial finding and the specific time course proposed for control processes in the DMC, provide a useful tool to examine reactive and proactive control processes in young and older adults. For instance, to identify an ERP correlate for reactive control, Czernochowski et al. (2010) compared response-locked ERP averages during a cued task-switch paradigm, in which conflict increased along with task difficulty for older adults in particular. Slow and fast responses for each task condition were selected to contrast responses based predominantly on reactive or proactive control. For young adults, a negative ERP modulation preceding the response at left frontal electrode sites (pre-response negativity or PRN) was observed along with behavioral costs selectively for slow responses during high-conflict trials taken to reflect predominantly reactive control. By contrast, as predicted by the DMC, the corresponding ERP modulation as well as pronounced RT costs were observed less selectively in older adults, and related to slow, but very accurate responses. Together, these results suggest that young adults employed reactive control only when necessary to support performance for high conflict trials, whereas older adults relied predominantly on reactive control, as evident in additional neuronal activity preceding the response.

The DMC also has important implications regarding the role of motivation to mitigate age differences in cognitive control. Notably, the DMC model explicitly posits that older adults suffer from a specific neurocognitive deficit in maintaining context representations. Hence, older adults would be compelled to rely predominantly on reactive control processes. In line with a true deficit in recruiting proactive control, age differences in terms of qualitatively different modes of controlled processing should be relatively stable across time and experimental incentive conditions. Alternatively, reactive control – sharing a number of characteristics with prioritizing accuracy over speed of responding as typically observed in older adults (cf. Rabbitt, 1979) – might at least to some extent reflect a deliberate or customary choice of strategy. In this scenario, older adults' preference for reactive control should be less stable and modifiable by introducing incentives. As reviewed in Section "Motivational Influences on Cognitive Control," introducing monetary rewards or penalties does not appear sufficient to induce qualitative changes in the type of control processes recruited by older adults. By contrast to young adults, a lack of motivation to select more effortful strategies to promote task performance does not appear to be the critical limiting factor for older adults (see also Braver et al., 2014). In fact, one of the first studies to report changes in control modes in older adults relied on a strategy training rather than reward incentives (Braver et al., 2009). This finding has important implications: despite age-related neurocognitive changes in the dopaminergic system and structural changes to dorsolateral PFC, the use of proactive control is feasible in older adults. However, at the same time this finding underlines the fact that old age is associated with a less flexible use of cognitive control. For young adults, providing monetary incentives or strategy training promotes proactive control, whereas potential monetary losses or introducing NoGo-trials discourages the use of proactive control (Gonthier et al., 2016). Monetary incentives or performance feedback may promote modes of cognitive control in older adults only under specific circumstances which are currently not evaluated in sufficient detail, for instance when sufficient time and processing resources are available (e.g., Schmitt et al., 2017). Another step may include more explicit explanations on the relative importance of rapid and correct responses for many laboratory paradigms, which typically differ between older and young adults.

## OPEN ISSUES, CAVEATS, AND FUTURE DIRECTIONS

On a more general note, motivational factors are not only a promising tool for mitigating age-related reductions in performance monitoring and cognitive control, intrinsic motivational age differences participants bring to the lab are likely to affect how incentives are processed and which ones are prioritized. In line with this, older participants often appear particularly motivated to reach good performance, although this is rarely formally assessed (for an exception, see Staub et al., 2014). To further complicate matters, increased motivation is likely to result in increased effort mobilized for the task, but this may not necessarily translate to better performance, particularly in old age. For instance, Ennis et al. (2013) compared young and older participants during a modified Sternberg memory search task and compared how much effort each group invested, as indexed by an increase in systolic blood pressure. Importantly, they also varied objective task difficulty and recorded motivation to do well as well as perceived control. In line with prior investigations, memory performance declined as a function of task difficulty and age. Extending prior work and in contrast to behavioral performance levels, findings suggest that older compared to younger participants invested more effort at all levels of task difficulty. However, as time on task increased and at the highest level of difficulty, older adults disengaged from the task and reduced their effort more than the young. Notably, motivation to do well and higher perceived control was associated with increased effort only for older participants (Ennis et al., 2013). Thus, not only individual participants but also young and older participants vary systematically in terms of how much effort they are willing – and able – to allocate to a task at hand. Unfortunately, increased effort does not translate linearly to better performance and also depends on task difficulty, time on task, and motivation to perform well. Finally, participants in aging research vary tremendously in terms of chronological age (in the studies reviewed above, age range extends from 48 to 85 years), but also other factors not routinely reported (years and type of education, health parameters, etc.). As a result, even before introducing experimental manipulations, we might compare a highly selective group of older adults in full sprint with young adults routinely jogging at a leisurely pace. In such a scenario, it should not be too surprising that only young adult samples can be motivated by incentives to improve/modulate performance. Given the increased variability in aging, it is likely that sub-groups may use cognitive reserve to compensate difficulties (cf. Czernochowski et al., 2008). As long as older adults have room to compensate by recruiting additional brain areas, there will be no general behavioral age differences in performance levels unless more sophisticated methods are used to quantify evidence for different strategies.

Neuro-scientific studies have begun to help to dissociate behavioral differences and to which extent they might be a result of extensive efforts to compensate age-related decline.

A second open issue concerns the nature and complexity of paradigms used in aging research. Overall difficulty, type of control needed to perform successfully, and precise timing vary considerably, and can account for at least some of the inconsistencies reported above. As reviewed above, timing and the role of speeded responses may be critical for advance preparation, but also has important implications for performance feedback, in particular when older adults invariably receive negative performance feedback based on their overall slower responses and relatively strict algorithms defining response deadlines. To avoid inconclusive results in future studies, some means of comparison of older adult samples across studies would be extremely useful. For instance, including basic measures of working memory spans or performance in simple speed tasks without major demands on cognitive control could help to create a more meaningful overview of performance in old age. Conversely, paradigms used for young and older adults sometimes may need to vary in important details. For instance, the timing of advance cues is of particular relevance when comparing age groups, as older adults typically need additional time for task preparation but may overcome their difficulties with longer cue-target intervals (Czernochowski, 2011).

Particularly useful to delineate specific age-related differences are task variants demonstrating the lack of age differences for selected conditions, or even paradox performance advantages (e.g., weak context representations in the AX-CPT reducing interference in B-X trials). Moreover, indices of effort put into task by each individual and age group, independent of behavioral outcome, could help to shed more light on complex motivation–cognition interactions and avoid circular argumentations. The precise implications of a lack of controlled processing in young adults with healthy PFC functions for potential aging effects in the same task remain unclear. Again, neuro-scientific measures can be fruitful for this endeavor in the future, but at present inter-individual variability in the strategies employed during a specific task or in cognitive reserve more generally, limit viable interpretations of task-unspecific brain activations. The DMC framework has been very instrumental in dissociating cognitive control processes, and spurred empirical evidence of how motivational factors can moderate cognitive control in young and older adults. Conversely, a clear taxonomy of paradigms used to investigate these effects and their implications cognitive control and its specific timing (e.g., with-in trial for self-paced designs or between-trial effects for speeded designs) is still missing to date.

## CONCLUSION

We report empirical findings demonstrating that incentives can modulate performance monitoring and cognitive control. Although studies examining age-related differences across adulthood are scarce, the existing ones indicate that under specific circumstances incentives can ameliorate age-related deficits. However, even apparently subtle inconsistencies between paradigms may have important implications seriously limiting the conclusions that can be drawn at this point. Clearly, future research is needed to clarify (a) the specific circumstances under which incentives can reduce rather than enlarge age-related impairments, (b) which types of incentives are most effective in which age group, and (c) the role of increased effort in overcoming individual differences in ability underlying performance differences in young but especially among older adults. Critically, due to compensatory use of differential strategies or increased effort, the true amount of age-related deficits may be systematically underestimated. While both ways to ameliorate performance deficits are useful and should be encouraged, they cannot be maintained over a longer period, hence it is important to differentiate between typical performance in old age and what can be achieved using all available resources and highest level of motivation. To achieve this, careful and innovative analyses on several aspects of behavioral performance are needed along with neuroscientific methods that together can shed light on the specific neuronal substrates and cognitive processes involved in successful task performance. We also noted several general caveats impeding research in this area, including the fact that participants differ in their long-term motivation to take part in research which can mask age-differences as long as (some) older adults are able to compensate. This substantiates the need to focus on neural activation patterns that can uncover both cognitive and motivational mechanisms underlying age differences in performance.

## AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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# Does the Effort of Processing Potential Incentives Influence the Adaption of Context Updating in Older Adults?

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A number of aging studies suggest that older adults process positive and negative information differently. For instance, the socioemotional selectivity theory postulates that older adults preferably process positive information in service of emotional well-being (Reed and Carstensen, 2012). Moreover, recent research has started to investigate whether incentives like gains or losses can influence cognitive control in an ongoing task. In an earlier study (Schmitt et al., 2015), we examined whether incentive cues, indicating potential monetary gains, losses, or neutral outcomes for good performance in the following trial, would influence older adults' ability to exert cognitive control. Cognitive control was measured in an AX-Continuous-Performance-Task (AX-CPT) in which participants had to select their responses to probe stimuli depending on a preceding context cue. In this study, we did not find support for a positivity effect in older adults, but both gains and losses led to enhanced context processing. As the trial-wise presentation mode may be too demanding on cognitive resources for such a bias to occur, the main goal of the present study was to examine whether motivational mindsets, induced by block-wise presentation of incentives, would result in a positivity effect. For this reason, we examined 17 older participants (65–76 years) in the AX-CPT using a block-wise presentation of incentive cues and compared them to 18 older adults (69–78 years) with the trial-wise presentation mode from our earlier study (Schmitt et al., 2015). Event-related potentials were recorded to the onset of the motivational cue and during the AX-CPT. Our results show that (a) older adults initially process cues signaling potential losses more strongly, but later during the AX-CPT invest more cognitive resources in preparatory processes like context updating in conditions with potential gains, and (b) block-wise and trial-wise presentation of incentive cues differentially influenced cognitive control. When incentives were presented block-wise, the above described valence effects were consistently found. In contrast, when incentives were presented trial-wise, the effects were mixed and salience as well as valence effects can be obtained. Hence, how positive and negative incentive cues influence cognitive control in older adults is dependent on demands of cue processing.

**Keywords: motivational incentives, proactive/reactive cognitive control, context processing, aging, ERPs**

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# INTRODUCTION

In daily life, motivation and cognition interact in many ways to determine goal-directed behavior. Motivational influences on goal-directed behavior become especially important in old age, when failures of cognitive functioning dramatically affect individual autonomy (Schmitt and Kray, 2015). The aim of the present study was to investigate how a specific motivational mindset, i.e., an induced cognitive orientation toward positive (anticipating monetary gains) and negative events (anticipating monetary losses), modulates cognitive control functioning in older adults. We were specifically interested in whether a positive or negative mindset would differentially influence cognitive control functioning.

In their dual-mechanisms-of-control (DMC) theory, Braver and Barch (2002) suggested that age-related impairments in a variety of cognitive tasks can be ascribed to age-related neuro-biological changes in the prefrontal cortex (PFC) and the dopamine (DA) system (Suhara et al., 1991; Raz, 2000; Bäckman and Farde, 2005) associated with the ability to process and update context information. Although the definition of "context" might differ between research domains (Ibañez and Manes, 2012), context information in the DMC theory refers to task instructions, rules and goals that, akin to a mindset, are actively maintained in memory to optimally adjust behavior (cf. Braver et al., 2005). In particular, the DMC theory proposes an age-differential pattern of cognitive control associated with processing and updating context information. It assumes that younger adults predominantly engage in proactive control, i.e., an early selection, updating, and maintenance of contextual information to bias subsequent cognitive processing. Functional magnetic resonance imaging (fMRI) studies indeed show that proactive control in younger adults is related to sustained and anticipatory activity of the lateral PFC and that the midbrain dopamine system supports the updating of PFC-representations in advance preparation prior to task execution (Braver and Barch, 2002; Braver and Bongiolatti, 2002; Bugg, 2013). Older adults, in turn, more heavily rely on reactive control, i.e., a bottom-up manner of processing contextual information when needed to resolve interference in an ongoing task. Accordingly, reactive control in older adults was associated with a transient activation of the lateral PFC as well as an activation of the anterior cingulate cortex (ACC) serving the detection of conflict during task execution (Paxton et al., 2006; Braver et al., 2008; Jimura and Braver, 2009; Braver, 2012).

Using the high temporal resolution of event-related potential (ERPs), our previous studies support differential time courses of pro- and reactive control during context processing across age groups (Schmitt et al., 2014a,b). In these studies, we applied a variant of the AX-CPT (cf. Lenartowicz et al., 2010), consisting of context-dependent (c-dep) and context-independent (c-indep) trials. On c-dep trials, correct responses to one of two probes are directly dependent on a preceding cue. On c-indep trials, the correct response to one of two probes is always the same, irrespective of the preceding context cue. Accordingly, context processing should occur to a lesser extent on c-indep trials as the cue is irrelevant for inferring the correct response. Thus, less cognitive control is needed. Our results in the cue interval indicated that older adults updated more task-relevant context cue information as reflected in a larger P3b (Donchin and Coles, 1988) whenever the identity of the context cue changed, while younger adults showed more updating only in the demanding c-dep trials. We also found a context effect in the contingent negative variation (CNV) that was of the same size for older and younger adults, indicating that more task set maintenance is necessary (Kray et al., 2005) on c-dep than on c-indep trials. Thus, there were age-related differences in how effectively proactive control is applied during context cue processing (Schmitt et al., 2014a). Moreover, older adults exhibited a larger amplitude of the N450 to c-dep than c-indep trials in the probe interval. The N450 component has been interpreted as reflecting conflict processing in the ACC and behavioral adaptation during task execution (West and Alain, 2000a; West, 2004). Thus, larger amplitudes of the N450 to c-dep than c-indep trials may indicate the greater need to resolve response conflict at the time the probe is presented as predicted by a reactive control style (Schmitt et al., 2014b).

Recently, research has investigated the flexible engagement of pro- and reactive control in adapting to various environmental conditions, such as motivational goals. Motivational stimuli signaling potential reward (see Gruber and Otten, 2010; Halsband et al., 2012), have been shown to foster the gating of upcoming task-relevant context information to the PFC (D'Ardenne et al., 2012), and to improve proactive context updating in younger adults (Locke and Braver, 2008; Chiew and Braver, 2013). In contrast, the impact of motivationally negative stimuli (e.g., prospective punishment) on cognitive control processing has been widely neglected (Engelmann and Pessoa, 2007). Similarly, not much is known about how cognitive control functions can be influenced by motivational incentives in old age. In one of our earlier studies, we examined whether different motivational cues modulate the time course of context processing in younger and older adults. In this study, participants performed an adapted version of the AX-CPT that included a trial-wise presentation of motivational cues either announcing a potential monetary gain, loss, or neutral outcome depending on individual performance (Schmitt et al., 2015). The ERP data locked to the motivational cues showed larger P2 and P3b amplitudes to salient gain and loss cues as compared to neutral cues for older adults, indicating more automatic capture of attention (Carretié et al., 2004; for a review, see Olofsson et al., 2008) and more updating of task-relevant information (Donchin and Coles, 1988; Briggs and Martin, 2009; Krebs et al., 2013) in the case of salient motivational cue information. Similarly, in the context cue epoch, older adults displayed larger P3b amplitudes for c-dep than c-indep trials for motivationally salient gain *and* loss cues. Gains and losses also resulted in a temporally prolonged probe-locked P3b, suggesting that older adults invested more in context updating and task reconfiguration during response preparation and execution. Hence, the results suggested that motivationally salient information led to an early cue-locked representation of context conditions in older adults, indicating that potential gains and losses elicit a shift toward proactive control and also strengthen reactive control processes.

However, the finding that older adults did not differentiate between conditions with potential gains and losses was surprising as there is evidence from other cognitive domains showing a preference toward remembering positive information (Mather, 2006). According to the age-related positivity effect, older adults direct more attention to and have better memory of positive relative to negative and neutral information compared to younger adults (Mather and Carstensen, 2005). This effect has been explained in the framework of the socioemotional selectivity theory (SST), postulating that emotional satisfaction and well-being, for instance by remembering more positive events, is prioritized when future time horizons are restricted (Reed and Carstensen, 2012). In line with this idea, Samanez-Larkin et al. (2007) demonstrated that older adults show age-related impairments (reduced striatal and insular activation) during the processing of potential losses, but not during processing of potential gains. Similarly, ERP studies found that older adults' are less affected by negative feedback and rely more on positive feedback during learning (e.g., Eppinger et al., 2008; Pietschmann et al., 2011). However, results are far from consistent. For instance, Eppinger et al. (2013) found age-related impairments in learning from monetary rewards but not losses and Frank and Kong (2008) found that old–old adults (mean age = 77 years) as opposed to young–old adults (mean age = 67 years) were better in learning to avoid stimuli that had been coupled with negative feedback before (see also Hämmerer et al., 2010). Consequently, it is not quite clear to what extent the positivity-effect generalizes to other domains of cognitive functioning. Also, there is evidence for the absence of a positivity effect when less resources for cognitive control are available for the task at hand (Mather and Knight, 2005; Knight et al., 2007; Gorlick et al., 2013) or in individuals with low levels of cognitive control functioning (Reed and Carstensen, 2012). Thus, in our previous study (Schmitt et al., 2015), in which the motivational cue information switched on a trial-to-trial basis, older adults might have been strongly engaged in adapting behavior to relevant motivational cue information on each trial, leaving less cognitive resources for processing the valence of motivational cues and to adjust behavior accordingly.

The main goal of the present study was to investigate whether the valence of motivational information (i.e., cue stimuli indicating potential gains or losses) differently influences cognitive control functioning in older adults when cognitive demands on cue processing are reduced. To this end, older adults performed the AX-CPT containing motivational cues, indicating potential positive (i.e., reward), negative (i.e., punishment) or neutral outcomes, but these motivational cues did not change within the actual task block. We induced a motivational mindset by presenting motivational cues in a block-wise fashion and compared this to the trial-wise cue presentation mode from our earlier study (Schmitt et al., 2015). Motivational effects, i.e., salience and valence effects were operationalized by comparing performance and ERP components on neutral against motivational gain *and* loss blocks, and between loss and gain blocks, respectively (see Bromberg-Martin et al., 2010). Cognitive control functioning was operationalized by examining c-dep and c-indep trials in the AX-CPT (Braver, 2012). Our reasoning was that this block-wise presentation of incentive cues should reduce updating requirements and may lead to the emergence of a valence effect as older adults have sufficient cognitive resources to direct attention toward the processing of positive cue information (Reed and Carstensen, 2012). We assumed that if the preference to process positive information in older adults indeed depends on the amount of cognitive resources available, then older adults may show enhanced attention (as indexed by a larger P2) and more updating (as reflected in a larger P3b) after positive relative to negative and neutral cue information in the motivational cue epoch (i.e., a valence effect), when cognitive demands are reduced by a block-wise cue presentation. We further expected this positivity effect to transfer to the AX-CPT, indicating a selective strengthening of context updating when positive information is anticipated. Here, the valence effect should be reflected in an enhanced difference between c-dep and c-indep trials in P3b and CNV amplitudes in the context cue epoch and in N450 amplitudes in the probe epoch on monetary gain trials only.

## MATERIALS AND METHODS

### Participants

Twenty-three older adults, recruited from a subject pool at Saarland University, took part in the study. Three participants had to be excluded because their latencies and/or error rates (ERs) in the AX-CPT were more than three standard deviations above the group means, indicating that they either did not fully understand the task or the task was too difficult for them. Two further participants were excluded because the number of artifact-free trials for EEG analysis was too low (less than 16) and one because he had already participated in an earlier version of this experiment and had been invited by accident. Therefore, the final sample included 17 older adults (mean age = 71.8 years, age range = 65–76 years, 53% females). Informed consent was obtained from each participant. The study was approved by the local ethics committee at Saarland University and conducted in accordance with the Declaration of Helsinki. Subjects were paid eight Euros per hour with an additional reimbursement based on the money won in the motivational blocks (see **Table 1**). All participants had normal or corrected-to-normal vision, no signs of color-blindness, and were free of self-reported neurological

**TABLE 1 |** Sample characteristics and results of psychometric measures (means and standard deviations).

| | Older adults | |
|---|---|---|
| **Measure** | ***M*** | ***SD*** |
| *n* | 17 | |
| Mean age (years) | 71.8 | 3.0 |
| Age range (years) | 65–76 | |
| Gender distribution (% female) | 43% | |
| Digit symbol substitution test | 51.1 | 6.5 |
| Counting span | 29.7 | 7.6 |
| Spot-a-word | 28.7 | 3.4 |
| Money won (euro) | 7.2 | 1.3 |

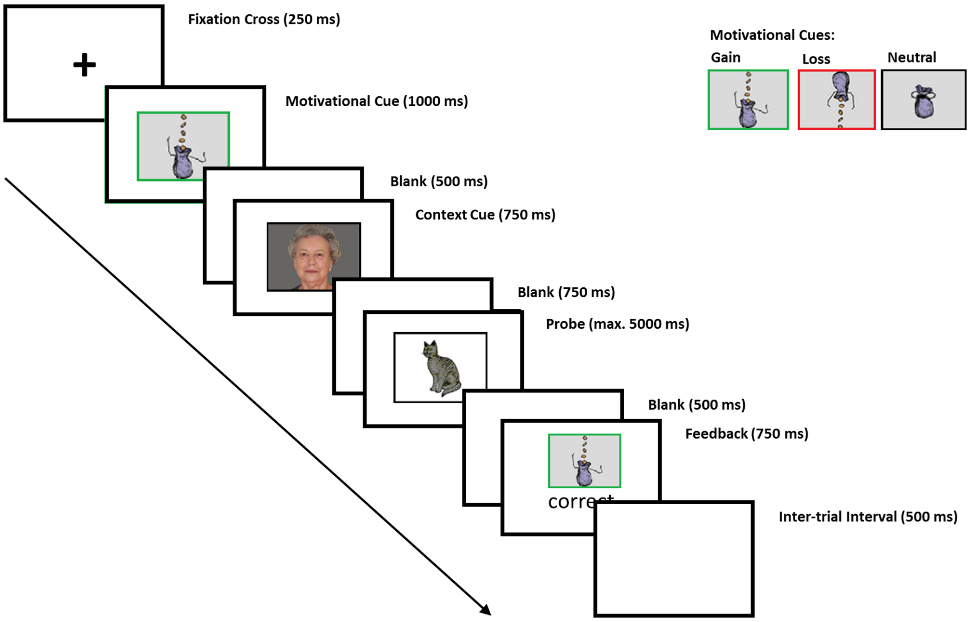

**FIGURE 1 |** Assignment of cues and probes to correct response keys on c-dep and c-indep trials. On c-dep trials, the correct responses to probes (as indexed by the pictures of the bird and the cat) after presentation of the cues (as indexed by the pictures of the younger woman and the older man) are exactly reversed for the two cues; i.e., participants have to press the left response key in case the bird follows the younger woman, whereas they have to press the right key in case the bird follows the older man. On c-indep trials, correct responses to the probes (as indexed by the pictures of the fish and the rabbit) are identical for both cues (as indexed by the pictures of the younger man and the older woman); i.e., participants always have to press the left key if they see the picture of the fish and the right key if they see the picture of the rabbit (Facial pictures by Minear and Park, 2004, pictures of animals by Rossion and Pourtois, 2004).

or psychological disorders. All subjects also performed three psychometric tests of cognitive functioning: The Digit-Symbol-Substitution Test (DSST, adapted from Wechsler, 2008) measured speed of processing, the Counting Span task (CS; adapted from Unsworth et al., 2005) served as a WM span measure, and the Spot-a-word test (Lehrl, 1977; Lindenberger et al., 1993) was used as an indicator of vocabulary. The results of the three cognitive control variables and the characteristics of the sample are displayed in **Table 1**. All participants performed well within their normal age range (cf. Myerson et al., 2003; Kray et al., 2008; Elliot et al., 2011; Ferdinand and Kray, 2013).

The participants described above performed the AX-CPT with incentive cues presented in a block-wise fashion (block-wise group) and were compared with the older participants from our previous experiment (for a detailed sample description, see Schmitt et al., 2015), who performed the AX-CPT with incentive cues presented in a trial-wise fashion (trial-wise group).

## Tasks and Stimuli

A modified version of the AX-CPT was applied using E-Prime 2 (Psychology Software Tools) in which subjects saw cue-probe combinations (for a detailed description, see Schmitt et al., 2015; adapted from Lenartowicz et al., 2010; see **Figure 1**). We used four pictures of young and old men and women (Minear and Park, 2004) as context cue stimuli and four pictures of animals (i.e., rabbit, bird, cat, and fish from the database by Rossion and Pourtois (2004)) as probe stimuli. On c-dep trials, correct responses to subsequent probes were dependent on the preceding context cue. For instance, subjects were instructed to press the *left* key when the picture of the *bird* followed the picture of the *young woman* and the *right* key when the picture of the *cat* followed the picture of the *young woman*. These stimulus-response assignments were reversed when the "bird" and the "cat" followed the picture of the old man. On c-indep trials, correct responses to probes were independent of the preceding context cue. Subjects were instructed to press the *left* key when the picture of the *rabbit* followed the picture of the *old woman* and the *right* key when the picture of the *fish* followed the picture of the *old woman*. The same stimulus-response assignments were required when the "fish" and the "rabbit" followed the picture of the young man. Note that subjects were instructed to respond to four cue-probe combinations and were not informed about the two different trial types (i.e., c-dep and c-indep trials).

Prior to the cue-probe combinations, participants received three variants of motivational cues (see **Figure 1**). The "neutral" motivational cue was a picture of a (closed) moneybag surrounded by a black frame. The motivational gain cue was a picture of a gain moneybag, i.e., money falling into the bag, which was surrounded by a green frame. The loss cue was a picture of a loss moneybag, showing money dropping out of the bag, was surrounded by a red frame. Participants were instructed that the gain cue indicated the possibility to win money if they responded correctly, and that the loss cue indicated the risk to lose money if they responded incorrectly. On neutral blocks, the monetary value remained constant irrespective of the response accuracy. Stimuli were presented in a 3.5 cm × 5.5 cm black frame on the center of a 24 in. monitor on a gray background and participants' viewing distance was approximately 80 cm. The assignment of context-cue conditions to response keys was pseudo-random across participants with the only constraint that a young and an old facial picture were presented in both trial types for each participant. This led to four context conditions that were equally assigned to male and female subjects.

## Procedure

Subjects first filled in an informed consent, a demographic and health questionnaire, and a handedness rating (Oldfield, 1971). Afterward, they were tested on the three control variables described above and the AX-CPT. All subjects were initially taught the meaning of the motivational cues and then performed three practice blocks of the AX-CPT. To familiarize participants with both trial types, the first practice block consisted of c-indep trials only, the second block of c-dep trials only, and the third practice block included both c-dep and c-indep trials. In case subjects did not understand the task during the first practice run, practice blocks were repeated. None of the subjects had more than two repetitions of any practice block.

Each participant performed the AX-CPT under three motivational mind-sets that were induced by block-wise instructions for three cue conditions (neutral, gain, or loss). In the first three task blocks, the three motivational conditions (neutral, gain, and loss) were presented successively in a random order. This order was then exactly repeated in the next three blocks, yielding a total of six motivational blocks. Each motivational block consisted of 48 c-dep and 48 c-indep trials. As a result, the AX-CPT consisted of a total of 96 c-dep and c-indep trials for each of the three motivational conditions (neutral, gain, and loss). After each block, a rest period was mandatory. In the rest period, participants received feedback about the amount of money they had earned so far, which was calculated by subtracting the amount of money lost on loss blocks from money won during gain blocks. In a single trial, there was no direct association between performance and the exact amount of money won or lost. Instead, the correctness of the response was indicated by abstract feedback (the respective money bag) together with the words "correct" or "incorrect!". After each block, the outcome was calculated by the difference between correct responses during gain and incorrect responses during loss trials, for both c-dep and c-indep trials. Since performance on c-indep trials was close to ceiling, only ERs below 5% were rewarded the highest amount of 75 cents, with decreasing rewards as ERs increased. Overall, the achieved outcome was always greater than zero. At the end of the whole experiment, subjects again received feedback about the total amount of money won over the course of six blocks. Participants were instructed to respond as quickly and as accurately as possible.

Within a block of the AX-CPT, each trial started with a fixation cross (250 ms), followed by a motivational cue (1000 ms) indicating the incentive value (potential gain, potential loss, and neutral outcome) of the subsequent cue-probe combination. The motivational cue was followed by a blank interval (500 ms), the context cue (750 ms), and another blank (750 ms). The context cue indicated whether the following trial was c-dep or c-indep. C-dep and c-indep trials were randomly mixed within the task. Probes were presented for 5000 ms or until the subject responded, i.e., if the response was not given within 5000 ms, the trial was considered as a time-out. The probe was followed by another blank (500 ms). Finally, feedback ("correct," "incorrect," or "too slow") was presented for 750 ms containing information about the response correctness and the achieved outcome. The inter-trial interval was 500 ms (see Schmitt et al., 2015).

## EEG Recording and Pre-processing

Participants were seated in a dimly lit, electrically shielded, and sound-attenuated chamber. EEG and electro-ocular activity (EOG) were recorded simultaneously by Brain Vision Recorder (Brain Products, Germany) with 59 Ag/AgCl active electrodes places in an elastic cap (extended international 10–20 system; Jasper, 1958). The left mastoid served as a reference and the ground electrode was placed at AFz. Impedances were kept below 20 kΩ. The EOG measured vertical eye movements from two electrodes above and below the right eye, and horizontal eye movements from the outer canthi of both eyes. EEG and EOG were low-pass filtered online (250 Hz), analog-to-digital converted (500 Hz SR), re-referenced to linked mastoids, and band-bass filtered offline from 0.01 to 30 Hz prior to statistical analysis. Whenever the standard deviation in a moving 200 ms time interval exceeded 30 μV in ocular electrodes or 20 μV in the representative electrode Cz, data were marked as artifacts. Recording epochs including eye-movements were corrected by using a linear regression approach (Gratton et al., 1983). The remaining artifacts were excluded after segmentation of the data by excluding the respective trials. Data pre-processing also included a visual screening for artifacts in all electrodes and trials with additional artifacts were removed before averaging. For visual presentation in **Figures 3** and **5**, the waveforms were low-pass filtered at 12 Hz. Offline EEG processing was done using EEProbe (ANT).

## Data Analysis

Practice blocks and trials with reaction times (RTs) faster than 100 ms were excluded from analysis (<0.1% of trials). The analysis of latencies was based on correct responses. The analysis of ERs included incorrect responses without time-outs. ERPs were recorded time-locked to the onset of the motivational cue, the context cue, and the probe and were analyzed at three midline electrodes over frontal (Fz), central (Cz), and parietal (Pz) areas. A 100 ms pre-stimulus baseline was used for all ERP averages. Note that we had to exclude one participant from the probe data due to less than 16 artifact-free trials for probe analysis. The selection of the time interval and the electrodes for statistical analyses of the EEG components was based on the literature and our previous ERP-analysis on the AX-CPT, together with visual inspection of peak latencies of the components obtained. In the motivational cue interval, we analyzed mean P2 amplitudes in a time window from 150 to 250 ms (cf. Olofsson et al., 2008), and mean P3 amplitudes in a time window from 500 to 700 ms after cue onset (cf. West and Alain, 2000b; Karayanidis et al., 2003; West et al., 2005; Friedman et al., 2008). In the context-cue interval, the analyses focused on the amplitude of the P3b and the CNV in time windows ranging from 450 to 650 ms and 1000 to 1500 ms after presentation of the context cue, respectively (cf. Karayanidis et al., 2003). Visual inspection of the ERPs in the probe epoch indicated that there seemed to be substantial component overlap between a centrally focused N450 and a parietally focused P3b. Because this makes it very difficult to draw conclusions regarding the underlying cognitive processes, we refrained from analyzing the probe-locked data.

In order to focus on motivational influences on context processing, and to analyze cue salience and valence effects, the effects of the motivational manipulation (for behavioral data and ERPs) were analyzed in terms of two *a priori* defined orthogonal contrasts: The first contrast (termed Salience effect) compared mean performance and ERPs on neutral blocks against the two motivational (gain and loss) blocks. The second contrast (termed Valence effect) compared mean performance and ERPs on loss vs. gain blocks. Consequently, for ERP data in the motivational cue interval, salience and valence effects were analyzed in ANOVAs including the additional factors Experimental Group (trial-wise vs. block-wise manipulation) and Anterior–Posterior (electrodes Fz, Cz, Pz). For behavioral data and ERPs in the context-cue interval, the effects of the Salience and Valence contrasts were analyzed in ANOVAs including the additional factors Experimental Group, Context Condition (c-dep, c-indep trials) and – for ERP data only – Anterior–Posterior (electrodes Fz, Cz, Pz). Additionally, to avoid unnecessary comparisons between electrode sites, the factor Anterior–Posterior was analyzed using repeated contrasts, i.e., Fz vs. Cz and Cz vs. Pz, that were defined *a priori*. For reasons of clarity, all significant ($p < 0.05$) and marginally significant ($p < 0.10$) effects are reported in the results section, non-significant effects are mostly omitted.

For all analyses, the alpha level was set to $\alpha = 0.05$. Bonferroni–Holm corrections were applied on non-planned *post hoc* comparisons and the corrected $p$-values are reported. If necessary, Greenhouse–Geisser corrections for non-sphericity (Keselman and Rogan, 1980) were applied and epsilon corrected $p$-values are reported together with epsilon values ($\varepsilon$) and uncorrected degrees of freedom.

# RESULTS

## Behavioral Data

The ANOVAs with the factors Experimental Group (trial-wise vs. block-wise manipulation), Context (c-dep vs. c-indep), and the two planned contrasts reflecting Salience (motivational vs. neutral blocks) and Valence (gain vs. loss blocks) revealed a main effect of Context Condition for both, ERs, $F(1,33) = 36.1$, $p < 0.001$, $\eta_p^2 = 0.52$, and reactions times, $F(1,33) = 57.1$, $p < 0.001$, $\eta_p^2 = 0.63$, indicating higher ERs and longer latencies on c-dep than c-indep trials (see **Figure 2**). For ERs, there was also a marginally significant interaction of Experimental Group and Salience, $F(1,33) = 3.0$, $p = 0.09$, $\eta_p^2 = 0.03$. However, *post hoc* analyses did neither reveal a significant effect of Salience in one of the experimental groups (all $p$-values $> 0.15$), nor a significant effect of Experimental Group for salient or neutral cues (all $p$-values $> 0.15$).

## ERPs Locked to the Motivational Cue

### P2

The ANOVAs with the factors Experimental Group, Anterior–Posterior, and the two planned contrasts reflecting Salience and Valence on the mean P2 amplitudes revealed significant effects of Experimental Group, $F(1,33) = 5.6$, $p < 0.05$, $\eta_p^2 = 0.15$, Anterior–Posterior (Fz/Cz contrast), $F(1,33) = 8.5$, $p < 0.01$, $\eta_p^2 = 0.21$, and of Salience, $F(1,33) = 15.4$, $p < 0.001$, $\eta_p^2 = 0.32$, and Valence, $F(1,33) = 5.2$, $p < 0.05$, $\eta_p^2 = 0.14$. It also resulted in interactions between Experimental Group and Salience, $F(1,33) = 5.9$, $p < 0.05$, $\eta_p^2 = 0.15$, Salience and Anterior–Posterior (Cz/Pz contrast), $F(1,33) = 10.2$, $p < 0.01$, $\eta_p^2 = 0.24$, Experimental Group and Valence, $F(1,33) = 5.2$, $p < 0.05$, $\eta_p^2 = 0.14$, and Experimental Group and Anterior–Posterior. To dissolve these interactions, separate analyses were calculated for the two experimental groups.

In the trial-wise manipulation group, we found a main effect of Salience, $F(1,17) = 22.8$, $p < 0.001$, $\eta_p^2 = 0.57$, denoting that salient trials elicited a larger P2 than neutral ones, and an interaction between Salience and Anterior–Posterior (Cz/Pz contrast), $F(1,17) = 8.3$, $p < 0.05$, $\eta_p^2 = 0.33$. This interaction was due to a larger central P2 for salient cues [P2 larger for salient than neutral cues at Cz: $F(1,17) = 20.1$, $p < 0.001$, $\eta_p^2 = 0.54$, P2 larger for salient than neutral cues at Pz: $F(1,17) = 8.4$, $p < 0.05$, $\eta_p^2 = 0.33$; P2 marginally larger at Cz than Pz for salient cues only, $F(1,17) = 3$, $p = 0.09$, $\eta_p^2 = 0.17$].

In the block-wise manipulation group, we found a main effect of Anterior–Posterior (Fz/Cz contrast), with larger P2 amplitudes at central than frontal sites, $F(1,16) = 11.6$, $p < 0.01$, $\eta_p^2 = 0.42$, as well as a significant effect of Valence, $F(1,16) = 7.3$, $p < 0.05$, $\eta_p^2 = 0.31$, indicating larger P2 amplitudes for loss vs. gain cues (see **Figure 3**). To check whether this P2 valence effect is reduced with repeated cue presentation, we additionally analyzed the first against the second half of trials within a block by means of *post hoc* tests. Results indicated that the P2 valence effect was marginally significant in the first half ($p = 0.07$), while a significant effect occurred in the second half of blocks, $F(1,16) = 7.9$, $p < 0.025$, $\eta_p^2 = 0.33$ (see **Figure 4**).

### P3b

The ANOVAs with the factors Experimental Group, Anterior–Posterior, and the two planned contrasts reflecting Salience and Valence on the P3b amplitudes revealed a main effect of Anterior–Posterior, i.e., a parietal distribution of the P3b [larger P3b at Pz than Cz: $F(1,33) = 6.6$, $p < 0.05$, $\eta_p^2 = 0.17$; larger P3b at Cz than Fz: $F(1,33) = 5.6$, $p < 0.05$, $\eta_p^2 = 0.14$]. It also showed effects of Salience, $F(1,33) = 17.0$, $p < 0.001$, $\eta_p^2 = 0.34$, and Valence, $F(1,33) = 18.5$, $p < 0.001$, $\eta_p^2 = 0.36$, as well as an interaction between Experimental Group, Anterior–Posterior (Fz/Cz contrast), and Salience, $F(1,33) = 4.6$, $p < 0.05$, $\eta_p^2 = 0.12$, and a marginally significant interaction between Experimental Group, Anterior–Posterior (Fz/Cz contrast), and Valence, $F(1,33) = 3.2$, $p = 0.08$, $\eta_p^2 = 0.09$.

Separate analyses in the trial-wise and the block-wise Experimental Group showed significant effects of Salience, indicating a larger P3b for salient motivational than neutral

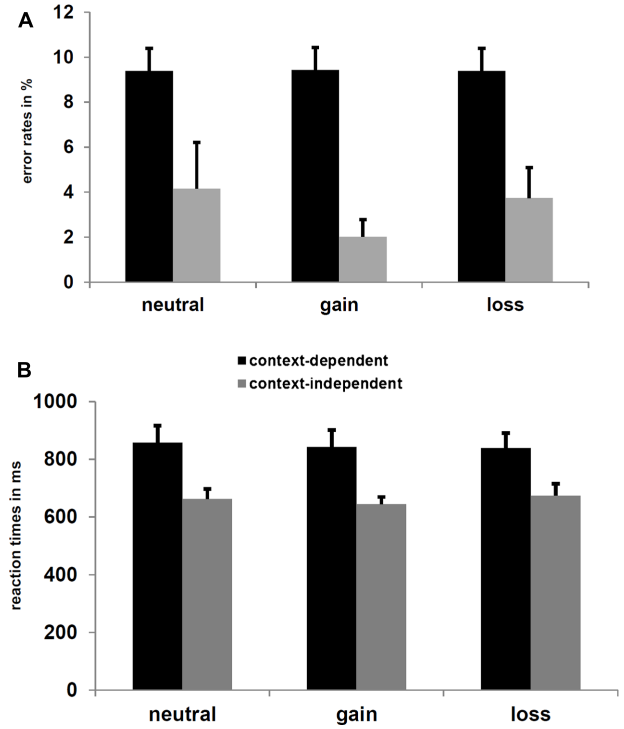

**FIGURE 2 | (A)** Mean error rates (ER) and **(B)** reaction times for c-dep and c-indep trials on neutral, gain, and loss blocks. Error bars represent standard errors of the mean. Significant differences were found between c-dep and c-indep trials.

cues [trial-wise: $F(1,17) = 10.8$, $p < 0.01$, $\eta_p^2 = 0.39$, block-wise: $F(1,16) = 6.4$, $p < 0.05$, $\eta_p^2 = 0.29$], and significant effects of Valence, i.e., a larger P3b amplitude for loss than gain cues [trial-wise: $F(1,17) = 8.7$, $p < 0.01$, $\eta_p^2 = 0.34$, block-wise $F(1,16) = 10.5$, $p < 0.01$, $\eta_p^2 = 0.40$]. To investigate why the interaction with Experimental Group occurred in the overall analysis, we additionally calculated *post hoc* analyses. These revealed that the salience effect in the block-wise group was due to a significant difference between loss and neutral cues, $F(1,16) = 12.6$, $p < 0.025$, $\eta_p^2 = 0.44$, but not between gain and neutral cues ($p = 0.58$, see **Figure 3**). In contrast, in the trial-wise group, there were significant differences between loss and neutral, $F(1,17) = 14.7$, $p < 0.025$, $\eta_p^2 = 0.46$, and gain and neutral cues, $F(1,17) = 5.9$, $p < 0.025$, $\eta_p^2 = 0.44$. This means that while there is a genuine effect of Salience and Valence in the trial-wise group, only loss cues induced a larger P2 and P3b during cue processing in the block-wise manipulation group.

## ERPs Locked to the Context Cue

### P3b

The ANOVAs with the factors Experimental Group, Context, Anterior–Posterior, and the two planned contrasts reflecting Salience and Valence on P3b amplitude showed significants main effects of Valence, $F(1,33) = 5.9$, $p < 0.05$, $\eta_p^2 = 0.15$, and Anterior–Posterior (Cz/Pz contrast), $F(1,33) = 31.5$, $p < 0.001$, $\eta_p^2 = 0.49$, and interactions between Anterior–Posterior (Fz/Cz contrast) and Experimental Group, $F(1,16) = 12.6$, $p < 0.01$, $\eta_p^2 = 0.44$, and Anterior–Posterior and Valence, $F(1,33) = 8.3$, $p < 0.01$, $\eta_p^2 = 0.20$. It also showed a marginally significant interaction between Anterior–Posterior (Fz/Cz contrast) and Salience, $F(1,33) = 3.0$, $p = 0.09$, $\eta_p^2 = 0.08$. Dissolving the interaction between Salience and Anterior–Posterior (Fz/Cz contrast) did not lead to any significant differences (all $p$-values $> 0.34$). Dissolving the interaction between Valence and Anterior–Posterior demonstrated that gain cues had larger P3b amplitudes than loss cues at central electrodes, $F(1,34) = 8.4$, $p < 0.01$, $\eta_p^2 = 0.20$ (see **Figure 5**).

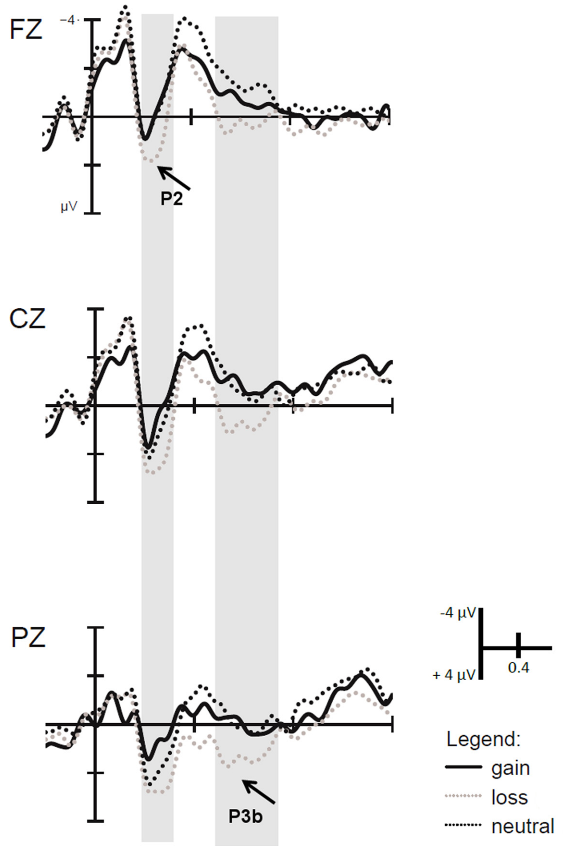

**FIGURE 3 |** Event-related potentials (ERPs) time-locked to the motivational cue. Larger P2 amplitudes in the time window ranging from 150 to 250 ms were found for loss than gain cues. In the time window from 500 to 700 ms, larger P3b amplitudes were found for motivationally salient trials relative to neutral trials due to larger P3b amplitudes on loss trials.

### Contingent Negative Variation (CNV)

The ANOVAs with the factors Experimental Group, Context, Anterior–Posterior, and the two planned contrasts reflecting Salience and Valence on CNV amplitudes showed a significant effect of Context, $F(1,33) = 19.8$, $p < 0.001$, $\eta_p^2 = 0.38$, indicating a larger (more negative) CNV for c-dep than c-indept trials, and of Anterior–Posterior [Fz > Cz contrast: $F(1,33) = 17.1$, $p < 0.001$, $\eta_p^2 = 0.34$; Cz > Pz contrast: $F(1,33) = 48.8$, $p < 0.001$,

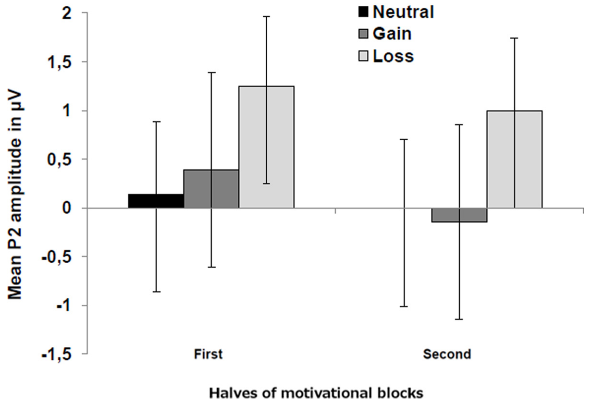

**FIGURE 4 |** Mean P2 amplitudes for neutral, gain, and loss motivational cues presented separately for the first (including trials from 1 to 48) and second half (including trials from 49 to 96) of motivational blocks. Error bars represent standard errors of the mean. Results indicated that the P2 valence effect was stronger in the second half of blocks.

$\eta_p^2 = 0.60$], indicating a centrally focused CNV distribution. We also found a marginally significant effect of Experimental Group, $F(1,33) = 3.8$, $p = 0.06$, $\eta_p^2 = 0.10$ with larger CNV amplitudes for the trial-wise group. Additionally, significant interactions between Salience, Context, and Anterior–Posterior (Cz/Pz contrast), $F(1,33) = 4.5$, $p < 0.05$, $\eta_p^2 = 0.12$, and Valence, Experimental Group, and Anterior–Posterior (Fz/Cz contrast), $F(1,33) = 4.7$, $p < 0.05$, $\eta_p^2 = 0.13$, were obtained.

To dissolve the interaction including the factor Salience, separate ANOVAs were calculated for motivationally neutral and motivationally salient (gain and loss) trials. For salient trials, the CNV was larger at central than parietal electrodes for c-indep, $F(1,34) = 34.4$, $p < 0.001$, $\eta_p^2 = 0.50$, and c-dep trials, $F(1,34) = 44.6$, $p < 0.001$, $\eta_p^2 = 0.58$. Additionally, there was a context effect that was more pronounced at central as compared to parietal electrodes [Cz: $F(1,34) = 13.6$, $p < 0.01$, $\eta_p^2 = 0.29$, Pz: $F(1,34) = 6.4$, $p < 0.05$, $\eta_p^2 = 0.16$], as indexed by the effect sizes. In contrast, only a general effect of CNV distribution was found for neutral trials, with larger CNV amplitudes at central electrodes, $F(1,34) = 45.5$, $p < 0.001$, $\eta_p^2 = 0.57$.

To dissolve the interaction including the factor Valence, different ANOVAs were computed for each Experimental Group. These analyses revealed that for the block-wise group only, there was an interaction between Valence and Anterior–Posterior (Fz/Cz contrast), $F(1,16) = 5.6$, $p < 0.05$, $\eta_p^2 = 0.26$. *Post hoc* analysis showed that this interaction was due to a larger CNV for gain than loss cues at frontal electrodes, $F(1,16) = 5.6$, $p < 0.05$, $\eta_p^2 = 0.26$, as well as a larger CNV on central than frontal areas for loss cues, $F(1,16) = 7.6$, $p < 0.05$, $\eta_p^2 = 0.32$ (see **Figure 5**).

## Summary of Results

In sum, our behavioral results showed a reliable context effect that was not modulated by gain and loss cues and did not differ between the experimental groups. In contrast, for the ERP data we did find differential Group effects. In the motivational cue epoch, salient gain and loss cues elicited a larger P2 and P3b than neutral cues and additionally loss cues elicited a larger P3b than gain cues in the trial-wise group. In contrast, in the block-wise group only the valence effects, i.e., a larger P2 and P3b for loss than for gain cues, remained significant. For the processing of the following context cue, however, we obtained a larger P3b to gain cues that was independent of Experimental Group. In the CNV after the context cue, we obtained a context effect, i.e., a larger CNV for c-dep than c-indep trials, for motivationally salient gain and loss trials in both experimental groups. Additionally, we obtained a larger CNV for gain than loss trials in the block-wise group only. Against our hypotheses, this effect did not interact with the context effect.

# DISCUSSION

The aim of the present study was to examine whether a motivational mindset, i.e., a cognitive orientation toward positive (potential monetary gain) or negative (potential monetary loss) outcomes induced by a block-wise presentation of incentive cues, differentially influences the implementation of cognitive control in older adults. To this end, a block-wise presentation off incentive cues was compared with a trial-wise presentation. Cognitive control was measured by means of the AX-CPT in which older adults had to select their responses to a probe either dependent or independent of a context cue, thus creating a situation with changing demands on cognitive control. Moreover, we applied an ERP approach to examine (a) whether gain and loss cues are processed differently, and (b) whether these incentive cues affect the amount of cognitive control exerted during the following AX-CPT.

## Context Effects

The behavioral data showed longer latencies and higher ERs for c-dep than c-indep trials. This context effect reflects the fact that more cognitive control is necessary to successfully work on the more demanding c-dep trials (cf. Lenartowicz et al., 2010; D'Ardenne et al., 2012; Schmitt et al., 2014a). This behavioral context effect is in line with the ERP results, showing a larger CNV in the context cue epoch to c-dep than c-indep trials. The CNV context effect is thought to reflect the increased need of proactive task preparation in the more demanding c-dep trials and replicates our earlier findings in the AX-CPT without motivational incentives (Schmitt et al., 2014a).

Interestingly, motivational incentives (gains and losses) modulated the context effect in the CNV in the context-cue epoch irrespective of whether incentive cues were presented trial-wise or block-wise: In motivationally salient gain and loss trials, a context effect was obtained, while it was absent for neutral trials. This reflects that gain and loss cues increased task preparation in the more demanding c-dep trials. In the block-wise presentation group, we had expected that a positivity effect would emerge, i.e., that gains would enhance the context effect due to the induction of a motivational mindset. However, this was not found. One simple explanation for this lack of a positivity effect

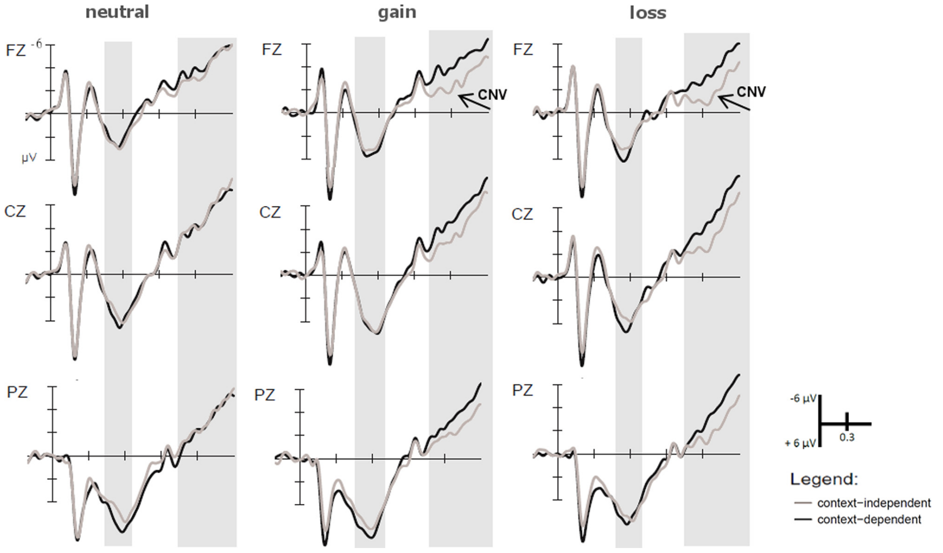

**FIGURE 5 |** ERPs time-locked to the context cue. Marginally larger P3b amplitudes were found for gain than loss blocks in the time window ranging from 450 to 650 ms after context cue onset at central electrodes (Cz) only. In the time window from 1000 to 1500 ms, CNV amplitudes were larger for gain than loss cues at frontal (Fz) electrodes.

could be that older adults may have ignored the cues because they were constant across a block and thus, in principle, redundant. However, our ERP findings in the motivational cue and the context cue interval speak against this idea because they show that (a) the motivational incentive cues were processed differently than neutral cues (see Processing of Motivational Cues) and (b) they do influence cognitive processes during task preparation even after repeated presentation (see Motivational Influences on Cognitive Processing during the AX-CPT). This implies that trial-wise presentation of incentive cues affects cognitive processing in a different way than block-wise presentation of incentive cues, which evokes a more transient motivational mindset. Thus, a more likely explanation is that block-wise in comparison to trial-wise presentation reduces working memory load for older adults to a level that allows them to perform the task similar to when no incentive cues are presented. This is, however, not reflected in a modulation of context effects.

## Processing of Motivational Cues

In the motivational cue epoch, we found that P2 amplitudes were larger after salient gain and loss cues than after neutral cues in the trial-wise group, while they were larger for loss than gain cues in the block-wise group. P3b amplitudes were larger for motivationally salient than neutral cues in the trial-wise group and also larger after loss than gain cues. In the block-wise group, in contrast, we did not obtain a salience effect, but a larger P3b for loss than gain cues. The P2 is known to be associated with a rapid allocation of attention toward a stimulus (Luck and Hillyard, 1994). It has not only been observed in purely cognitive paradigms, but also in terms of an increased orienting of attention toward emotional stimuli (e.g., Ito et al., 1998; Carretié et al., 2001; Huang and Luo, 2006; Kanske and Kotz, 2007; Kanske et al., 2011). The P3b has been linked to the strategic updating of an internal model of the environment by task-relevant information and the relevance ascribed to the motivational cue (Donchin and Coles, 1988; Briggs and Martin, 2009; Krebs et al., 2013). Thus, when presented with incentive cues in a block-wise fashion, older adults seem to allocate more attention to loss cues and invest more in updating task-relevant information after having been presented with a loss cue.

In line with this result, there is evidence that the cognitive processes reflected in the P2 and P3b can be applied relatively flexible. For example, Kanske and Kotz (2007) observed a larger P2 amplitude for emotionally positive as opposed to neutral words while younger adults performed a lexical decision task (see also Kanske et al., 2011). This attention capture effect is not uniformly found toward positive but also toward negative stimuli (e.g., the presentation of negative IAPS pictures; Ito et al., 1998; Carretié et al., 2001; Huang and Luo, 2006). In a similar vein, Zinchenko et al. (2015, 2017) demonstrated that positive as well as negative emotional stimuli lead to increased attention allocation as reflected in an enhanced P200 during conflict processing. Moreover, it has been found that in conditions of heightened state anxiety, there is increased attention allocation to stimuli in a threatening context (Mercado et al., 2006). Although these studies examine emotional rather than motivational manipulations, they show that the attention allocation as reflected in the P2 can be applied relatively flexible, depending on task characteristics. Similarly, it has been demonstrated that P3b amplitude can be influenced by subjective processes of stimulus categorization (Mecklinger and Ullsperger, 1993). Together, this evidence suggests that orienting of attentional resources and updating of task-relevant information can be flexible and depend on task and or person characteristics.

In the present study, inducing a motivational mindset via block-wise presentation of motivational incentives increased the rapid allocation of attentional resources (as reflected in the larger P2 for losses than gains) and the updating of task-relevant information (as reflected in the larger P3b for losses than gains) toward cues signaling potential losses. In the experimental group with trial-wise presentation of incentive cues, this valence effect was only found for the P3b. However, in this group, a salience effect was found in the P2 and the P3b, i.e., older adults paid more attention to all motivationally salient gain and loss cues. As outlined above, this operationalization probably imposed higher demands on working memory resources than a block-wise manipulation, especially for older adults. Thus, it could be speculated that working memory demands might be an additional task characteristic that changes the rapid allocation of attentional resources toward motivational cues. In the case of a high working memory load, older adults might mainly classify the different cues into "salient" vs. "neutral," while under conditions in which they have more resources left, losses might play a more important role. However, this idea needs to be tested more directly in future research by explicitly manipulation working memory load.

Because it has been demonstrated that this rapid allocation of attentional resources decreases with repetition of the same stimulus (Luck and Hillyard, 1994), we additionally investigated in a control analysis whether this valence effect diminishes over the course of time when participants become familiar with the stimuli. This analysis found quite the reverse pattern, namely that the effect was stronger in the second half of the motivational block. Thus, unlike for the repeated presentation of motivationally neutral stimuli, the rapid allocation of attentional resources toward cues indicating potential losses did not abate over time in older adults. This is especially interesting because, in principle, the motivational cues were redundant and hence could mean that they were not able to ignore the negative value of the loss cues specifically.

## Motivational Influences on Cognitive Processing during the AX-CPT

Although motivational cues did not modulate context effects (except for the salience effect in the CNV, see section "4.1 Context Effects" and below), they did influence cognitive processing in the AX-CPT. However, in contrast to the motivational cue epoch where losses were of greater importance, ERP data in the context cue epoch of the AX-CPT showed stronger reactivity to motivational gain cues. Here, we found a larger P3b in the context cue epoch after gains than losses for both experimental groups. Note, however, that when the trial-wise group of older adults was compared to a trial-wise group of younger adults in our previous study (Schmitt et al., 2015), a larger P3b had been found for salient than neutral trials. This salience effect did not reach significance in the present comparison of the two older participant groups.

In the CNV of the context cue epoch, we found larger amplitudes for potential gains and losses in both experimental groups. This salience effect interacted with context (larger CNV for c-dep than c-indep trials after salient cues, see section "Context Effects" above). Only in the block-wise experimental group an additional valence effect emerged, i.e., in this group gain trials elicited a larger CNV than loss trials. These results indicate that (a) during actual task preparation (as opposed to motivational cue processing), potential gains seem more important than potential losses and (b) in the block-wise group, this effect is even stronger than in the trial-wise group because they not only show more updating of task-relevant information (as reflected in the P3b) but also more maintenance and response preparation (as reflected in the CNV) under conditions with potential gains. Unfortunately, due to component overlap, we were not able to analyze the influence of motivational incentives on response-related processes in the probe interval.

Together, our results from the context cue epoch demonstrate that incentives can lead to the implementation of enhanced task preparation in older adults. This adds to previous research showing that older adults control style can be changed to become more proactive by extended practice on the task (Braver et al., 2009). Our results also show that trial-wise and block-wise presentation of incentive cues change preparatory processing in different ways: while during block-wise presentation only gain cues influence proactive processing, the evidence from the trial-wise presentation group is mixed with gains enhancing working memory updating (P3b) but gains and losses enhancing maintenance and response preparation (CNV). As described in detail above, a trial-wise presentation of the motivational cues imposes high demands on working memory because the cues are not redundant. This may have resulted in a different categorization of the cues and thus a different focus.

To sum up, the results from the motivational cue epoch indicate that older adults are more sensitive to the presentation of a loss cue. This would speak in favor of the notion that the prevention of losses is more relevant to older adults than the receipt of gains as would be predicted by the model of Selection, Optimization, and Compensation (SOC) by Baltes and Baltes (1990; for a similar view, see Brandtstädter, 2009). In contrast, the pattern of results from the context cue epoch imply that older adults invest more cognitive resources under conditions in which potential gains can be obtained. This result would be expected according to the age-related positivity effect as assumed by the SST (e.g., Mather and Carstensen, 2005). This pattern of results seems contradicting at first glance, however, it indicates several important issues that need further consideration. First, the SST and the SOC model were developed in a different research context that aimed at explaining a means to regulate emotional well-being and goal motivation in old age and might not be easily transferred to cognitive control processes. Second, it hints at the possibility that the processing of motivational cues and the allocation of attentional and control processes is more flexible than would be expected by a age-related positivity effect or loss-prevention mindset that are constantly in effect, namely that it is dependent on the task, the person, and the availability of cognitive resources. This idea is consistent with recent behavioral studies showing that older adults prioritize the processing of negative over positive information when it holds survival value (such as the processing of negative emotional faces, Reed and Carstensen, 2012) and that a positivity effect is not obtained in older adults when avoiding negative information has detrimental effects while attending to negative information is behaviorally adaptive (Reed and Carstensen, 2012). Third, it hints at a possible dissociation between the immediate (and probably more automatic) reaction to stimuli holding motivational value vs. the more strategic and goal-directed use of controlled processing. In this sense, the present study found a strong initial reaction to stimuli signaling potential losses that may serve a kind of arousal function and support orienting of attention to an alerting stimulus. Although they are, in principal, redundant, older adults are not able to ignore these potential loss stimuli even after prolonged presentation. Hence, the processing of the loss cues may indicate a genuine processing bias in older adults. On the other hand, older adults show increased investment in preparatory processes when gains can be obtained by optimal performance and sufficient cognitive resources are available to perform the task at hand.

## Limitations and Future Research Directions

The present findings demonstrate that older adults react more strongly to cues signaling potential losses, but invest more cognitive resources during the preparation for an upcoming probe stimulus in conditions where gains can be obtained when a motivational mindset is induced by block-wise presentation of gain, loss or neutral cues. However, it should be noted that the present study did not involve a younger control group, although by definition, the age-related positivity effect and the loss aversion of older adults usually is examined as a relative difference between older and younger people (Baltes and Baltes, 1990; Reed and Carstensen, 2012). Therefore, we can only make conclusions about the impact of a motivational mindset in older adults. Whether younger and older adults differ in valence processing during block-wise presentation of motivational cues needs to be investigated in future work.

Recent research has begun to investigate the time-course of processing incentive and task-cue information on cognitive control to investigate its additive or interactive nature (Chiew and Braver, 2015). Regarding the present study, we found no actual interaction between incentive and task-cue information in the block-wise group. However, there is evidence from younger adults that during trial-based motivational cueing, the timing of informative and incentive cue presentation critically affects its impact on proactive control performance (Chiew and Braver, 2015). Hence, future work may more thoroughly manipulate the timing and nature of combined reward and context cues in an ERP approach and extend this relationship toward the understanding of cognitive aging. Besides, both incentive processing and the updating of contextual information seem to rely on dopaminergic activation. As we only used behavioral and ERP data to investigate salience and valence effects, it might therefore be necessary to use molecular imaging techniques to link the processing of motivational cues to salience and valence effects on the neuronal level. At this point, is important to note that most aging studies so far only applied reward motivations, but not penalties on cognitive control tasks, so that the precise nature of age differences in salience and valence effects remains unknown (cf. Chiew and Braver, 2011; Ferdinand and Kray, 2013).

# CONCLUSION

Taken together, the findings of the present study show that when motivational cues signal that potential gains, losses, or neutral outcomes can be obtained depending on performance in the following task, older adults initially react more strongly to cues signaling potential losses, but then invest more cognitive resources during the preparation for an upcoming probe stimulus in conditions with potential gains. Additionally, presenting incentive cues on a trial-wise or block-wise basis makes a difference. During block-wise presentation valence effects are consistently found. The effects during a trial-wise presentation mode are rather mixed and salience as well as valence effects can be obtained. This is probably due to the trial-wise presentation being more demanding. By this, the study furthers our understanding of how motivational incentives modulate task-related processing and the implementation of cognitive control. It also emphasizes the need for further studies focusing on task characteristics and individual differences that influence the availability of cognitive resources in cognitive-affective interactions.

# ETHICS STATEMENT

This study was carried out in accordance with the recommendations of the Declaration of Helsinki and approved by the local ethics committee of Saarland University. All subjects gave written informed consent and were paid 8€ per hour with an additional reimbursement based on their money won during the experiment.

# AUTHOR CONTRIBUTIONS

HS, NF, and JK conceived the research design of the study. HS and NF carried out the statistical analyses and interpretations. All authors contributed to the writing of the manuscript.

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