INFANTS' UNDERSTANDING AND PRODUCTION OF GOAL-DIRECTED ACTIONS IN THE CONTEXT OF SOCIAL AND OBJECT-RELATED INTERACTIONS

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INFANTS' UNDERSTANDING AND PRODUCTION OF GOAL-DIRECTED ACTIONS IN THE CONTEXT OF SOCIAL AND OBJECT-RELATED INTERACTIONS

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Four month old infant reaching for an object handed to her by an adult.
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Since the discovery of mirror neurons, the study of human infant goal-directed actions and object manipulation has burgeoned into new and exciting research directions. A number of infant studies have begun emphasizing the social context of action to understand what infants can infer when looking at others performing goal-directed actions or manipulating objects. Others have begun addressing how looking at actions in a social context, or even simply looking at objects in the immediate environment influence the way infants learn to direct their own actions on objects. Researchers have even begun investigating what aspects of goal-directed actions and object manipulation infants imitate when such actions are being modeled by a social partner, or they have been asking which cues infants use to predict others' actions. A growing understanding of how infants learn to reach, perceive information for reaching, and attend social cues for action has become central to many recent studies. These new lines of investigation and others have benefited from the use of a broad range of new investigative techniques. Eye-tracking, brains imaging techniques and new methodologies have been used to scrutinize how infants look, process, and use information to act themselves on objects and/or the social world, and to infer, predict, and recognize goal-directed actions outcomes from others. This Frontiers Research topic brings together empirical reports, literature reviews, and theory and hypothesis papers that tap into some of these exciting developmental questions about how infants perceive, understand, and perform goal-directed actions broadly defined. The papers included either stress the neural, motor, or perceptual aspects of infants' behavior, or any combination of those dimensions as related to the development of early cognitive understanding and performance of goal-directed actions.

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EDITORIAL
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Editorial: Infants' Understanding and Production of Goal-Directed Actions in the Context of Social and Object-Related Interactions

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Editorial on the Research Topic

Infants' Understanding and Production of Goal-Directed Actions in the Context of Social and Object-Related Interactions

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Goal-directed actions are central to our everyday lives. They are also considered a hallmark of prospective control. Indeed, in order to attain an intended goal (whether a wanted object or an aimed location in space), a certain amount of anticipation and forward planning is necessary. In humans, early signs of anticipation of actions can be detected as early as *in utero* (Myowa-Yamakoshi and Takeshita, 2006; Zoia et al., 2007), but significant changes in goal-directed actions happen in infancy, specifically around the age of 3–5 months, when infants start to produce their first reaching attempts toward an object in their vicinity (Thelen et al., 1993; Corbetta et al., 2014). Other precursor behaviors of anticipation and goal-directedness can also be seen in the previous months or weeks preceding reach onset, and occur in the form of anticipatory gaze responses or tracking of visual events (see for example, Haith et al., 1988; Wentworth and Haith, 1992; Hofsten and Rosander, 1997; Agyei et al.). The action of reaching, however, is the first behavior in early infancy that brings together a deliberate movement of the hand toward an object-goal visually attended.

The emergence of reaching undeniably marks an important milestone in early development. This has been acknowledged for decades. But in recent years, it has been discovered that the emergence of reaching triggers a rapid developmental cascade that has far and wide implications for infants' cognitive and sensorimotor development. From about 12 weeks of age, infants already begin to display predictive looking behaviors and pick up cues from moving objects (Rosander and von Hofsten, 2004; Agyei et al.). As reaching emerges, they learn to pick up even more sophisticated cues to direct their actions within their surroundings, scenes, and people in their immediate social environment (Fagard et al.; Fantasia et al.; Filippi and Woodward; Williams and Corbetta), they learn to plan their movements accordingly (Fantasia et al.; Williams and Corbetta), and they also begin to understand other people's actions and intentions in the context of social interactions (Zmyj et al.; Filippi and Woodward; Robson and Kuhlmeier).

The goal of this research topic is to bring together these exciting and recent developments. Much of the manuscripts in this research topic address novel aspects of infants' production and understanding of goal-directed actions in relation to object and others. The first half of the articles focus on the origins, changes, and brain activities related to the prospective control of infants' own goal-directed actions. Two articles discuss the very first behaviors that are preceding and subsequently leading to the formation goal-directed actions. Agyei et al. review the early development of prospective control in infancy, particularly in the case of visual motion perception, while Thomas et al. focus on the spontaneous self-touching behaviors in the first 6 months of life that form the foundation of goal-directed reaching and grasping. Williams and Corbetta center on the emergence of reaching and investigate how novice reachers quickly learn from the consequences of their own actions to modulate their arm response depending on whether they are aiming for a continuously moving target or a target that moves only in response to successful contacts with the object target. Both Agyei et al. and Kaur et al. extend these research questions to special populations. Agyei et al. report preliminary differences in prospective control between full-term and pre-term infants, and Kaur et al. show that over the 2 first years of life, infants at risk of Autism Spectrum Disorder show less manual exploratory behaviors of objects compared to same age typically developing infants. Two papers also use brain imaging techniques to capture developmental changes in goal-directed behaviors. Agyei et al. illustrate how Visual Evoked Potentials (captured via EEG) can reveal impaired functioning in the dorsal visual stream of preterm infants, while Nishiyori demonstrates how functional near-infrared spectroscopy (fNIRS) can be a useful tool to capture cortical activity as infants develop goal-directed actions (see also Nishiyori et al., 2016).

The second half of the papers in this research topic focus more specifically on how infants understand intents and goal-directed actions performed by others. Since the discovery of the mirror neuron (Buccino et al., 2001) there has been growing evidence showing that infants' emerging ability to reach influences not only their ability to act on their environment, but also their ability to understand and anticipate the actions of others (e.g., Falck-Ytter et al., 2006; Cannon et al., 2012). Several contributions in this research topic build on these prior findings. Fantasia et al., for instance, provide compelling evidence that at 3-months-old infants already, not only plan ahead and adjust their posture in preparation for being picked up by their caregiver (Reddy et al., 2013), but show also sensitivity to change in timing in the pick-up sequence as provided by the adult. To older infants, Fagard et al. presented a variety of tool use demonstrations (modeled by an adult) to retrieve an object out of reach. They find that when the actor first displays its intentions, infants are more likely to learn how to use the tool successfully than when a simple demonstration of how to use the tool is provided. Clearly, infants use intent-based cues provided by their social partner to position themselves in the interaction or solve problems. The way infants use social cues provided by a partner in the context of object-directed actions to attribute goals and understand others action is elegantly reviewed by Robson and Kuhlmeier. We know also that the cue details that infants pick up from social actors can be quite specific. Filippi and Woodward show that infants with anticipatory reaching experience can also visually anticipate the goal-object being reached by a partner based on the orientation of their hand and its congruency with the object goal orientation. Finally, a study from Zmyj et al. examines the extent to which older infants understanding of false-beliefs (perpetrated by an agent) is related to their working memory. They test infants in two tasks designed to assess working memory but find no relations between tasks and thus no direct relation between working memory and false-belief understanding.

In conclusion, the ensemble of research showcased in this research topic capture the breath of the questions that relate to infants' understanding and production goal-directed actions in the context of social and object-related interactions.

AUTHOR CONTRIBUTIONS

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

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HYPOTHESIS AND THEORY
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Development of Visual Motion Perception for Prospective Control: Brain and Behavioral Studies in Infants

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During infancy, smart perceptual mechanisms develop allowing infants to judge time-space motion dynamics more efficiently with age and locomotor experience. This emerging capacity may be vital to enable preparedness for upcoming events and to be able to navigate in a changing environment. Little is known about brain changes that support the development of prospective control and about processes, such as preterm birth, that may compromise it. As a function of perception of visual motion, this paper will describe behavioral and brain studies with young infants investigating the development of visual perception for prospective control. By means of the three visual motion paradigms of occlusion, looming, and optic flow, our research shows the importance of including behavioral data when studying the neural correlates of prospective control.

Keywords: brain and behavioral development, visual motion perception, optic flow processing, perceptual information for action, prospective control

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According to Gibson's ecological theory of visual perception, direct and precise specification of objects and events in the environment provides information for direct perception through the pattern of light reflected from the surrounding to an observer (Gibson, 1966, 1979). Integral to this theory is the concept of affordances, which refers to what the environment affords or offers the observer. For example, surfaces of the environment may afford the observer locomotion, collision with other objects, and other behaviors that may be beneficial or injurious. Thus, it is important for affordances to be perceived efficiently. According to the theory, information for visual perception is inherent in the ambient light when an observer looks at a visual scene. As such, information about the surface layout and layouts of different objects and places in the environment projects from the dynamic ambient optic array of light that reaches the eye, which then specifies action possibilities to the observer. With movement, the dynamic optic array (flow field) specifies information about direction of motion and the relative movement of objects and the observer. This pattern of visual information that results from an observer's own motion is referred to as optic flow (Gibson, 1979).

The visual motion perception that is achieved by changes in optic array information becomes crucial for environmental navigation. Optic flow patterns afford the adjustment of posture, perception of time-to-contact, avoidance of obstacles, and reaching a target efficiently by specifying the appropriate heading direction. Infants respond to radial flow patterns using defensive responses such as backward head movements and eye blinks (e.g., Kayed and van der Meer, 2000, 2007). Such responses suggest that young infants use perceptual information to execute adaptive motor responses (Shirai and Yamaguchi, 2010). In this paper, we discuss the development of the visuo-cognitive systems, especially visual motion perception for the control of anticipatory actions during early infancy. We provide information that contributes to the understanding of the development of visual motion perception for prospective control and the developmental impairments associated with motion perception following preterm birth. Understanding functional brain development and the possible developmental anomalies of premature birth is important to ensure early intervention and diagnosis of preterm infants at risk of developing neurological impairments.

INFORMATION FOR PROSPECTIVE CONTROL

For effective navigation to reach a destination, it is vital to perceive the visual scene and then guide forthcoming actions through the coupling together of perceptual information, cognition, and the subsequent motor execution of intended actions. This ability is referred to as prospective control (Lee, 1993, 1998; von Hofsten, 1993). Prospective control is primarily concerned with future events or future goals to be realized (see also Turvey, 1992). Without sufficient prospective control, individuals may experience problems when responding to changes in the environment. Problems may include difficulties with performing everyday tasks such as the control of walking speed and direction to reach an intended destination. Controlling speed and direction during locomotion may depend on the extent of the complexity or familiarity associated with the visual flow information. As the speed of simulated forward motion increases, latencies in response to motion activity become longer (Vilhelmsen et al., 2015a). Thus, visual scenes that are perceived as being complex and naturally infrequent or unfamiliar may affect the output of cortical responses. Constant modification of integrated inputs from the visual system concerning the nature of the visual scene is therefore necessary. This modification must be dynamic enough to incorporate the constantly changing contextual information from the environment to provide accurate prospective control information.

During visually guided actions, an observer reaches an ideal state when he acts to produce a certain pattern of visual flow. This pattern is characterized by an invariant property that is left unchanged across conditions whenever the observer is in the ideal state (Fajen, 2005). Thus, when current conditions are set constant, information about one's future trajectory is used to modify deviations from the ideal state in order to eventually reach the intended outcome or destination. Over the years, models of visually guided actions for locomotion have been proposed (see Fajen, 2005). Among these models are the bearing angle model and the affordance-based model. In the bearing angle model (e.g., Lenoir et al., 1999; Fajen and Warren, 2007), an observer is on a collision course with an object if the object's bearing remains constant. Thus, to avoid collision an observer must change his speed and/or direction if there is a fixed bearing angle between the observer and the object (see also recent studies by Bootsma et al., 2015 for an extension of this model). The bearing angle model has been used by numerous studies over the years to investigate interception and detection of collisions, and obstacle avoidance in humans and other animals (see e.g., Cutting et al., 1995; Chardenon et al., 2004; Ghose et al., 2006). However, its numerous limitations (see review by Fajen, 2013) including failure to take locomotor capabilities and limits of observers into consideration, and to account for coordination of speed and direction during locomotion, have made its approach unsuitable to predict guided movement of observers in the presence of other moving objects (Fajen et al., 2013). The affordance-based model, which originates from Gibson's ecological theory, rectifies such limitations. It incorporates the ability to choose actions and guide locomotion by taking into account body dimensions and dynamics (Warren and Whang, 1987; van der Meer, 1997; Fajen, 2007, 2013). It also accounts for how speed and direction are coordinated (Warren and Rushton, 2007, 2009; Bastin et al., 2010). However, specific actions observers have to select to actualize the intended motor outcome, and the directions observers have to follow to reach their desired target fall outside the scope of what this model predicts. For successful performance during visually guided action, it is ultimately important for an observer to perceive the available possibilities for action and to behave in order to keep the desired prospective action within the range of possible actions (Fajen, 2007).

According to Gibson's ecological theory, it is important to identify stimulus variables that are necessary to specify perceived aspects of the environment. Specifying variables (optical invariants) are patterns of ambient-energy arrays that are left unchanged by certain transformations (Fajen, 2005). Tau (Lee, 1976) is an example of a specifying variable that estimates time-to-contact information for timing interceptive actions. Further studies show that an alternative source of optical information when estimating time-to-collisions is the use of non-specifying variables (e.g., visual angle and expansion rate) that do not relate to specific environmental factors (see Michaels et al., 2001; Smith et al., 2001; Jacobs and Michaels, 2006). Thus, in contrast to optical invariants such as tau that is unaffected by changes in environmental conditions, non-specifying variables are influenced by environmental factors such as speed and size of objects (Runeson and Vedeler, 1993; van der Meer et al., 1994; Fajen, 2005). Studies have shown that in estimating time-to-collision, observers may use tau information independently (e.g., Yilmaz and Warren, 1995) or in conjunction with the use of non-specifying variables (e.g., Jacobs et al., 2001; Smith et al., 2001). In this paper, studies are presented that show age-related differences in the use of specifying and non-specifying optical variables, as well as the developmental changes in the use of such variables for prospective control during perceptuo-motor tasks in infants.

Perception of visual information for locomotion includes being able to accurately time and efficiently guide movements. The introduction of the tau-coupling theory has helped to explain how organisms are able to guide their movements through the closure of motion gaps (van der Weel et al., 2007). Tau of a motion gap is the time to closure of the motion gap at its current rate (Lee, 1998). When two or more taus are coupled over a period of time, they remain in constant proportion over the specific time period (Lee, 2009). Their relationship is defined by the coupling constant, K, which defines the speed profile of the gap closure. When reaching with the hand to catch a moving object, motion gaps exist between the hand and the object, or between the hand and the estimated interception point of the object, or between the object and the interception point. For the hand to be at the correct place to catch the moving object, tau of the motion-gap between the hand and the interception point, and the tau of the motion gap between the object and the interception point must be coupled together. Thus, external information about the motion of the object tau-guides the hand in an extrinsic tau-coupling process (Lee et al., 2001). In an intrinsic tau-coupling, tau of the gap between the hand and the stationary object is performed when self-guided action is coupled with an intrinsic tau value generated in the nervous system (Lee, 2009). Tau information is in the form of electrical energy that flows in neuronal assemblies in the nervous system. Tau information in the nervous system serves as a template for movement control upon which proprioceptive feedback can be used for prospective control (Lee, 2009). Intrinsic tau-coupling activity can be observed, for example, during the control of sucking in infants where the sucking pressure follows a pressure curve predicted by tau-coupled movement (Craig and Lee, 1999), or during the control of balance in children and adults (Austad and van der Meer, 2007; Spencer and van der Meer, 2012).

THE NEURONAL BASIS OF VISUAL MOTION PERCEPTION

In determining how visual perception is mediated in the brain, studies in humans and other primates have investigated the cerebral networks specialized for perception of visuo-spatial information over the past years. Several studies associate the structural and functional organization of the dorsal and ventral streams in the overall processing of visual information (e.g., see review by Creem and Proffitt, 2001). Perception of spatial aspects of stimuli such as the direction and speed of motion is processed via the dorsal visual stream (Creem and Proffitt, 2001), with the ventral visual stream primarily suggested to be involved in object recognition (Milner and Goodale, 2008). Neurons within the middle temporal complex (MT/V5+) of the dorsal visual stream are generally sensitive to radial motion processing including information from looming stimuli (Greenlee, 2000). The dorsal medial superior temporal (dMST) area is specifically implicated in optic flow processing (Duffy and Wurtz, 1991; Greenlee, 2000). The MT+ complex has also been found to play an important role in the control of continuous eye movement and in catch-up saccades to a moving target during the perception of motion information (Orban de Xivry and Lefèvre, 2007).

Over the years, non-invasive electroencephalogram (EEG), with its high temporal resolution in the millisecond scale, has been used to study the neuronal basis of motion perception and the functional specializations of cortical structures. EEG records brain electrical activities primarily from pyramidal neurons. In visual perception tasks, visual evoked potential (VEP) waveforms in EEG are generally assumed to represent responses of cortical neurons to changes in afferent activity (Brecelj, 2003). VEP waveforms are dominated by a motion-sensitive negativity (N2) during visual motion processing. The N2 is assumed to originate in area MT/V5, with adult N2 latencies reported around 130–150 ms (Probst et al., 1993; Heinrich et al., 2005) and around 180–220 ms in 8-month-old infants (van der Meer et al., 2008a).

Together with VEPs, EEG analysis in the time-frequency domain is used to isolate event-related frequency changes that reflect oscillatory mechanisms underlying neuronal populations (Hoechstetter et al., 2004). Event-related time-frequency responses (TSE, time spectral evolution) represent interactions of local cortical neurons that control the frequency components of an ongoing EEG (Pfurtscheller and Lopes da Silva, 1999). Using spectral profiles within specific frequency bands, different classes of oscillations have been distinguished over the years: delta-band (1–4 Hz), theta-band (4–7 Hz), alpha-band (7–13 Hz), beta-band (13–30 Hz), and gamma-bands (30–150 Hz). These rhythms are thought to reflect neurophysiological processes that exhibit functionally different roles. These roles include signal detection and decision making with the use of delta frequency (Başar et al., 2000), the control of inhibition and cortical processing with alpha-band waves (Klimesch et al., 2007), involvement in multisensory stimulation and the shifting of neural systems to a state of attention using beta-band activity (Khader et al., 2010), and the utilization of bottom-up and top-down memory matching of information for perception using gamma frequency (Herrmann et al., 2010). Several adult studies have found evidence for the modulation of the natural frequencies by motion stimuli (e.g., see review by Saby and Marshall, 2012), with little evidence for such activity reported in infants. Low-frequency EEG rhythms are reported in infants (e.g., Orekhova et al., 2006), with event-related theta oscillations found to provide information for impending collisions in the infant brain (van der Weel and van der Meer, 2009). Some of the studies presented in this paper will show further evidence for the use of theta-alpha and other frequency oscillations during the processing of visual information for the control of prospective actions in infants.

EARLY DEVELOPMENT OF VISUAL PERCEPTION FOR PROSPECTIVE CONTROL

Since perception of information for prospective control plays an important role for everyday survival, the developmental processes that mediate visual perception throughout life are expected to be increasingly efficient after birth. One of the earliest indicators of prospective control behavior in infants is the ability to continuously pursue a moving target with head and eye movements (von Hofsten and Rosander, 1996). Smooth visual pursuit of a moving target involves fixing gaze on the target and matching eye movements with the speed of the moving target. This helps to anticipate and predict the target's trajectory. Rudimentary perception of visual flow appears within the first weeks after birth (Shirai and Yamaguchi, 2010). Infants younger than 6–8 weeks are unable to efficiently discriminate between motion directions or smoothly pursue small moving objects, but they show rapid improvements between 6 and 14 weeks of age (Gilmore et al., 2007; Rosander et al., 2007). Young infants exhibit sensitivity to information for impending collision very early in development, with infants between 3 and 6 weeks shown to perceive optical collisions by responding with defensive blinks and head movements (e.g., Náñez, 1988). Even neonates as young as 3 days old exhibit responses through backward head movements when exposed to backwards flow stimuli (Jouen et al., 2000; Shirai and Yamaguchi, 2010). Such responses in very young infants may be the result of multimodal integrative and cooperative processes in which visual, vestibular, and proprioceptive senses are involved rather than a direct consequence of motion perception (Jouen et al., 2000).

Around 2 months of age, infants are already able to show prospective control as they continuously track objects using smooth pursuit eye movements and a gain geared to the velocity of the moving target (Rosander and von Hofsten, 2002). From 3 to 5 months, infants discriminate between virtual flow displays that depict at least 22° changes in heading direction (Gilmore et al., 2004). Around 6 months of age, they further follow moving objects on a linear path using predictive head and eye movements (Jonsson and von Hofsten, 2003). At this age, infants reach for a moving target by not aiming for the current position of the object but predictively aiming for a position further ahead on the path where the hand and the object will meet (van der Meer et al., 1994; von Hofsten et al., 1998; Jonsson and von Hofsten, 2003). When moving objects that are being tracked move temporarily out of view, infants should anticipate where and when the object would reappear again. This ability seems to be developed around 6 months of age (Johnson et al., 2003).

Studies using anticipatory and compensatory postural adjustment to study prospective control have found mobile infants around the end of the first year of life to show peak postural compensation to visual flow information (e.g., Bertenthal et al., 1997; Lejeune et al., 2006). Witherington et al. (2002) studied infants between 10 and 17 months of age to investigate early development of anticipatory postural activity in support of pulling action. Infants retrieved toys by pulling open cabinet drawers while a force resisting the pulling action was applied to the drawers. Infants' anticipatory postural adjustments and the temporal specificity of anticipatory activities progressively improved with age as infants learned to stand and walk. By improving anticipatory postural responses, balance control is also enhanced (Santos et al., 2010). Thus, prospective control plays an important role in keeping balance during standing and locomotion. In evaluating whether infants who are able to walk show greater sophistication compared to non-walking infants when anticipating postural disturbances induced by a continuously moving platform, Cignetti et al. (2013) reported that the acquisition of independent walking improves sensorimotor control of posture. Other studies also show that infants with locomotor experience typically respond more to peripheral flow than pre-locomotor infants and that the developmental shift in using flow-field information for postural control may be more closely linked to locomotor experience (e.g., Higgins et al., 1996). With the development of self-generated actions including self-locomotion experience, what is perceived and the ensuing anticipatory actions considerably improve in the developing brain (van der Meer et al., 2008a; James and Swain, 2011). Thus, the functional detection of visual flow information develops hand in hand with self-produced locomotion in normally developing infants (van der Meer et al., 2008a).

Unlike normally developing full-term infants, preterm infants show differential brain development that is particularly evident from abnormalities in tissue microstructure, cerebral morphology, and white matter damage (see review by Counsell and Boardman, 2005). Preterm infants are therefore at a higher risk of developing neurological and perceptuo-motor problems (see Taylor et al., 2009). These abnormalities underlie various cognitive and behavioral impairments, including deficits in visual perception and other neurodevelopmental disorders that are associated with preterm birth (de Jong et al., 2012). Preterm children show deficits in perception of global motion, global form, and biological motion, with impairment of the dorsal visual stream particularly implicated as a possible cause of such developmental problems (Taylor et al., 2009). Because of these impairments, identifying at-risk preterm infants is necessary to offer appropriate early intervention to those who need it.

By using brain and behavioral data mainly from occlusion, looming, and optic flow studies, we further discuss the development of visual perception for the control of prospective actions during the first year of life. Prospective control behavior in infants is shown through predictive gaze and reaching movements, and different timing strategies for obstacle avoidance. We show that the development of prospective control substantially improves with age. We illustrate how preterm infants show developmental delays in the processing of prospective control information by comparing full-term infants' responses with responses of preterm infants. The relationship between behavioral development and the development of the underlying neuronal processes is highlighted through EEG measurements of neuronal electrical activity as a function of perception of visual motion information.

INTERCEPTION TASKS WITH TEMPORARY OCCLUSION

With visual occlusion tasks, we investigated infants' prospective control and the ability to maintain object permanence—the understanding that an object exists even if it is out of sight. The development of the mediating neural structures of such processes was also studied. By combining behavioral measurements of eye, head, and hand-reaching movements together with EEG analysis of neuronal gamma oscillations, we could study infants' ability to follow, maintain attention on, and predict the arrival of a moving object as it disappears behind an occluder and reappears shortly afterwards.

When reaching for a moving object, infants must use prospective control to guide their hand-reaching movements to intercept the moving object. To study prospective control in catching, van der Meer et al. (1994) investigated the control of hand and gaze movements as infants reached for a toy moving at different speeds. The toy was occluded from view by a screen during the final part of its approach. Infants could reach to catch the toy when it was at a certain distance or time away from them. To effectively catch the toy, a strategy based on distance is less efficient as it is dependent on the approach velocity of the toy. Thus, reaching to catch the toy when it is approaching at a fast velocity leaves very limited time to extend the arm to make an interceptive movement. A strategy based on time-to-contact, however, is most efficient since it leaves the same amount of time to carry out the interceptive movement irrespective of the toy's approach velocity. Infants around 11 months of age anticipated with their gaze and hand the reappearance of the toy as it emerged from behind the occluder. Their hands started moving forward before the toy had even disappeared behind the occluder in order to catch the toy as soon as it reappeared. Prospective gaze and hand action was coupled to certain times before the toy's reappearance. Thus, information that was picked up before the disappearance of the toy behind the occluder was used to regulate gaze and hand movement. When infants between 20 and 48 weeks of age were studied longitudinally, infants' gaze anticipated the reappearance of the moving toy as soon as they were able to successfully catch the toy. Infants' anticipatory gaze movements suggest that this ability is a prerequisite for the onset of reaching for moving objects. As corroborated by various studies (e.g., Aguiar and Baillargeon, 1999), the findings indicate that object permanence is present in infants earlier than the suggested 8 months by Piaget (1954). The ability to successfully catch a fast-moving object coincides with infants' ability to use perceptual information to initiate a reaching movement. Initiation of the hand movement should begin when the toy is a certain time away from them, instead of a certain distance away, thus making available the same average time for the catching movement whether the toy is moving slowly or quickly.

How do neurologically at-risk preterm infants perform in comparison with full-term infants on tasks that rely heavily on prospective control? van der Meer et al. (1995) studied healthy full-term infants and low-birthweight preterm infants longitudinally between 20 and 48 weeks of age to investigate whether infants classified as being neurologically at-risk of brain damage have similar prospective control ability as full-term infants, and if not, whether their lowered ability could be indicative of brain damage. Infants' ability to reach for a toy moving at different speeds was studied. At the first reaching session each infant's gaze successfully anticipated the reappearance of the moving toy. However, reaching onset and prospective control of gaze and hand movements varied considerably between the full-term and preterm infants. From 24 weeks onwards, the full-term infants anticipated the moving toy with their gaze, but gaze anticipation was delayed in all the preterm infants until 40 or 48 weeks of age. As a group, the preterm infants started reaching late for the toy. Three started to reach at 28 weeks corrected age, 8 weeks later than the full-term control infants. Some preterm infants geared their actions to the distance instead of the time that the toy was from the catching point, which caused problems with faster moving toys. Almost all the preterm infants anticipated the reappearance of the moving toy with their hand at the final testing session at 48 weeks of age. They also started showing signs of using the time strategy to adapt their actions according to the length of time that the toy was from the reappearance point at this age. Two of the preterm infants still appeared to be using the less efficient distance strategy when shifting their gaze and initiating their hand movement to reach for the toy at 48 weeks of age. The same two infants also showed the poorest anticipation of the toy's reappearance. These two preterm infants were later diagnosed with mild and moderate cerebral palsy at around 2 years of age. Hence, poor development of prospective control on the catching task could potentially serve as an indicator of possible brain damage.

Further, with normally developing full-term and preterm infants between 22 and 48 weeks of age, we longitudinally investigated the timing strategy infants use to initiate and guide the hand when catching a moving object and whether the guiding action is influenced by the use of timing strategies (Kayed and van der Meer, 2009). Little difference was found between full-term and preterm infants' use of timing strategies. Preterm infants showed about the same development as full-term infants both in timing the catch and in continuously guiding hand movement. Variation in the functionality and length of the tau-coupling between the hand and the toy was influenced by the timing strategy the infants were using to initiate the hand movement. The younger preterm and full-term infants used a distance strategy to initiate hand movement when they started to reach for the moving toy. This resulted in a high number of unsuccessful attempts at catching the toy. They performed shorter and less functional tau-coupling that was characterized by non-controlled collisions with the hand accelerating toward the toy when they used the distance strategy. However, the older infants around the end of the first year of life switched to a time strategy when reaching for the moving toy. They performed longer and more functional tau-coupling between the hand and the toy, with better controlled collisions with the hand decelerating toward the toy. They showed a marked improvement in the number of successful catches. One preterm infant failed to switch to a time strategy and showed poor prospective control with a higher number of unsuccessful catches compared to other infants. This preterm infant may later have perceptuo-motor problems.

To further investigate the use of prospective control in catching and how it could be used as a tool to detect signs of brain dysfunction, Aanondsen et al. (2007) studied adolescents between 14 and 15 years of age who were either born as preterm very-low-birthweight (VLBW), full-term small for gestational age (SGA), or full-term appropriate for gestational age (AGA) infants. They were presented with a moving target that approached from the side at three different accelerations. The experiment was conducted as a blind study without knowing beforehand the participants' neurological status such as birth status, gestational age, birthweight, and their cerebral magnetic resonance imaging (MRI) results. All participants used the time-to-contact strategy to initiate their hand movements except three adolescents (two preterm VLBW and one full-term SGA). They rather used the less advanced distance or velocity timing strategy to guide the initiation of at least one of their hands to catch the moving target. Based on their timing strategies, the three adolescents were classified as at risk for neurological problems. Their cerebral MRI confirmed this classification. It showed them to have reduced white matter tissue, dilation of the ventricular system, and/or pathology in the corpus callosum. The findings showed that the ability to use prospective information for catching could be a reliable tool to help detect diffuse signs of motor dysfunction that may not be readily detectable using only standard neuropsychological tests.

To investigate the neural correlates underlying prospective control, Holth et al. (2013) coupled adults' gaze control during deceleration in a visual tracking task with their EEG activity. Participants followed with their gaze a horizontally moving car that was temporally occluded and pushed a button to stop the car as soon as it reappeared from behind the occluder on a large screen placed 80 cm in front of them (see **Figure 1A**). The car moved under three different constant decelerations. The button-press response was defined as either a hit or a miss depending on how much of the car was visible in the target area when it was stopped. A hit response was defined as at least half of the car being visible after pressing the button. Different events were used to time-lock the averaged event-related potential (ERP) waveforms, including stimulus onset, push-button responses, and eye jumps across the occluder. When ERP waveforms were time-locked to the prospective gaze shift over the occluder, participants were successful in discriminating between the three decelerating speeds. Thus, participants' parietal activity indicated that they were able to differentiate between the different car decelerations but only when their averaged EEG was time-locked to the eye jump event and only when they managed to stop the car successfully. No such effect was found when ERP waveforms were time-locked to any of the other events. The findings indicate that a traditional stimulus-onset time-locking procedure is likely to distort the averaged EEG signal. This distortion may consequently hide important activity differences, especially in the parietal cortex that may provide information about the prospective timing of decelerating object motion during occlusion. The observations strongly suggest active incorporation of behavioral data into EEG analysis to provide valuable information that would be lost otherwise, when studying the neural correlates of prospective control.

Further longitudinal EEG studies showed that infants' ability to smoothly track a moving object undergoing occlusion (see **Figure 1A**) and to predict its reappearance increases considerably between the ages of 4 and 12 months (Twenhöfel et al., 2013). Infants showed more instances of shifting gaze predictively over the occluder with age (**Figures 1B,C**). The older infants showed a more consistent pattern of anticipatory eye movements in response to the moving target. The results corroborate previous studies showing that anticipatory eye movements improve considerably in the course of the first year of life (see e.g., Gredebäck and von Hofsten, 2004). In order to successfully track an object over an occlusion period, object permanence must be developed. Rosander and von Hofsten (2004) suggested that smooth pursuit of moving targets and predictive occluder tracking depend on the ability to anticipate future motion based on the prediction of a continuous motion trajectory of a moving object. Because of a 100–200 ms visuo-motor delay that the smooth pursuit system has to overcome during the tracking of moving objects (see Schlag and Schlag-Rey, 2002), smooth pursuit must be adjusted predictively to compensate for this delay within which a visual target may have moved significantly. With the development of object permanence, the older infants may have used visuo-motor integration to successfully predict the object's trajectory and to continuously track its movement.

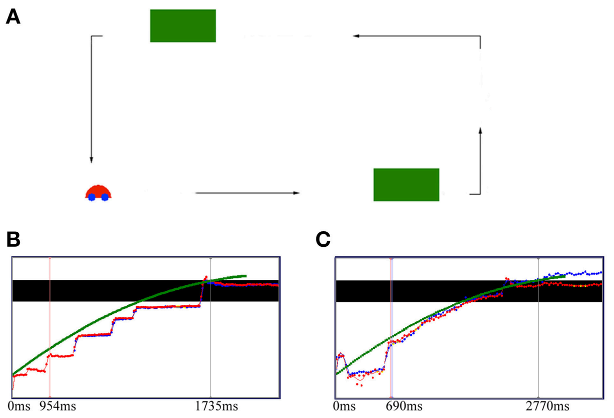

FIGURE 1 | Occlusion experimental set-up (A), and gaze data (↑ position and → time) for a typical slow deceleration in a 4-month-old infant (B) and a 12-month-old infant (C). (A) The car traveled horizontally on a rectangular path under one of three deceleration conditions, fast (10% deceleration), medium (50% deceleration), and slow (90% deceleration). The two green boxes temporarily occluded the car from its path of travel. **(B,C)** The black bar represents the occluder, and the green squares represent the car motion, while the red and blue dots represent the right and the left eye, respectively. Yellow dots are missing data. The left markers in each graph represent the catch up event (the moment at which the horizontal eye velocity equals the speed of the car for the first time), while the right markers represent the point in time at which the car starts to reappear from behind the occluder. The 4-month-old infant shows typical saccadic tracking to keep up with the target motion **(B)**, whereas the 12-month-old infant follows the car with smooth pursuit **(C)**. The 12-month-old infant shows an anticipatory saccade to the end of the occluder before car reappearance, while the 4-month-old infant shows no such prospective eye movement.

The predictive gaze shift was accompanied by a divergence and a shift in gamma band topography with age. Neuronal gamma band topography shifted from occipital areas in the dorsal stream in the younger infants to anterior temporal areas in the ventral stream in the older infants when the underlying neuronal source activities were analyzed. The divergence in gamma band topography may possibly reflect developmental changes in neuronal mechanisms serving object tracking over transient occlusion periods during the course of the first year of life. Previous studies have also implicated gamma activity in complex object processing in regions distributed along the ventral and dorsal pathways (e.g., Lachaux et al., 2005; Hoogenboom et al., 2006). The shift of gamma activity in neuronal regions may suggest different strategies of occluder tracking with age. Younger infants may be guided mainly using spatio-temporal information processed via the dorsal pathway to fill perceptual gaps over transient occlusions. The ventral pathway activation in the older infants may suggest further incorporation of object features during perceptual representations of moving objects. Thus, the gamma activation could represent top-down processing (high-speed memory comparison) of the object template that was maintained over the perceptual gap with the perceived stimulus (see Herrmann and Mecklinger, 2001). The ventral stream activation is in accordance with the suggestion that vision for perception (a typical ventral stream task) could replace vision for action (mainly a dorsal stream task) in order to successfully guide 11-month-old infants' arm reaching movements in an occlusion situation (van Wermeskerken et al., 2011). The developmental progression in regional cortical shift of oscillatory activity suggests that the development of object permanence and prospective control become more prominent around the end of the first year of life.

Unlike full-term infants, preterm infants show delayed development in the continuous eye tracking of moving objects. While full-term infants around 12 months smoothly followed the moving target in 64% of all trials, preterm infants around the same age (corrected for prematurity) showed smooth pursuit in only 35% of the presented trials. The lower proportion of predictive eye movements in the preterm infants compared to the full-term infants may be a reflection of a weak object representation (Munakata, 2001) and a delay in the influence of functional object representations on eye movements (Hollingworth et al., 2008). However, their ability to make anticipatory eye movements was relatively similar to the full-term infants. Thus, they were able to disengage attention from tracking the moving object during an occlusion period and then predictively re-orient gaze over the occluder after the object's reappearance despite showing difficulties with smooth pursuit. Disturbances in the development of the motion perception pathways and other complications associated with premature birth may impair motion processing and contribute to preterm infants' reduced ability to track moving objects. To compensate for their less functioning smooth pursuit system, it has been suggested that preterm infants may use saccadic eye movements and head movements to continuously follow a moving target, although this results in less efficient smooth pursuit than that observed in full-term infants (Grönqvist et al., 2011).

LOOMING VIRTUAL STIMULI ON A COLLISION COURSE

How does the infant brain process information about imminent collisions? By simulating a looming object on a direct collision course toward infants, it is possible to investigate brain activities in response to looming information. Looming refers to the last part of the approach of an object that is accelerating toward the infant (Kayed and van der Meer, 2007). To prevent an impending collision with the looming object, infants must use a timing strategy that ensures they have enough time to estimate when the object is about to hit them in order to perform the appropriate behavioral response. Defensive blinking is widely considered as an indicator for sensitivity to information about looming objects on a collision course. Infants must use time-to-collision information to precisely time a blinking response so that they do not blink too early and reopen their eyes before the object makes contact or blink too late when the object may have already made contact. An accurate defensive response helps to prevent injury to the infants. For a successful defensive response to avoid collisions, development of prospective control is important. Infants must use looming visual information to correctly time anticipatory responses to avoid impending collisions.

The timing strategies that infants use to determine when to make a defensive blink to a looming virtual object on a collision course were investigated using full-term infants between 22 and 30 weeks of age in a cross-sectional behavioral study (Kayed and van der Meer, 2000). The youngest infants used a strategy based on visual angle (analogous to the distance strategy) to time defensive blinks. Thus, they blinked too late when the looming object approached at high accelerations. The oldest infants, on the other hand, used a time strategy allowing them to blink in time for all the approach conditions of the virtual object. When precise timing is required, the use of the less advantageous visual-angle strategy may lead to errors in performance compared to the use of a time strategy that allows for successful performance irrespective of object size and speed.

Further longitudinal studies of full-term and preterm infants at 22 and 30 weeks of aged showed that with age, the majority of infants switched from using a strategy based on visual angle to a strategy based on time to time their blinks (Kayed and van der Meer, 2007; Kayed et al., 2008). Some of the infants used a time strategy even already at 22 weeks, with such infants maintaining the use of this strategy on subsequent testing sessions. None of the infants switched back to using a strategy based on visual angle after using a time strategy. One preterm infant showed delayed development compared to the other infants since he was using a timing strategy based on visual angle for all loom speeds. This caused him to blink late on the majority of trials even when he was 30 weeks of age. In infants, the inability to switch from a timing strategy that is susceptible to errors to a strategy that affords successful defensive blinking might reflect an inadequate potential for flexibility. Flexibility may be required to help adjust appropriately to local environmental conditions and to successfully interact with the environment, especially since good timing is essential to avoid obstacles during navigation.

With the presentation of a looming virtual object on a direct collision course, we then investigated the developmental differences between full-term and preterm infants using high-density EEG. Infants were studied longitudinally at 4 and 12 months. The looming stimulus was programmed to loom toward the infant with different accelerations, which finally came up to the infant's face to simulate a visual collision experience (see **Figure 2A**). Looming-related peak VEP responses were analyzed using source dipoles in occipital areas. Results showed a developmental trend in the prediction of an object's time-to-collision in full-term infants. With age, average VEP duration (processing time) in full-term infants decreased, with peak VEP response closer to the loom's time-to-collision (van der Weel and van der Meer, 2009; van der Meer et al., 2012). Full-term infants around 12 months of age used the more sophisticated and efficient time strategy to time their brain responses to the virtual collision. Their looming-related brain responses were fixed at a constant time-to-collision irrespective of visual loom speed (**Figure 2B**), an indication of the development of prospective control at this age (van der Meer et al., 2015). The use of such

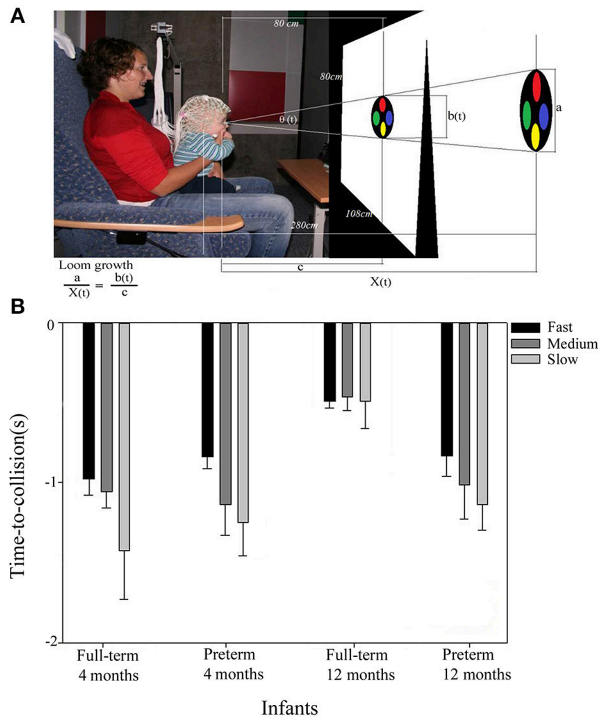

FIGURE 2 | Looming experimental setup (A), and averaged looming-related VEP peak responses (with SDs) in full-term and preterm infants (B). (A) Infants were shown a flat 2-dimensional circle filled with four smaller colored circles. The looming stimuli simulated an object approaching from a distance on a direct collision course under constant accelerations of −21.1, −9.4, −5.3 ms^{-2} for fast loom (2 s), medium loom (3 s), and slow loom (4 s), respectively. The bottom left equation describes the growth of the visual loom. The looming stimuli approached the infant as the image on the screen grew symmetrically and stopped when the image filled the entire screen. **(B)** With increasing age, the full-term infants responded significantly closer to the loom's time-to-collision compared to the pre-term infants. Only the older full-term infants responded at a fixed time-to-collision irrespective of loom speed, an indication that only the full-term infants at 12 months had switched from a visual angle strategy to the more sophisticated time strategy when timing their looming-related VEP peak responses.

a timing strategy based on a fixed time-to-collision may reflect infants' levels of neural maturity and locomotion experience. Maturity and experience are important factors needed for accurate timing of prospective actions in response to looming objects to ensure successful evasive maneuvers during navigation.

However, unlike full-term infants, preterm infants did not show such improvements with age but continued to use the less efficient timing strategy based on the loom's visual angle even at 12 months (**Figure 2B**). This suggested that preterm infants have problems with prospective control during the first year of life, showing their brain responses too early in the looming sequence and therefore not adequately taking into account the loom's different accelerations.

By localizing brain source activity for looming stimuli approaching at different speeds and using extrinsic tau-coupling analysis, the temporal dynamics of post-synaptic neuronal activity in the first year of life was further investigated (van der Weel and van der Meer, 2009). Tau-coupling analysis calculated tau of the peak-to-peak source waveform activity and the corresponding tau of the loom speeds. Source dipoles that modeled brain activities within the visual areas of interest, O1, Oz, and O2 were fitted around peak looming VEP activity to give a direct measure of brain source activities on a trial-by-trial basis. Using full-term pre-locomotor infants at 5–7 and 8–9 months and crawling infants at 10–11 months of age, synchronized theta-band activity in response to the looming stimulus was found. This was consistent with other studies that identified oscillations in the theta range as important for registration and processing of visual perceptual information (e.g., Kahana et al., 2001). Extrinsic tau-coupling analysis on the source waveform activities showed evidence of strong and long tau-coupling in all infants. The oldest infants showed brain activity with a temporal structure that was consistent with the temporal structure present in the visual looming stimuli. Thus, in the course of development, the temporal structure of different looming stimuli may be sustained during processing in the more mature infant brain. Sustaining the temporal structure may provide increasingly accurate time-to-collision information about looming danger as infants become more mobile with age. Infants at 10–11 months differentiated well between the different loom speeds with increasing values of the tau-coupling constant, K, for the faster loom. The younger infants were not able to differentiate between the looms, with the worst performance observed in infants at 5–7 months. The findings may suggest mature neural networks for processing impending collision information in the oldest infants compared to the youngest. At 5–7 months, such neural networks may not have been developed but could rather be in the process of being established at 8–9 months of age, which coincides with the onset of crawling in infants. Thus, with better control of self-produced locomotion, the perceptual ability to recognize looming danger, and perform the necessary prospective action to avoid impending collision markedly improves.

In the developing brain, not only is visual information important for the performance of prospective actions, but also integration of information from multiple senses is necessary and fundamental to perception. To investigate whether the auditory system also plays a role in prospective control, van der Meer et al. (2008b) used an auditory-guided rotation paradigm in a behavioral study of infants at 6–9 months of age. Infants lay in a prone position with magnetic sensors fastened to their head and body to measure direction and velocity of rotation as they responded to auditory stimulation from their mothers. Infants were able to consistently choose the shortest way over the longest way to rotate to their mothers who were positioned behind them. The infants showed prospective control by rotating with a higher peak velocity as the angle to be covered between themselves and their mother's position increased. In line with affordance theory, we showed that the auditory system can function as a functional listening system. Auditory information may be used as a source of perceptual information to help guide behaviors adequately in the environment. Mobile infants may use auditory information that offers them the most efficient method for action relative to their own position in space and a desired position to reach in the environment (also see Morrongiello, 1988; Middlebrooks and Green, 1991; van der Meer and van der Weel, 2011).

However, when visual and auditory looming information are simultaneously present in an audiovisual looming stimulus, prelocomotor full-term infants show earlier looming-related brain responses to the auditory loom than to the visual loom (Agboada et al., 2015). Longitudinal studies show that peak visual and auditory looming activation responses in infants at 3–4 months occur earlier in the looming sequence compared to older infants at 9–10 months. The results indicate a developmental trend in the prediction of time-to-collision information in infancy where the recruitment of neuronal assemblies in higher cortical areas, particularly in the parietal cortex, is implicated in the processing of looming-related information as infants age. With an evolutionary bias for survival prioritizing an early auditory response over that of visual response in audiovisual looming perception, it is likely that audiovisual integration in infants could be heavily influenced by their spatial attention being captured by a visual loom. In order words, visual looming-related responses that appear relatively late in a looming sequence could be a reflection of infants' active attention shown to a visual loom over that of an auditory loom (see Corbetta et al., 1990).

OPTIC FLOW INFORMATION SIMULATING SELF-MOTION

With an optic flow paradigm, we have explored the development of visual motion perception during the first year of life by using both evoked (VEP) and induced (time-spectral evolution, TSE) brain responses to simulated self-motion. Using EEG in 8-month-old infants and adults, van der Meer et al. (2008a) studied brain electrical activity as a function of perception of structured optic flow and random visual motion. Brain activities related to the processing of motion stimuli were different in infants and adults both in VEP and induced activities of EEG. Adults and infants had shorter N2 latencies for structured optic flow than random visual motion. Infants showed longer latencies in both motion conditions compared to adults, with the longest latencies observed for random visual motion. While infants used the slower theta-band frequency during the processing of visual information, adults used the faster beta-band activity in response to the motion conditions. The findings show that infants that are not yet capable of walking may detect optic flow less efficiently compared to adults and they may be more affected by the lack of structure present in random visual motion. When the speed of structured forward optic flow information was varied in adults and infants at 4–5 and 8–10 months, Vilhelmsen et al. (2015a,b) showed that differences in N2 peak latency occurred in the adults and the older infants but not in the infants at 4–5 months. N2 latencies were found to decrease with age, with shortest N2 latency observed for the lowest speed of motion. Unlike the younger infants, the older infants may have had a more developed neurobiological system that contributed to an improved detection of visual motion, similar to the adult participants. Motion-sensitive cortical areas continue to develop through infancy to adulthood (Gilmore et al., 2007), which lead to more efficient processing of different speeds of motion with age.

In relating behavioral changes such as locomotion experience to accompanying changes in brain activities, prelocomotor infants at 3–4 months and infants at 11–12 months with self-produced locomotion experience were longitudinally studied using an optic flow paradigm (Agyei et al., 2015, 2016). Both full-term and preterm infants were studied to investigate the effect of prematurity on the processing of optic flow information. The infants were presented with three motion conditions (forwards and reversed optic flow, and random visual motion) together with a static non-flow condition. The younger infants had no crawling experience while the older infants had on average, about 2.5 months of crawling experience.

Full-term infants differentiated between the three motion conditions with shortest latency for forwards optic flow and longest latency for random visual motion, but only at 11–12 months (**Figure 3**). This improvement in visual motion perception with age was possibly due to significant neural developments such as increasing myelination of connecting fibers (Paus et al., 2001; Grieve et al., 2003; Loenneker et al., 2011) and maturation of local glucose metabolic rates (Chugani et al., 1996; Klaver et al., 2011). Thus, rapid progressive improvement in the functional processing of motion information as infants get older may account for the shorter latencies observed in infants at 11–12 months. The shortest latency for forwards optic flow could suggest faster sensitivity development to radial motion that corresponds to forward movement rather than to reversed or random directions. Further, when mothers carry infants, the infants experience passive locomotion where they are tuned to the dominant statistics of their experienced visual environment (Raudies et al., 2012; Raudies and Gilmore, 2014). Infants' passive experience of visual flow, especially during fast flow speeds, occurs as a result of their downward head direction and closer proximity to ground surfaces when being carried (Raudies et al., 2012). However, only self-generated actions may lead to a stronger link between perception and action in the developing brain (James and Swain, 2011). Thus, only the older full-term infants who had crawling experience from self-movement were better at distinguishing between the motion conditions compared to the younger infants who only had passive locomotion experience from being carried around.

The preterm infants did not differentiate between the three motion conditions at 11–12 months or improve their latencies with age. Studies show that preterm infants at corrected age of 2–3 months are delayed several weeks compared to full-term infants when differentiating between changes of direction (e.g., Braddick et al., 2005; Birtles et al., 2007). Considering that the preterm infants had similar crawling experience as the full-term infants, their inability to differentiate between the motion conditions when older could have resulted from abnormalities in white matter that may underlie impairment of the dorsal visual stream. Thus, axonal electrical impulses could be impaired, resulting in unimproved latencies with age. It is possible that preterm infants' unimproved latencies with age could also reflect a normal delay related to premature birth that could be recovered at a later age. However, at 3–4 months and irrespective of visual motion condition, preterm infants had significantly shorter latencies than full-term infants. Since the preterm infants were tested corrected

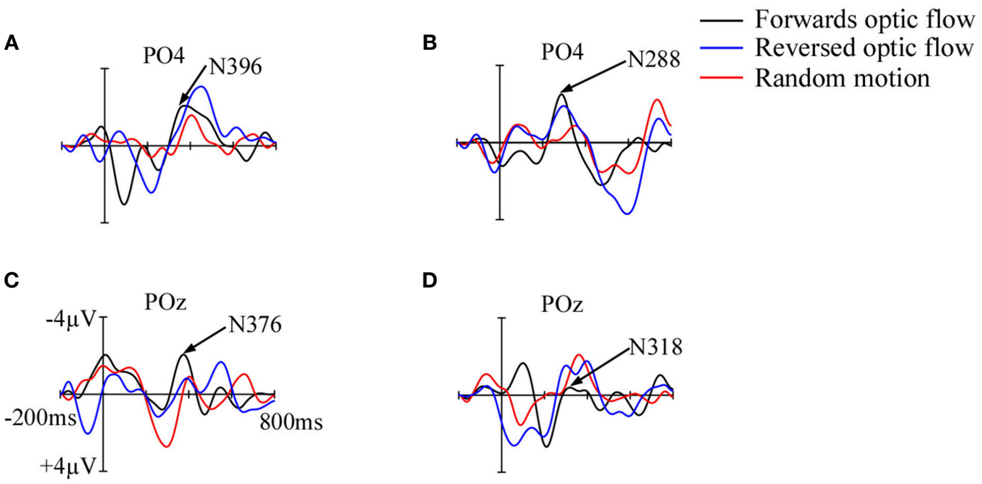

FIGURE 3 | Grand average motion VEPs in full-term infants at 3–4 months (A) and 11–12 months (B), and in preterm infants at 3–4 months (C) and 11–12 months (D). Amplitudes are on the y-axis and latencies on the x-axis. The actual N2 peak latencies for forwards optic flow are indicated at PO4 in full-term infants and POz in preterm infants. Differences in N2 peak latencies for the three motion conditions were observed only in full-term infants at 12 months where latency increased from forwards optic flow to reversed optic flow and random motion.

for prematurity, one contributing factor to this faster perceptual response could be the longer exposure to and experience of visual flow in the younger preterm infants compared to the term infants at 3–4 months.

When TSE of the motion conditions were compared with TSE of the static non-flow dot pattern, both infant groups showed desynchronized theta-band activity that was more prevalent in the younger infants (**Figure 4**). Low-frequency theta-band oscillation is a general sign of immaturity in infancy (e.g., Orekhova et al., 2006). The more prevalent theta-band desynchronization in the younger infants could suggest relatively larger neural networks and lesser specialization when processing radial motion information at this age. Further, synchronized alpha-beta band activity was seen only in the full-term infants at 11–12 months. The emergence of faster alpha-beta band frequency activity only at 11–12 months could indicate a gradual progression from less specialized, slower oscillating, and relatively immature larger oscillatory cell assemblies at 3–4 months to a more adult-like pattern of motion specialization where cell assemblies have fewer but more specialized neurons. This could explain why full-term infants at 11–12 months are better at establishing more rapid coupling between spatially separated brain regions, allowing for improved visual motion perception.

The possible impairment of the dorsal stream responsible for processing visual motion could be the reason why the preterm infants at 11–12 months showed no such progression in oscillatory patterns. Since the dorsal visual stream develops and matures relatively early (Hammarrenger et al., 2007), being born preterm may have disrupted the association fibers and synaptic development in the dorsal stream that help to fine-tune cortical growth during late fetal and early extrauterine life (Huppi et al., 1998; Mewes et al., 2006). The disruption in the development of the dorsal visual stream because of premature birth may have impeded efficient cortical growth and contributed to the absence of higher frequency oscillatory activities when the preterm infants were older. Further, individual analysis showed abnormally high latencies in response to optic flow in three preterm infants (see also van der Meer et al., 2015). Because of the possible greater degree of impairment of the dorsal stream in these preterm infants, a follow-up study when the preterm infants reach school age is necessary to investigate whether these infants still have impaired dorsal stream-related functions, and the effect of the impairment on everyday life.

CONCLUSION

Information about how the visual system responds to visual motion through the interconnection of behavioral and neural processes has been presented to help advance our understanding of the development of visual perception for prospective control in infancy. Infants show a developmental progress with age as they use visual perceptual information to help guide the execution of anticipatory actions of eye, head, and hand movements. The processing of visual information and the development of object permanence become more efficient around the end of the first year of life. Infants show marked improvements in looming-related brain responses and the ability to switch from a distance or visual-angle strategy to the more efficient time strategy to help tau-guide their reaching movements. With age, infants recognize and differentiate between different radial motions, and show a progression from low- to high-frequency neuronal oscillations during the processing of visual information. Self-produced locomotion experience and the ongoing neural maturational processes may be factors that contribute to the efficiency of visual motion perception during development. Unlike full-terms, preterm infants may have impairments in the

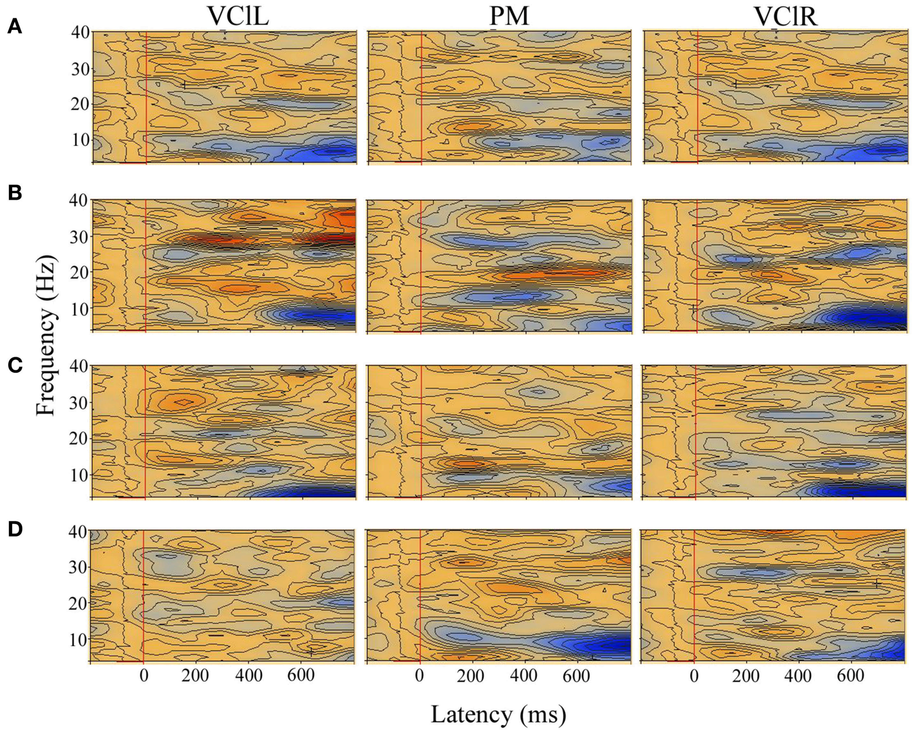

FIGURE 4 | TSE plots across brain regions of interest (VCIL, visual cortex lateral left; PM, parietal midline; VCIR, visual cortex lateral right) when the motion conditions were compared with the static non-flow condition in a typical full-term infant at 4 months (A) and 12 months (B), and in a typical preterm infant at 4 months (C) and 12 months (D). Induced synchronized and desynchronized activities appear in red and blue colored contours, respectively. Induced theta-band desynchronized activities were observed in all the visual areas of interest in the full-term and preterm infants at both ages, with induced alpha-beta band synchronized activities observed in two or more visual areas only in the full-term infants at 12 months. Stimulus onset is the vertical red line at 0 ms, with epoch from −200 to 800 ms.

functioning of the dorsal visual stream. Impaired functioning of the dorsal stream may contribute to their relatively poorer performances during the processing of visual information. Early detection and identification of preterm infants who could be at risk for developmental problems is thus necessary to help provide early intervention programmes required for their optimal development. When studying the neural correlates of prospective control in infancy, it is of the utmost importance to incorporate behavioral data into EEG analyses to get a better understanding of how the development of brain and behavior is intimately linked.

AUTHOR CONTRIBUTIONS

SA, FW, and AM have contributed equally to the conception and design of the work and are accountable for all aspects of the work. SA has drafted the work, FW and AM have contributed equally to revising it critically for intellectual content.

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Independent development of the Reach and the Grasp in spontaneous self-touching by human infants in the first 6 months

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The Dual Visuomotor Channel Theory proposes that visually guided reaching is a composite of two movements, a Reach that advances the hand to contact the target and a Grasp that shapes the digits for target purchase. The theory is supported by biometric analyses of adult reaching, evolutionary contrasts, and differential developmental patterns for the Reach and the Grasp in visually guided reaching in human infants. The present ethological study asked whether there is evidence for a dissociated development for the Reach and the Grasp in nonvisual hand use in very early infancy. The study documents a rich array of spontaneous self-touching behavior in infants during the first 6 months of life and subjected the Reach movements to an analysis in relation to body target, contact type, and Grasp. Video recordings were made of resting alert infants biweekly from birth to 6 months. In younger infants, self-touching targets included the head and trunk. As infants aged, targets became more caudal and included the hips, then legs, and eventually the feet. In younger infants hand contact was mainly made with the dorsum of the hand, but as infants aged, contacts included palmar contacts and eventually grasp and manipulation contacts with the body and clothes. The relative incidence of caudal contacts and palmar contacts increased concurrently and were significantly correlated throughout the period of study. Developmental increases in self-grasping contacts occurred a few weeks after the increase in caudal and palmar contacts. The behavioral and temporal pattern of these spontaneous self-touching movements suggest that the Reach, in which the hand extends to make a palmar self-contact, and the Grasp, in which the digits close and make manipulatory movements, have partially independent developmental profiles. The results additionally suggest that self-touching behavior is an important developmental phase that allows the coordination of the Reach and the Grasp prior to and concurrent with their use under visual guidance.

Keywords: reach, grasp, prehension, self-touch, sensorimotor development, development of reaching, development of grasping

INTRODUCTION

The Dual Visuomotor Channel theory proposes that visually guided reaching consists of two movements, the Reach and the Grasp, each mediated by separate visuomotor pathways from occipital to parietofrontal neocortex (Arbib, 1981; Jeannerod, 1981, 1999; Rizzolatti et al., 1998; Tanné-Gariépy et al., 2002; Culham and Valyear, 2006; Cavina-Pratesi et al., 2010; Filimon, 2010; Karl and Whishaw, 2013). The Reach transports and orients the hand in relation to the extrinsic (location) features of a target while the Grasp opens, shapes, and closes the hand for target purchase in relation to the intrinsic (size, shape) features of the target. Visual fixation of a target from movement onset to target contact integrates the Reach and the Grasp into a seamless act (de Bruin et al., 2008; Sacrey and Whishaw, 2012). In a number of situations in which online vision is not available to guide reaching, the Reach and the Grasp can become uncoupled, each becoming directed by somatosensory guidance. Proprioception guides the Reach to locate the target whereas the Grasp is initiated from information obtained after the target is touched (Karl et al., 2012a; Karl and Whishaw, 2013; Hall et al., 2014). Visually guided reaching is likely accomplished through the same parietofrontal Reach and Grasp pathways that mediate somatosensory guided reaching (Dijkerman and de Haan, 2007; Fiehler et al., 2009; Fiehler and Rösler, 2010; Karl et al., 2012b). In short, anatomical, electrophysiological, brain imaging and behavioral evidence provide support for the idea that reaching consists of two movements, the Reach and the Grasp, which can be configured in various ways depending upon the availability of sensory guidance from different sensory systems.

At the present time, little is known about how the Reach and the Grasp become integrated as a seamless visually guided act but it is reasonable to suppose that development in infancy plays a formative role. A number of prereach and pregrasp movements displayed by infants at different stages of development can be viewed as supporting the idea that the Reach and the Grasp have independent developmental origins. Prior to the onset of visually guided reaching, prereach movements include first orienting the eyes and head to a visual target (Greenman, 1963; Kremenitzer et al., 1979; von Hofsten and Rosander, 1997), then reaching for an object with the mouth by thrusting the head forward and flexing the abdominals (Foroud and Whishaw, 2012), and eventually swiping at a visual target with a fisted or open hand (White et al., 1964; von Hofsten, 1982, 1984). Pregrasp movements include orienting the hand to, and closing the fingers on, an object that contacts the hand (Twitchell, 1965), performing spontaneous hand and grip configurations during vacuous hand babbling (Wallace and Whishaw, 2003), and manipulating objects (Lobo et al., 2014). Some prereach and pregrasp movements likely begin in utero (Myowa-Yamakoshi and Takeshita, 2006). The descriptions of these prereach and pregrasp movements indicate that they are not only made in relation to visual stimuli but they are importantly associated with somatosensory stimulation derived from hand contact with a target (Lockman et al., 1984; Newell et al., 1993; Corbetta et al., 2014).

One prediction of the Dual Visuomotor Channel theory of reaching is that development should feature independence in the maturation of the Reach and the Grasp. Indeed, a number of previous lines of investigation have noted that reaching without grasping occurs at an earlier developmental age than reaching with grasping (Von Hofsten and Lindhagen, 1979; von Hofsten, 1984; Savelsbergh and van der Kamp, 1994; Wimmers et al., 1998a,b). Nevertheless, there are divergent predictions related to the significance of the independence of behaviors described as reaching and grasping. For example, catastrophe theory proposes that during development, reaching gives way to grasping and that the transition point or cusp is associated with enabling morphological changes such as those of hand size, arm size, and torso strength (Wimmers et al., 1998a,b). In contrast, Dual Visuomotor Channel theory would favor the idea that the Reach and Grasp remain independent but that development also fosters conditions in which they can be combined, as occurs when the Reach and the Grasp are integrated together under online visual or somatosensory guidance (Karl and Whishaw, 2013; Corbetta et al., 2014).

Many of the studies that have investigated infant reaching have focused on visually guided reaching and so have used older infants that display visually guided reaching and grasping. Somatosensory guided reaching has received less study (but see Corbetta et al., 2014). The present study was prompted by the observation by Wallace and Whishaw (2003) that at approximately 4 months of age there is a decrease in the spontaneous vacuous arm and hand movements made by infants that is seemingly replaced by self-grasping of the body and clothing. These self-grasping movements have not received experimental analysis and we hypothesized that they could provide insights into the development of infant reaching behavior and the organization of visuomotor systems. First, they would indicate whether there is a phase of somatosensory-related reaching/grasping that precedes and/or is integrated with the onset of visually guided reaching. Second, the analysis of these movements could provide further support for the theory that the Reach and the Grasp are behaviorally independent but can be integrated through experience. Third, analysis of these movements could test the notion that the Reach and the Grasp are supported by at least partially independent neural channels. The present ethological study was therefore directed toward characterizing self-touching behavior in developing human infants over the first 6 months of life.

An important feature of the analysis included determining the relationship between infant age, the location of hand contact, and the type of hand-to-body contact. Accordingly, self-touching movements were coded in relation to the part of the hand that contacted the body (i.e., Dorsum—side or back of the hand, or Palmar—digit surface and palm) and the location on the body at which the contact was made (i.e., Rostral—head or torso, or Caudal—legs or feet). In addition, any self-grasping movement with a digit or number of digits on the body or clothes was also documented. Video recordings of the infants were made across the first 6 months of life because this time period includes the age at which self-grasping movements have been documented and precedes the age at which visually guided reaching becomes a frequent infant activity.

MATERIALS AND METHODS

RESEARCH PARTICIPANTS

Forty-two normal, full term infants (21 boys and 21 girls) participated in the study. None of the infants had sensory or motor impairments. The initial observations were made within a few days of birth and filming sessions ended when the infants were approximately 24 weeks old (Wallace and Whishaw, 2003). This period precedes the age at which visually guided reaching becomes pronounced.

Infants were recruited from acquaintances of the authors, private day homes, the University of Lethbridge Daycare, and a local Montessori preschool (Sacrey et al., 2012). The daycare, preschool, and day homes provided the age of the child in weeks to the experimenters. Informed consent was obtained from the parent(s) prior to their child participating in the study. The University of Lethbridge Human Subjects Research Committee approved the study. All parents were naïve to the purpose and hypothesis of the study.

VIDEO RECORDING

Participants were recorded using a Sony Hi8 video camera, a Sony MiniDV video camera, or a Casio Exilim digital camera. All Hi8 and MiniDV tapes were converted to digital formats. The scorers analyzed the video recordings using slow-motion playback on QuickTime Player 7.

FILMING PROCEDURE

For filming, the infants were either lying on their back or sitting in baby seats, with the older infants usually supported in a baby seat or sometimes supported by a parent (see Lobo and Galloway, 2013, **Figure 2** for illustration of infant supported in baby seat). The seating arrangement was in part determined by parental transport preference. Nevertheless, because Savelsbergh and van der Kamp (1994) have found that body orientation to gravity influences early infant reaching, as does the location of target objects relative to the upper and lower visual fields, every attempt was made to maintain a relatively constant body orientation for the participants across the study period.

The infants were required to be unencumbered by long cuffs that covered the hands or blankets that covered their hands, body, or legs. The infants were filmed from a front view in such a way that the entire infant was visible. This necessitated placing the camera above infants that were lying on their back and before infants that were sitting. The infants did not have toys or other objects present that would otherwise distract them from spontaneous activity.

DATA COLLECTION

At least 10 min duration of spontaneous activity was filmed for an infant on each filming session. At each sampling age, between 8 and 10 infants comprise the final data set. Some of the infants were available for repeated filming ($n = 4$ for all sessions), whereas others were filmed at only a few time points. There were no obvious differences in the data obtained from infants that were repeatedly filmed and those that were filmed only once. The samples were taken as close as possible to the 2 week interval markers (i.e., when the infant was exactly 2 weeks old, 4 weeks old, etc.) as long as the infants were alert during these recordings.

SCORING

The actions of both hands were coded separately. Because no differences in the frequencies of the types of movements were found between the two hands, the results from the two hands were combined for analyses. The infants made a large number of arm and hand movements during the recording sessions, but only punctuate contacts by the hand with the body were subject to analysis. Hand contacts were classified according to contact location (Rostral or Caudal body contacts) and hand posture (Dorsum, Palmar, or Grasp contacts).

1. *Rostral vs. Caudal Body Contacts*. Rostral contacts (**Figures 1A,B**) were any self-contacts by a hand to the head, trunk, arm, or other hand. Caudal contacts (**Figures 1C,D**) were any self-contacts by a hand to the hips, upper leg, lower leg, or feet.
2. *Dorsum vs. Palmar.* Dorsum contacts (**Figures 2A,B**) were any self-contact with the dorsal aspect of the hand, including the back of the digits or the sides of the hand. Hand shapes could include a fist shape, a semi-closed hand with the thumb often tucked under or over the fingers, or an open hand. Palmar contacts (**Figures 2C,D**) were any self-contact with the Palmar aspect of the hand, including the fingertips, the palm, or the ventral sides of the hand. Hand shapes could include a partially open hand in which only the Palmar digit tips were in contact, or a more open hand in which the digits, palm, or digits and palm were in contact.
3. *Grasp contacts.* Grasp contacts (**Figures 2E,F**) were defined as the closing of one or more of the digits around the infant's body or clothing (Wallace and Whishaw, 2003). These Grasps included pre-precision grasps, in which only one or a few digits were involved in grasping, and whole hand Grasps, in which all digits were involved. A note was also made with respect to whether a grasped target was manipulated after grasping.

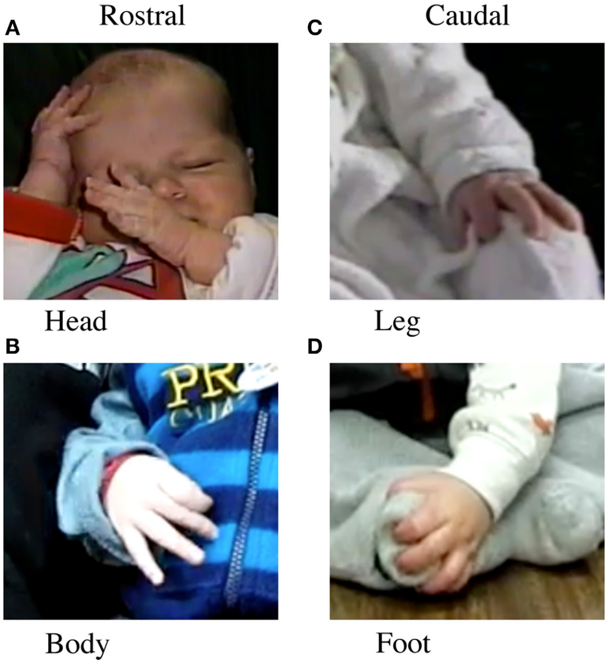

FIGURE 1 | Location of body contact. Left. Rostral contact on **(A)** the head, **(B)** the trunk. **Right:** Caudal contact on **(C)** leg and **(D)** foot.

For each sampling period for each infant, the first 40 instances of self-touching behavior were documented, irrespective of which hand was used. The duration of the positioning of each hand movement was not noted, but most contacts were discrete in that the contact was broken shortly after it was made. One investigator (BLT) scored all of the behavior while two other investigators (JMK, LAL) scored samples of behavior in order to establish rater reliability. Inter-rater reliability for whether the hand contacted the body, whether contact was Rostral or Caudal, and whether contact was Dorsum, Palmar, or Grasp exceeded 95% agreement between the raters.

STATISTICAL ANALYSIS

The frequency of body contacts and hand posture contacts, as a function of infant age, were subject to statistical analyses using the computer program SPSS (v. 21.0.0.0). To accommodate uneven data points across infants, results were evaluated using repeated-measures mixed linear models (MLM; Verbeke, 2009; Heck et al., 2014). Age (0, 2, 4, 6, 8, 10, 12, 14, 16, 18, and 20 weeks) served as the within-subjects factor. A p-value of 0.05 was considered significant.

RESULTS

From birth through 6 months of age, infants displayed many spontaneous contacts of the hands with the body. The ethogram in **Figure 3** illustrates a sample of the hand shapes/body location for the first 10 contacts made by infants at three different

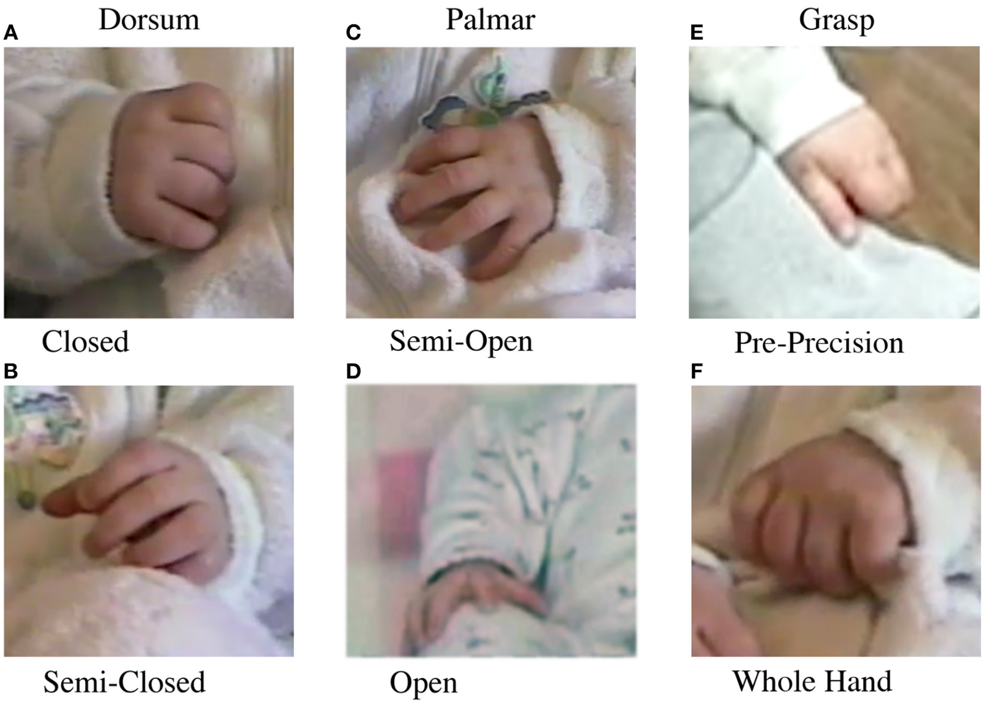

FIGURE 2 | Hand posture during contact with the body. Left: Dorsum contacts, **(A)** contact with the back of the digits with the hand closed, **(B)** contact with the back of the digits with the hand semiclosed. **Middle:** Palmar contact, **(C)** contact with the digit pads and partially open hand, **(D)** contact with the fully open hand. **Right:** Grasp contacts, **(E)** pre-precision grasp between the thumb and side of the index finger, **(F)** whole hand grasp.

4 Weeks	L-FT-H L-SC-T R-SC-H R-SC-T L-FT-T L-SC-T R-O-H L-FT-T L-FT-H R-SC-H
12 Weeks	L-FT-Le L-FT-Le R-C-T R-C-T L-O-T R-FT-T L-FT-Le R-O-T L-C-T R-C-T
20 Weeks	L-FT-Le L-FT-Le L-FT-Le L-FT-Le R-O-Le L-O-F L-G-F R-FT-Le R-G-Le L-FT-F

FIGURE 3 | Sample coding of the ethogram illustrating some of the hand shapes/body location of the first 10 contacts made by one infant at three different ages (1, 3, and 6 months). (1) Hand: R, right; L, left; (2) Hand Shape: C, closed; SC, semi-closed; FT, fingertips; O, open; (3) Location: H, head; T, torso; Le, legs; F, feet.

ages. Note that these samples were collected in an average of 21 s of observation time at each age (10–39 s). There was no evidence for differences in the location or hand posture of contacts according to hand or sex. Thus, sex and hand were compiled in the results. Infants ages 20, 22, and 24 weeks were also combined for this analysis, as behavioral results were asymptotic for these ages. Overall, the results show that there is a developmental transition from Rostral to Caudal contacts, a developmental transition from Dorsum to Palmar contacts, and a developmental point at approximately 16 weeks of age at which infants show an increased proportion of Grasp contacts.

ROSTRAL vs. CAUDAL BODY CONTACTS

Figure 4 illustrates the percent of hand-to-body contacts to the Caudal portions of the body (legs and feet) as a function of age (Video 1). In the earliest weeks, the infants mainly made contacts to the Rostral region of the body, including the head, torso, arms and hands. Rostral hand-to-body contacts were restricted to the areas of the body within immediate proximity of the hand. And so, for an arm that was largely flexed at the elbow, contact was made with the head or torso. At approximately 12 weeks of age onwards, increased numbers of contacts were made with Caudal regions of the body (including the hips, legs and eventually the feet). Caudal hand-to-body contacts began with contacts to the hips and upper thighs, and expanded toward the knees and feet at approximately 20 weeks of age. Hand-to-body contacts with the knees and feet frequently involved bending of the knees and bringing the feet up toward the torso, especially when the infant was lying on his or her back.

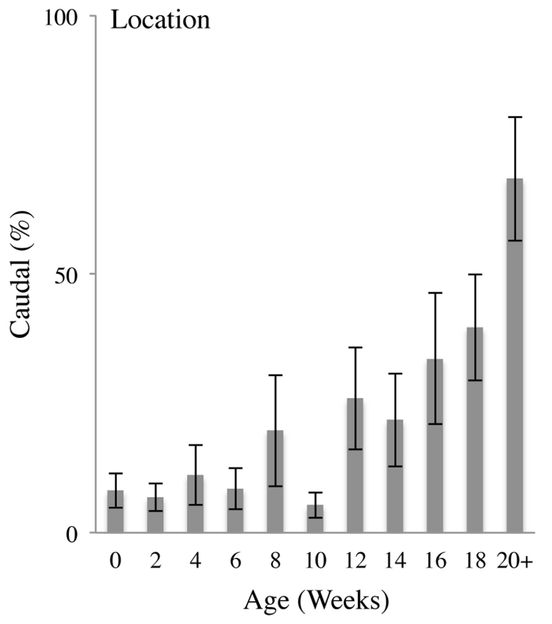

FIGURE 4 | Caudal body contacts. Percent (mean and standard error) of contacts with the hand on the Caudal portions of the body (legs and feet) relative to all contacts as a function of age.

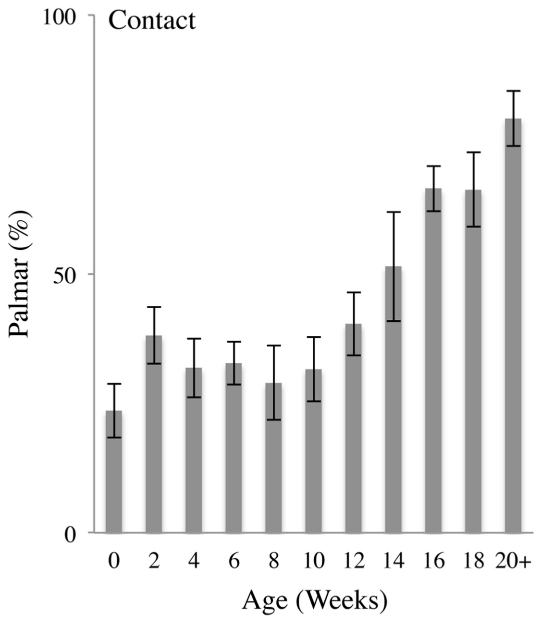

FIGURE 5 | Palmar body contacts. Percent (mean and standard error) of Palmar contacts (contact with the digit pads or palm) relative to all contacts as a function of age.

In sum, Caudal contacts began to occur with increasing frequency at approximately 14 weeks of age, progressing from contacts with the head and trunk to contacts with the hips, legs, and feet. Thus, as a proportion of all body contacts, Caudal contacts increased as a function of age as indicated by a repeated measures MLM for Caudal contacts that gave a significant effect of Age [$F_{(10,\ 13.037)} = 5.633$, $p < 0.01$]. *Post-hoc* comparisons revealed that, compared to 0 weeks of age, the percentage of Caudal contacts was significantly increased at 14 ($p < 0.05$), 16 ($p < 0.05$), 18 ($p < 0.01$), and 20+ ($p < 0.001$) weeks of age.

DORSUM vs. PALMAR CONTACTS

Figure 5 illustrates the percent of Palmar contacts as a function of age. In the earlier weeks, the infants mainly contacted the body using the Dorsum of the hand, with a high frequency of self-contacts made with a fist, progressing to Dorsum contacts with a semi-closed hand, including contacts with the back of the fingers and the side of the hand. Duration of hand-to-body contact length was brief, marked mainly by contact and release (Video 2). At 8–12 weeks, hand-to-body contacts become increasingly exploratory with increased contact duration, digit manipulation, and movement. By 12 weeks Hand-to-body contacts were increasingly made with the Palmar aspect of the hand and became more complex, often involving rotation of the hand at contact, dragging the palm or fingertips along the surface of the body, and dynamic and complex hand shaping sequences.

In sum, Palmar contacts began to occur with increasing frequency at approximately 12 weeks of age, progressing from contacts with the pads of the fingertips, to dynamic contacts with the open palm. As a proportion of all body contacts, Palmar contacts increased as a function of age as indicated by a repeated MLM for Palmar contacts that gave a significant effect of Age [$F_{(10,\ 20.125)} = 7.092$, $p < 0.001$]. *Post-hoc* comparisons revealed that, compared to 0 weeks of age, the percentage of Palmar contacts was significantly increased at 12 ($p < 0.05$), 14 ($p < 0.05$), 16 ($p < 0.001$), 18 ($p < 0.001$), and 20+ ($p < 0.001$) weeks of age.

GRASP CONTACTS

Figure 6 illustrates that the incidence of Grasps as a percentage of all hand contacts was low in infants aged 0–14 weeks and then increased at 16–20 weeks. The self-directed preGrasps that occurred within the first week of infancy continued to occur at a relatively low frequency across the 24 weeks of study whereas whole hand Grasps became prominent at 16 weeks of age. As a proportion of all body contacts, Grasp contacts increased as a function of age as indicated by a repeated MLM for Grasp contacts that gave a significant effect of Age [$F_{(10,10.547)} = 3.935$, $p < 0.05$]. *Post-hoc* comparisons revealed that, compared to 0 weeks of age, the percentage of Grasp contacts was significantly increased at 16 ($p < 0.05$), 18 ($p < 0.05$), and 20+ ($p < 0.05$) weeks of age.

DEVELOPMENTAL PATTERNS

Normalized regression curves for Caudal, Palmar, and Grasp contacts are shown in **Figure 7**. Spearman's correlations gave a significant Caudal vs. Palmar Rho = 0.806 ($p = 0.005$), a significant Palmar vs. Grasp Rho = 0.770 ($p = 0.009$), but no Caudal vs. Grasp Rho = 0.503 ($p = 0.138$). The regression curves suggest that increases in Caudal and Palmar contacts are of a comparable magnitude and follow a similar developmental time course. By contrast, the regression curve for Grasps is reduced and shifted to

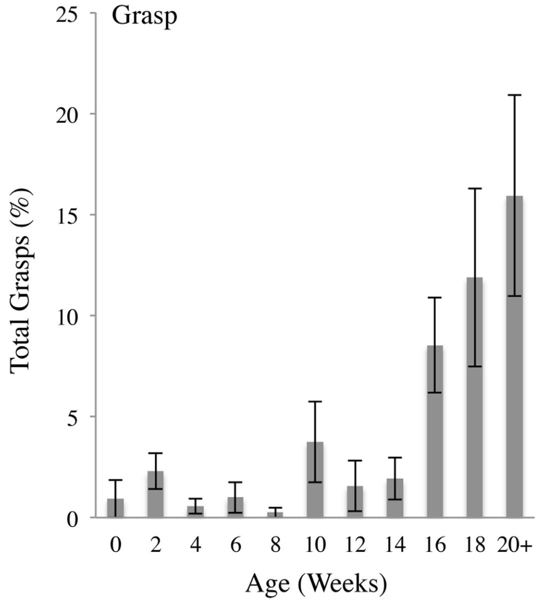

FIGURE 6 | Grasp body contacts. Percent (mean and standard error) of Grasp contacts (pre-precision or whole hand) relative to all contacts as a functions of age.

the right, indicating that the incidence of Grasps did not become prominent until somewhat later. These relations are also reflected by follow-up tests described in the Dorsum-Palmer, Rostral-Caudal, and Grasp sections above. The significant relationship between Grasp and Palmar is likely due to the fact that a Grasp is dependent upon a Palmar contact.

DISCUSSION

There are two novel contributions of this study. First, it was found that otherwise resting infants in the first 6 months of life made many, almost continuous, forelimb movements that resulted in hand contacts with the body. These contacts eventually included grasping and manipulating the body and clothes in all regions of the body. Thus, self-touching behavior in infants is revealed to be a behavior in which infants can practice reaching, and perhaps additionally acquire body awareness in relation to a hand-related schema. Second, the analysis of self-touching movements suggests that advancing the hand to different body targets and contacting the body with the digit tips and palm represent an early developmental phase of the Reach whereas grasping the body and clothes and performing manipulatory movements represent an early phase of the Grasp. Because Reach activities developmentally preceded Grasp activities, the results suggest some independence of the two movements. Taken together with previous work showing that infants do not need to view their own hand in order to transport it to a target (Clifton et al., 1993; Corbetta, 2010), the timing and the sophistication of hand contacts with the body observed in the present study suggest that reaching undergoes substantial preparedness under the auspices of proprioception and touch prior to and in concert with the emergence of visually guided reaching.

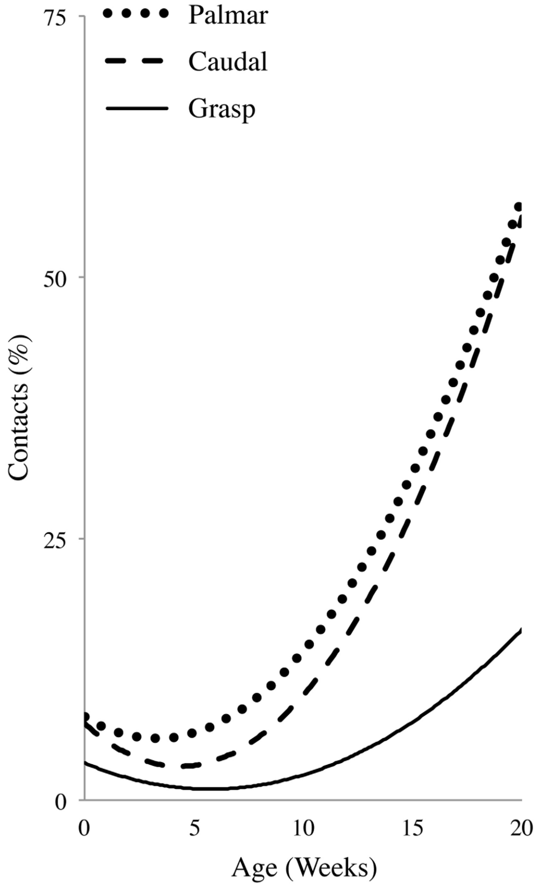

FIGURE 7 | First order polynomial regression illustrating the developmental profile of hand-to-body Palmar contacts, contacts to the Caudal region of the body, and Grasps. Note the differences between Palmar/Caudal contacts and Grasps.

It is important to note that the present study was primarily directed toward describing self-touching hand movements and secondarily at assessing the idea that during development there is some independence in the display of reaching and grasping movements as has been suggested in studies largely directed toward visually guided reaching (Von Hofsten and Lindhagen, 1979; Trevarathen, 1982; von Hofsten, 1984; Savelsbergh and van der Kamp, 1994; Wimmers et al., 1998a,b). Thus, although it is obvious that the spontaneous activity that we have observed is likely the result of interactions between nervous system development, morphological development of the body, the posture of the infants during testing, and the life history of the experimental subjects (Savelsbergh and van der Kamp, 1994; Thelen and Spencer, 1998; Heathcock et al., 2004; Lobo et al., 2014; Soska and Adolph, 2014), there was no intent in the present study to distinguish between these contributing factors. Rather, it was our view that any differences in the developmental profile of reaching and grasping might contribute to a growing body of evidence that the Reach and the Grasp are mediated by different sensorimotor channels (for a review of other infant work directed toward this question see Karl and Whishaw, 2014). As noted by Hebb

(1949) "The problem of understanding behavior is the problem of understanding the total nervous system and *visa versa (xiv)*."

Specifically, three aspects of hand-to-body contact were documented in relation to infant age: an increasing incidence of caudal body relative to rostral body contacts, an increasing incidence of palmar relative to dorsum hand contacts, and an increasing incidence of contacts that resulted in Grasps of the body and clothes. An increase in the incidence of palmar and caudal contacts occurred at a somewhat earlier age than did the increase in the incidence of Grasps. Because the Reach in adults is associated with forelimb movement and a more open hand to make palmar contact with a target, we suggest that the forelimb movement and palmar contact in infants is a manifestation of an infant Reach. Because the Grasp in adults includes digit flexion and closing to purchase and manipulate an object, we suggest that self-grasping in infants is an early manifestation of an infant Grasp. Thus, we suggest that the developmental pattern of these Reach and Grasp movements in infants supports the Dual Visuomotor Channel Theory, which proposes that the reaching act is enabled by separate Reach and Grasp neural systems. Of course, morphological development including increases in the length of the arms, the size of the hands, and body strength in all likelihood are also necessary for some part of the maturation of the movements. Nevertheless, the hand to body self-touching movements seen in the infants likely continue throughout life and likely continue to serve some of the same purposes in adults that they serve in infancy.

The design of the present experiment is similar to that of a number of our previous studies in that it is ethological, focuses on infant spontaneity, and searches for structural organization within this activity. It also featured a number of procedures to ensure accurate measurement of spontaneous hand-to-body contacts in infants (Wallace and Whishaw, 2003; Sacrey and Whishaw, 2010; Foroud and Whishaw, 2012). First, toys and other distractions were removed to ensure that self-directed movements were unbiased by extraneous influences. Second, to control for individual differences in the frequency of hand-to-body contacts, 40 consecutive contacts within each 10-min recording period were used for analysis. Third, high inter-rater reliability scores among 3 independent raters on the main behaviors that were measured confirmed the validity of the scoring method. These procedures ensured that the infants were similarly relaxed and alert and otherwise not disturbed and so were likely to engage in a common class of relatively spontaneous activities across the study period.

In many respects, this work differs from the more formal studies of visually guided reaching in which both the task and the outcome are constrained. For example, in the Wimmers studies (Wimmers et al., 1998a,b), described in the introduction, infants are encouraged to purchase a proffered object, resulting in seemingly age-related dichotomous behavior, reaching without grasping followed by reaching with grasping. Spontaneous self-directed movements of the hand described here also reflect a developmental profile in which the Reach matures before the Grasp, but one behavior does not completely replace the other. The spontaneous manual interaction with objects when documented in a ethological context also suggests that reaching without grasping and reaching with grasping co-occur (Lobo et al., 2014). Although the present study was not directed at examining how reaching and grasping occur, work with older infants suggests that there is a very prolonged developmental period, likely lasting beyond 2 years of age, in which the Reach and Grasp are not yet fully mature and not yet fully integrated (Karl and Whishaw, 2014). Further work using high speed filming of infant self-grasping could be used to examine the detailed architecture of the Reach and the Grasp in self-grasping because it might be expected that online somatosensory guidance of reaching matures before the online visual guidance of reaching (Karl et al., 2012b).

A number of caveats in relation to the present methods must be noted. First, infants were filmed in a variety of settings including the home and laboratory, the time of day during which filming occurred was variable, and the postures of the infants did vary somewhat depending upon their age, and all infants could not be filmed at every age. It might be considered, however, that such variation strengthens the ethological relevance of the sampling method. Second, infants were usually clothed and so it was not possible to confirm that similar hand-to-body behavior would be demonstrated in the absence of clothing. For example, the presence of clothing might serve to encourage grasping behavior. It was noted, however, that there were no obvious differences in the behavior of infants for whom clothes were tight fitting versus loose fitting. Third, the sampling periods were limited to resting behavior and did not include other activities, including breast or bottle feeding or interpersonal play, which could provide additional information concerning the development of hand contacts to the self and proximal objects. In addition, the infants' spontaneous activity included many other activities such as movements of the head, trunk, and legs and these activities were not documented. Nevertheless, the high number of hand-to-body contacts that occurred in each infant and the systematic changes in the location and way that the hand contacted the body across the developmental period examined suggests that this data sample is sufficiently robust to provide insights into an activity that must occur in infants many hundreds of times each day.

There are a number of features of the present results that we feel justify concluding that they reveal a novel insight into the developmental progression of reaching behavior and its relation to the distinctive Reach and Grasp movements of adults as characterized by the Dual Visuomotor Channel Theory. First, studies that have manipulated the visual contribution to reaching show that without vision the Reach consists of a movement of extending the arm and hand with open digits in order to make palmar contact with a target (Karl et al., 2012a; Karl and Whishaw, 2013). We suggest that in infants, the development of hand-to-body contacts from rostral to caudal body locations associated with the increasing frequency of opening the hand to make palmar contacts might be a developmental precursor of the adult manifestation of the Reach. That is, in the initial weeks of the samples, arm movements were largely movements around the shoulders with the digits in a mainly closed configuration (Sacrey and Whishaw, 2010) that resulted in incidental hand to body contact. Eventually, the arm movements included movements of the trunk and all of the forelimb joints, including extension of the digits. In doing so, they included palmar contact that began to have an exploratory character and that increasingly included the caudal regions of the body. The movements also became coordinated with other body movements as exemplified by reaches that contacted the feet and toes that were themselves in motion. It is also noteworthy in this respect that regression profiles of touches on caudal body locations and the use of palmar contacts were very similar. Thus, in their eventual configuration, infant reaches to touch the body resembled the Reach made by unsighted adults in that the arm carries an open hand to make a palmar contact with a target.

It is interesting that Pellijeff et al. (2006) show that reaches made by adults to their own hand, located near their own torso, are associated with fMRI activation in the cortical area of the anterior precuneus and medial intraparietal sulcus in the superior parietal lobe. This is the same region that is activated for both proprioceptively and visually guided reaching toward external objects (Filimon et al., 2009). Therefore, we suggest that infant reaches toward the torso and body are analogous to adult reaching to distal targets, adding support to our suggestion that caudal directed reaches and touches serve as a developmental precursor/addition to reaching to visual targets.

We were, of course, unable to determine the extent to which reaches to various body parts were vacuous versus goal directed but we propose that the scope and frequency of the movements provides ample room for arm movements to mature both in their configuration (von Hofsten, 1984) and intent (Lew and Butterworth, 1997). We note that after palmar contacts begin to occur they also begin to take on an exploratory character in frequently caressing the part of the body that is contacted. As such, the practice/development of these movements made to body targets might well be preparatory/facilitatory for reaches that will subsequently be directed to targets during visually guided reaching (White et al., 1964; McDonnell, 1975; von Hofsten and Fazel-Zandy, 1984; von Hofsten and Ronnqvist, 1988; Lobo et al., 2004; Lobo and Galloway, 2013). In the present study, we observed few movements directed toward the mouth, and accordingly did not separately document them, but other research has found that these movements only become frequent after about 4 months of age, an observation consistent with the present results that it is at about this age that hand movements are becoming goal directed (Lew and Butterworth, 1997; Sacrey et al., 2012).

According to the Dual Visuomotor Channel Theory, the Grasp preshapes the digits relative to target size and adjusts the digits for appropriate target purchase (Arbib, 1981). In the absence of vision, shaping and grasping are instructed by haptic information provided by touch (Karl et al., 2012a; Karl and Whishaw, 2013). In the infants examined in the present study, the first grasps featured hooking one or another digit into the clothing, they then involved clasping with the thumb or other digits, and by the end of the observational period they featured whole hand grasps that included manipulation. We suggest that this pattern features a progression in "maturation and learning to grasp." Our observations and interpretation are consistent with an extensive literature on infant and fetal hand use (Twitchell, 1965; Hepper, 1990; Hepper et al., 1991; Sparling and Wilhelm, 1993; Sparling et al., 1999). Nevertheless, prior to the various grasping acts, there was no obvious shaping of the digits prior to target contact nor was obvious hand shaping present between successive contacts. The absence of digit preshaping is not surprising because evidence from studies on the development of visually guided reaching suggests that hand preshaping continues to mature beyond 2 years of age (McCarty et al., 2001; Karl and Whishaw, 2014).

Evidence that grasping movements have a partially different developmental onset than reaching movements was supported by our finding that the developmental profile of grasping frequency was statistically unrelated to the Rostrocaudal profile of body contact and was only somewhat weakly related to the Dorsopalmar profile of hand contact, which were themselves tightly coupled. That is, the onset of frequent self-grasping occurred at a somewhat later age than the onset of frequent caudal body contacts and palmar contacts. We suggest that this difference provides further support for the idea that the Reach and the Grasp have different developmental onset. That is, our results suggest that the Reach, consisting of an ability to move the hand to a body target with the digits open to make a Palmar contact with the target, is achieved before the hand begins to engage in substantial object purchase, which characterizes the Grasp. Of course, the movements are not completely unrelated because a Reach with Palmar contact necessarily precedes a Grasp. Nevertheless, it is interesting that an examination of the early development of visually guided reaching similarly suggests that Reach maturation precedes Grasp maturation (Karl and Whishaw, 2014; see also Von Hofsten and Lindhagen, 1979; Trevarathen, 1982; von Hofsten, 1984; von Hofsten and Fazel-Zandy, 1984; Ruff, 1989; Savelsbergh and van der Kamp, 1994; Wimmers et al., 1998a,b; Corbetta and Snapp-Childs, 2009).

In previous work, we have suggested that the Reach and the Grasp have different evolutionary origins, the Reach derived from stepping and the Grasp derived from food handling movements (Karl and Whishaw, 2013). In light of this suggestion, the present findings might seem surprising because the development of self-touching Reach and Grasp movements occur both before the onset of walking (crawling) and the onset of hand use for self-feeding. In humans, however, self-feeding and walking are developmentally delayed. It is possible that the many leg movements associated with self-directed reaches to the caudal body are a developmental precursor for walking and may facilitate the development or refinement of neural circuitry in the superior parietal lobe that is common to both stepping and reaching (Bakola et al., 2010, 2013; Karl and Whishaw, 2013). Although leg movements were not analyzed in the present study, the relationship between arm movement and leg movement could be addressed by examining their relationship in human infants as well as their early development in other animal species, especially other primate species (e.g., Wallace et al., 2006). Similarly, hand movements in infants are often associated with mouth movements (Iverson and Thelen, 1999). It is possible that the species-typical developmental profile of humans results in suppression and reordering of the development of many movements (Schott and Rossor, 2003).

Speculatively, the present results could be related to the Dual Visuomotor Channel Theory in other ways, including the establishment of body spatial schema and hand action schema related to objects (Granmo et al., 2008; Yamada et al., 2013). In this respect it is relevant that the Reach is importantly directed to the extrinsic (e.g., location) properties of targets using egocentric coordinates provided by proprioception. Early prereach activity associated with self-touching could contribute to the development of egocentric coordinate systems. It is also relevant that the Grasp is importantly guided by the intrinsic properties (size, shape, etc.) of a target. Infant self-grasping acts could contribute to the development of a hand schema that provides an appreciation for the intrinsic properties of objects. Because both the body and hands are undergoing continuous morphological change (Newell et al., 1989, 1993), the high incidence of self-touching and grasping could contribute to updating hand and body schema.

In summary, developmental research presupposes that developing actions are the foundation for more complex adult behavior (Lobo and Galloway, 2008) and that development frequently has a proximodistal progression (Berthier et al., 1999). Although numerous hand-to-body contact behaviors and hand manipulative capabilities have been observed in development, including in fetal development (Hepper, 1990; Hepper et al., 1991; Sparling and Wilhelm, 1993; Sparling et al., 1999), the present results are consistent with these general sequences and also offer two new insights into the development of reaching. First, we suggest that hand-to-body contact is a formative stage in the development of the adult Reach. It is likely that the maturation of self-contact movements into self-grasping movements is an important preparatory stage for the development of the adult Grasp. Second, we suggest that the early development of arm movement and hand touching compared to the later development of the pattern of self- grasping and manipulation provide evidence that the Reach and the Grasp have at least partially separate developmental profiles. Finally, we suggest that the development of the Reach and the Grasp and their integration is importantly related to practice provided by the high incidence and changing patterns of hand self-contact behavior.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://www.frontiersin.org/journal/10.3389/fpsyg.2014.01526/abstract

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Assessing the Impact of Movement Consequences on the Development of Early Reaching in Infancy

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Prior research on infant reaching has shown that providing infants with repeated opportunities to reach for objects aids the emergence and progression of reaching behavior. This study investigated the effect of movement consequences on the process of learning to reach in pre-reaching infants. Thirty-five infants aged 2.9 months at the onset of the study were randomly assigned to 1 of 3 groups. Two groups received a 14-day intervention to distinct reaching tasks: (1) in a contingent group, a toy target moved and sounded upon contact only, and (2) in a continuous group, the toy moved and sounded continuously, independent of hand-toy contact. A third control group did not receive any intervention; this group's performance was assessed only on 2 days at a 15-day interval. Results revealed that infants in the contingent group made the most progress over time compared to the two other groups. Infants in this group made significantly more overall contacts with the sounding/moving toy, and they increased their rate of visually attended target contacts relative to non-visually attended target contacts compared to the continuous and control groups. Infants in the continuous group did not differ from the control group on the number of hand-toy contacts nor did they show a change in visually attended target versus non-visually attended target contacts ratio over time. However, they did show an increase in movement speed, presumably in an attempt to attain the moving toy. These findings highlight the importance of contingent movement consequences as a critical reinforcer for the selection of action and motor learning in early development. Through repeated opportunities to explore movement consequences, infants discover and select movements that are most successful to the task-at-hand. This study further demonstrates that distinct sensory-motor experiences can have a significant impact on developmental trajectories and can influence the skills young infants will discover through their interactions with their surroundings.

Keywords: motor development, infants, reaching, reinforcement learning, contingent reinforcement, developmental trajectories, sensorimotor experience

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INTRODUCTION

In typically developing infants, reaching emerges between 3 and 5 months of age (von Hofsten, 1984; Clifton et al., 1993; Thelen et al., 1993). The appearance of this behavior has significant cascadic effects on many areas of development. For example, it impacts gains in motor control and the emergence of novel exploratory abilities (von Hofsten, 1991; Konczak et al., 1995;

Thelen et al., 1996; Bhat et al., 2005), it offers new opportunities to learn about object properties (Gibson, 1988; Rochat, 1989; Bushnell and Boudreau, 1993; Lederman and Klatzky, 1993; Corbetta and Snapp-Childs, 2009; Lobo and Galloway, 2013), and triggers changes in the socioemotional context (Bakeman and Adamson, 1984; Fogel et al., 1992; Ruff and Rothbart, 1996; Fogel, 1997). Because of the conspicuous importance of such a behavior, developmental scientists have actively sought to understand how it forms in infancy. For many decades, researchers have carefully described the progression of this behavior over time by focusing mainly on the role that vision played in the guidance of the arm toward the target object (e.g., Piaget, 1952; White et al., 1964; von Hofsten, 1979, 1982, 1984; Bushnell, 1985). Since the late 1990s, however, researchers have come to understand that the emergence of reaching is the product of multiple interacting subsystems, not just vision (Thelen, 1992, 1995; Thelen and Smith, 1994, 1998; Spencer et al., 2000; Clearfield and Thelen, 2001; Cunha et al., 2015). As a result, research efforts have increasingly shifted toward identifying which types of early experiences can help the integration of these multiple systems in fostering the emergence of infant reaching.

Several groups of researchers have now published studies that examined the impact of varied types of sensory-motor experiences on the emergence of infant reaching. One such study from Lobo et al. (2004) discovered that both general movement and reaching-specific, or object-directed, movement experiences served to drive higher amounts of reaching behavior relative to a no experience control. However, infants in the reaching-specific condition, in which the successful movement consequence was hand-toy contact, displayed significantly higher amounts of reaching relative to infants in the general movement experience condition. Furthermore, Lobo and Galloway (2008) replicated the reaching-specific results of Lobo et al. (2004) but extended the findings to show that infants who received specific reaching experience, and even basic postural experience, significantly outperformed infants who received non-object-directed social experience.

These studies revealed that broad, non-specific arm movements and postural enhancements – two contributing sub-systems to learning to reach – can help the emergence and development of reaching, but specific reaching experiences always led to faster learning outcomes. Along the same line of inquiry, another group of studies also found that reaching-specific experience interventions significantly helped precipitate the development of reaching (Cunha et al., 2013, 2015; Soares Dde et al., 2013). More unexpectedly, these studies discovered that even very short-term durations of 1 or 2 days of reaching-specific intervention sufficed to drive significant results in the amount of reaching performed in babies, compared to control babies who only received a non-object-directed social intervention.

The fact that reaching-specific interventions seem to have an impact on learning to reach fits well with the idea that repeated opportunities to reach for and explore specific action consequences may facilitate the discovery of successful actions (Schlesinger et al., 2000; Bojczyk and Corbetta, 2004; Corbetta and Snapp-Childs, 2009; Williams et al., 2015a). Needham et al. (2002) and Libertus and Needham (2010, 2014) further examined this idea through a series of studies where they fitted pre-reaching infants with “sticky mittens” thereby providing *simulated grasping* experience when the object stuck to the mittens following hand-toy contact. In these studies, the action consequence during the learning to reach process was not just limited to making hand-toy contact, but also offered infants the enhanced ability to seemingly *pick up* the toy. Parents were instructed to provide 10 min of reaching exposure to their infant wearing the “sticky mittens” for 12–14 consecutive days. The “sticky mittens” group was also compared to other age-matched groups of infants who received other kinds of “more passive” experiences. In one study (Libertus and Needham, 2010), the object was placed by the parent directly in the infant’s hand while wearing the mittens. In another (Libertus and Needham, 2014), the object was attached to the wrist of the infant, or in another condition, the infant was not encouraged to reach. In all study variations, performances were always compared with an age-matched, no intervention control group. The researchers consistently found that infants in the “sticky mittens” group performed more toy-directed behaviors than infants in any of the other groups, which led them to conclude that the simulation of grasping provided by the mittens served to drive increased toy-directed behavior.

In these studies, however, it remained unclear if the “sticky-mittens” experience provided something truly additional to the learning to reach experience. Much of the other group interventions to which the “sticky mittens” were compared did not entail much reaching behavior. Further, many aforementioned studies reported increases in learning to reach simply by exposing infants to classic, reaching-specific experiences. If we follow the reasoning that the consequences of an action are an important factor in driving the learning to reach process, then one may ask what could be the relative impact of the “sticky mittens” simulated grasping experience on the formation of initial reaching behavior, compared to simply touching the target. In an effort to address this question, Williams et al. (2015b) examined the developmental trajectories of near-reaching infants receiving task-specific reaching experience wearing “sticky mittens” with an age-matched group of infants who wore “non-sticky mittens.” Both groups received 14 days of 10-min, experimenter-led exposure to the reaching task. In addition, Williams et al. (2015b) recorded the arm movement kinematics prior to and after the 14-day reaching experience. These researchers found that both mittens groups displayed significant gains in the amount of visually attended target reaching over the course of the study, however, only infants in the “non-sticky mittens” group showed a significantly higher amount of visually attended target reaching relative to the no-experience control group on the final day. The “sticky mittens” group did not. In addition, infants in the “non-sticky” group showed a decrease in movement speed between the first and last day of the study, as did the no-experience group, which is an indication of improved movement control. Infants in the “sticky” group, on the contrary, increased movement velocity between the first and last day, suggesting that they were possibly learning to swipe more at the toy to pick it up rather than slowing movement speed to contact the toy accurately (Williams et al., 2015b).

These results indicated again that varying experiences associated with distinct movement consequences of hand-toy contact could drive diverse developmental trajectories in the early learning to reach process. Specifically, Williams et al.'s (2015b) study revealed that learning to reach was not particularly enhanced by the provision of grasping simulation, but that making direct contact with the toy alone was sufficient to drive the process of action selection. Further investigations of the "sticky" group's performance led these researchers to pin point more accurately what might have driven the observed differences between mitten groups (Corbetta et al., 2015). Williams et al. (2015b) designed their mittens differently than the Needham group; the Williams et al. (2015b) mittens had openings for the fingers allowing infants in both groups to make direct haptic contact with the target depending on how the hand was directed at the toy at contact. Follow-up analyses revealed that the best performers in the "sticky mittens" group were the infants who made more direct bare finger contacts with the toy relative to simulated grasps. The data also revealed that the grasping simulation intervention with the open fingers mittens worked successfully – the toy stuck to the mitten at contact – but success at "picking-up" the toy via "sticky-mittens" with rare direct fingers-to-toy contact did not contribute to increased performance over time. Thus, those analyses indicated that reaching progression was driven more by direct haptic finger contact with the toys than by the provision of grasping simulation via "sticky-mittens" (Corbetta et al., 2015). This finding was in line with Schlesinger and Parisi's (2001) work indicating that tactile feedback is an important factor in driving the exploration and selection of reaching movements. Through this series of studies we learned that infants may indeed rely on the consequences of their actions to increasingly select their actions, but these consequences may be more directly tied to direct haptic hand-toy contact than grasping simulation *per se*. This finding is in line with the findings of the aforementioned groups of researchers who observed progression in reaching-specific interventions without "sticky mittens" (Lobo et al., 2004; Lobo and Galloway, 2008; Cunha et al., 2013, 2015; Soares Dde et al., 2013).

This line of research has theoretical implications. We know that the process through which novel behavior emerges and organizes is complex and that it begins in early development through repeated cycles of action and perception, during which infants learn about their actions and their associated consequences (Gibson, 1988; Gibson and Pick, 2000; Corbetta, 2009). When infants discover action consequences relevant to the task-at-hand, those actions become selected over time and used in future, similar situations. Dynamic Systems Theory, for example, purports that the selection process leading to more sophisticated levels of reaching behavior is heavily driven by repeated cycles of action and perception (Bojczyk and Corbetta, 2004; Corbetta and Snapp-Childs, 2009). Such repeated cycles are also tied to the process by which the brain learns, and the values it attributes to the consequences of actions. Recent neuroscientific research, specifically, perspectives on neural substrates of behavioral development such as Edelman's (1987) Theory of Neuronal Group Selection (TNGS) and Approximate Optimal Control Theory (Berthier et al., 2005) supplement Dynamic Systems to better explain the early emergence and development of behavior (see Williams et al., 2015a, for a more detailed account). In effect, both TNGS and Approximate Optimal Control provide potential neural mechanisms for the neuronal selection process that underlies behavioral change. Specifically, Edelman (1987) proposed that synaptic connections active during a successful behavior will be strengthened through signals sent from innate value systems which indicate that the most recent behavior performed was functionally valuable. Thus, those connections that receive signals from the positively activated value systems will be strengthened and more likely to be re-activated in similar future situations (Edelman, 1987; Sporns and Edelman, 1993). Approximate Optimal Control perspectives contribute to this view by providing a more continuous look at the selective process by applying principles of reinforcement learning to behavioral modeling technology. As a behavior aimed at a target is performed, a value function is created via continuous neural mapping of each system state during the behavioral sequence in relation to the goal. Behaviors during periods of activity that bring the infant closer to goal attainment are assigned a higher value and thus, the selection process is continuous and proceeds based on the associated potential reward returned by the value function based on the current state of the system (Berthier et al., 2005).

Many findings in other areas of motor development are consistent with such theoretical views. For example, research on infant kicking and early eye-hand coordination has shown that from very early in life, infants are able to engage in exploratory actions, discover the consequences of their actions, and select those actions that are adaptive to the task-at-hand (Rovee and Rovee, 1969; Thelen, 1994; van der Meer et al., 1995; Angulo-Kinzler, 2001). These studies clearly highlighted the importance of exploratory opportunities to the discovery and emergence of new skills in novel tasks. Discovery of new actions or patterns of action occurred through the exploration of varied movements and their consequences.

Bojczyk and Corbetta (2004) exemplified the importance of opportunities to discover movement consequences when they examined the impact of minimal, but repeated opportunities to explore an object-retrieval task on the emergence of successful bimanual coordination retrieval strategies. Prior research indicated that infants did not display such well-coordinated bimanual strategies in object-retrieval tasks until they reached 12–18 months of age (Bruner, 1970; Diamond, 1991). Bojczyk and Corbetta (2004) provided infants, beginning at 6 ½ months of age, with only six trials of weekly exposure to an object-retrieval task requiring bimanual coordination to retrieve a toy concealed in a box. They followed infants until they were able to perform well-coordinated bimanual patterns consistently. Compared to age-matched control groups that did not receive repeated exposure to the object-retrieval task, infants with repeated exposure showed significantly more well-coordinated bimanual strategies and they displayed these efficient strategies by the age of 8 and 9 months, which was much earlier than the ages of success reported for similar behaviors by prior object-retrieval studies (Bruner, 1970; Diamond, 1991). Thus again, repeated exposure to the task, which provided opportunities for the infants to perform various actions during the object-retrieval task, seemed to be enough to aid the selection process and enhance the development of successful bimanual coordination in much younger infants. In other words, through repeated actions and perception of action consequences, infants developed a value function that became tailored to the object-retrieval task and, in turn, facilitated the discovery of the most adaptive retrieval strategies for the task-at-hand. Gradually, over time the more successful strategies became increasingly selected and used more frequently (Bojczyk and Corbetta, 2004).

In the current study, we aimed to further explore the notion that direct hand-toy contact provides value for driving movement exploration, discovery, and selection of adaptive reaching responses around the time of the emergence of reaching. Specifically, we hypothesized that if hand-toy contact is particularly important for learning to reach, then emphasizing the consequence of such direct hand-toy contact may help precipitate the selection process and trigger a steeper developmental curve in reaching. If the engine of the selective process is the repetition of action and perception cycles in relation to discovered valuable action consequences, then task manipulations designed to highlight different movement consequences should spark and drive action-perception cycles selecting distinctive movement processes. With this scope in mind, this study aimed to manipulate the consequences of the immediate hand-toy contact to assess how variations in such movement consequences would lead to distinct developmental outcomes or different kinds of movement enhancement. We rooted our sensory-motor manipulations in two well-established lines of empirical research in order to examine the impact that each enhancement would have on the early reaching selection process.

First, work in the mastery motivation literature revealed that exposure to responsive toys, or toys activated contingently upon infants' actions, in the everyday environment drove higher levels of task persistence during the first year of life (Jennings et al., 1979). In this work, the researchers operationalized *persistence* as the continued search for feedback from objects. Thus, in the context of early reaching, exposure to responsive toys at contact may increase infants' persistence at reaching for and activating the toys and consequently enhance the discovery and selection process. To examine the initial trajectory of reaching as a function of repeated exposure to toys responsive to touch, we provided infants with 14 days of repeated reaching exposure with toys that moved and sounded *only* upon hand-toy contact. Working with the assumption that hand-toy contact providing haptic feedback is already a valuable movement consequence for the selection of appropriate reaching responses, we predicted that using contingently activated toys would further enhance the consequence of hand-toy contact and aid the creation of an even stronger reaching-specific value function over time. The discovery of the contingency between movement and consequence would drive infants' persistence to repeat such an event, and thus, enhance and sustain the action-perception cycle even more. This would lead to a significant increase in reaches over time, where the target is being visually attended relative to hand-toy contacts happening without visually attending the target. In addition, we would expect to see a change in movement patterns, as revealed by kinematic measures that are appropriate to the reaching context.

Second, work on infant attention suggests that we could also enhance infants' initial selective process by increasing infant object-directed attention. Specifically, empirical work guided by the intersensory redundancy hypothesis revealed that if an event's sounds and motions are synchronous in a visual scene, infants will attend and perceptually process that event more than any other elements in the scene (Bahrick and Lickliter, 2000; Bahrick et al., 2004; Reynolds et al., 2014). Thus, in the context of early reaching, exposure to autonomously activated, synchronous moving and sounding toys in the reaching space may increase infants' toy-directed attention. A by-product of such toy-directed attention may be greater attempts at toy-directed reaching activity, which could increase the likelihood of hand-toy contact and, subsequently, enhance infants' persistence at reaching for the toy. This persistence may ultimately aid the discovery and selection process. But, in this case, the task differed from the condition described above in the key point that toy motion is *independent* from hand-toy contact, and therefore not a direct consequence of contacting the toy. To examine the developmental trajectory of reaching as a function of autonomously activated, synchronous moving and sounding toys, we provided infants with 14 days of repeated exposure to such self-activated toys. We inferred that if the moving and sounding toy captured infants' attention, then infants would look at the toy more and show higher amounts of movement activity to attempt to reach for the toy. This, in turn, could increase the likelihood of hand-toy contact, thereby creating a reaching-specific value function possibly aiding the selection of successful movements for the reaching task. Also, with the increased reaching attempts we would expect a concomitant increase in movement kinematics appropriate to the reaching context over time.

MATERIALS AND METHODS

Participants

Thirty-five infants, recruited within the week prior to turning 3 months of age participated in this study. Twenty-two were randomly assigned to one of two conditions: (a) Contingent ($n = 11$; six females, five males): the toy motion and sound was contingent on hand-toy contact, and (b) Continuous ($n = 11$; six females, five males): the toy motion was independent from hand-toy contact. A Control group ($n = 13$; six females, seven males) was from Williams et al. (2015b): in this group the toy did not move or sound. Based on parental reports, all infants included in the final sample were born full term and possessed no known sensory, motor, or neurological impairments. Also, no infant demonstrated the ability to successfully reach for and contact toys on the first day of the study. We followed the 22 infants in our two intervention groups for 16 consecutive days (1 day pre-test, 14 days intervention, 1 day post-test). The 13 control infants were only seen on the first pre-test day and last post-test day, which corresponded to day 16 in the intervention groups. This study and all procedures were approved by the Institutional Review Board of the University of Tennessee. Parents received an explanation of the study procedures and were shown the laboratory and equipment to be used prior to consenting participation. They were informed that their participation was voluntary and that they could withdraw their child from the study at any time without penalty. Parents received $5 on day 1 and on day 16 and a baby book containing a collection of pictures capturing the daily progresses of their infant's reaching.

Materials

Infant Seat and Table

During all testing sessions infants sat in a custom-designed infant seat reclined 10 degrees from vertical. A foam strap around infants' torsos provided full postural support and permitted a full range of motion of the limbs. We placed the seat directly behind a wooden table (15″ wide × 25″ long × 15″ high) which we used for toy presentation. The table height was waist high for all infants (see **Figure 1**).

Laboratory Toys

Toys used in the laboratory sessions were a mixture of small, colorful plastic spheres (5 cm diameter) comprised of non-toxic materials. These objects did not move nor make sound even upon hand-toy contact. Toys used for laboratory sessions of the control infants were a mixture of small, visually attractive colorful Peek-a-Blocks and plastic animal squirt toys (5–6 cm in diameter; see Williams et al., 2015b). These toys were used with the control group infants in place of the colorful plastic spheres to maintain their attention and motivation to the task given that infants in this group were never exposed to sounding and moving toys.

Home Toys

Toys for the contingent group moved and sounded only upon hand-toy contact. We modified the small, colorful plastic spheres by placing a bell inside. For trials, we placed each toy atop a small, Velcro-covered platform on a 1 ½ inch stiff spring. The spring securely sat on top of a 3 ½ inches tall × 4 ½ inches wide wooden block which fit snuggly through a hole on the surface of the custom-made wooden table cover. Once the block was inserted in the table hole, its top was flush with the top of the table so that only the toy on the spring extended through the table. A plain uniformly colored cover atop the table provided a smooth surface around the toy. Toys mounted on the spring for the contingent group oscillated and sounded with the smallest of hand-toy contact.

Toys for the continuous group were the same small colorful plastic spheres as for the contingent group. However, they sat on top of a Velcro-covered platform on a 1 ½ inch stiff plastic rod. The rod rested securely into a 3 ½ inches tall × 4 ½ inches wide custom-designed toy motor. All parts of the toy motor were encased in a hard plastic covering which also fit snuggly in the table surface opening so that the top of the motor casing was flush with the table cover. A button located under the table on the side of the motor casing activated the toy such that the toy oscillated with the sounding bell inside in a left-right motion for one full minute and then autonomously shut off. Thus, toy oscillations were independent of hand-toy contact.

Behavioral Recording

For laboratory pre- and post-tests, three video cameras captured the looking and reaching behavior of the infants. One camera,

FIGURE 1 | Screenshot of gaze camera to depict the experimental setup for contingent (Left) and continuous (Right) conditions.

placed directly across the table at infant eye level captured gaze and reaching behavior while the two remaining cameras, situated 90 degrees left and right of the infant, captured the movements of each arm. A digital video switcher (Datavideo Corp., Whittier, CA, USA) merged the images from the two lateral cameras to create a split-screen image and sent it to a VCR for recording. For home sessions, only the video camera situated directly across the table at infant eye level was used. It captured both gaze and reaching behavior of the infants and recorded it to a VHS-C cassette.

During all laboratory sessions a Mini Flock of Birds motion analysis system (Ascension Technology Corp., Burlington, VT, USA) captured arm kinematics. The experimenter applied a mini bird marker (8 mm) to the dorsal side of each wrist and secured the wires up the arm and behind the infant seat with hypoallergenic tape. The Mini Flock of birds sampled movement at 120 Hz. We synchronized the video and kinematic recordings with a frame counter (Horita, Mission Viejo, CA, USA) superimposed on the video recording that started and stopped when the experimenter started and stopped the motion analysis system.

Procedure

Testing occurred in three phases: (a) Pre-intervention assessment (day 1 in laboratory), (b) 14-day sensory-motor intervention (days 2–15 in home), and (c) Post-intervention assessment (day 16 in laboratory). The contingent and continuous groups participated in all three phases of the study while the control group only participated in the pre- and post-assessment phases.

Laboratory Pre-intervention Assessment

During this phase, we established baseline measures of gaze and reaching. This phase was identical for all three groups of infants. The experimenter secured the infant in the seat and placed the seat behind the table. Prior to applying the Mini Flock of Bird markers, the experimenter collected one kinematic trial with one marker on the table top to denote the toy location for all trials. Trials began with one experimenter seated across the wooden table from the infant with a toy in hand. After capturing the infant's attention, the experimenter placed one toy on the pre-determined toy position at midline and 14 cm from the edge of the table where the infant sat (Williams et al., 2015b). Toys for this phase were all non-moving and silent. A second experimenter triggered the motion analysis system and tracked trial duration. Once the toy was on the table top, the experimenter situated across from the infant remained silent and did not interfere with infant behavior in the presence of the toy. We collected 10, 1-min trials. During each trial, all infants had the opportunity to repeatedly reach for and contact the toys. Only infants who performed zero hand-toy contacts during this initial phase of the study were entered in the study and continued to the next phase as done in Williams et al. (2015b).

Home Sensory-motor Intervention

Two experimenters traveled to the infants' homes for those assigned to the contingent and continuous groups to provide the 14 daily sensory-motor experience sessions. Home sessions occurred in a low distraction area of the home and in a similar manner as the pre-intervention assessment session. After securing the infant in the seat, one experimenter sat directly across the table from the infant, captured the infant's attention, and placed one object at midline and 14 cm in front of the infant. For the continuous group, the experimenter switched on the motor immediately after placing the toy on the table. Again, once the toy was in place, the experimenter remained silent and did not interfere with the infant's behavior while the second experimenter kept track of trial duration. As in the pre-intervention assessment session, we collected 10, 1-min trials. Again, on each trial, infants had the opportunity to repeatedly reach for and contact the toys.

Laboratory Post-intervention Assessment

During this phase, we reassessed all infants' gaze and reaching behaviors after the 14-day sensory-motor intervention, or no intervention (control). We conducted this session in exactly the same fashion as the pre-intervention assessment on the first day of the study.

Data Coding and Analysis

We coded all video recordings of gaze and reaching behavior with The Observer XT-9 (Noldus Information Technology, Wageningen, The Netherlands). All kinematic data were processed with a custom-made MATLAB program (The Mathworks, Inc., Natick, MA, USA). We conducted all analyses on the 1-min time periods when toys were in infants' reaching spaces. Also, with regard to statistical analyses, we used parametric analyses when data met all appropriate test assumptions. Otherwise, we used non-parametric analyses.

Reaching Measures

Two independent coders scored the number of hand-toy contacts (visually attended and non-visually attended). These coders overlapped on 20% of the sample in order to compute interobserver reliability, which reached a 91% agreement or above for each infant. As in Williams et al. (2015b), we coded a visually attended contact when the infant looked at the toy prior to, during the arm movement toward the toy, up until hand-toy contact. If the infant shifted their gaze away from the toy during this time reaching window we considered the hand-toy contact non-visually attended. Key computations included the total number of non-visually attended and visually attended target contacts, as well as a visually attended target contact index. In a similar way that Hinojosa et al. (2003) calculated handedness, we calculated the visually attended target contact index (a z-score), to capture the relative distribution in amounts of visually attended and non-visually attended target contacts in a single measure. Specifically, we calculated a difference score between the number of visually attended target contacts and the number of non-visually attended target contacts, then divided the difference by the square root of the sum of contacts. These standardized scores gave us clear benchmarks for comparison on amount of visually attended target reaching responses.

Looking Measures

The videos from the front camera capturing the infant gaze were coded in the Observer XT (Noldus, Inc.) by two trained independent coders who scored the onsets and offsets if the infant looking behavior according to five looking areas: Toy, experimenter, right hand, left hand, or elsewhere. Elsewhere was coded when infants looked anywhere other than the four areas (i.e., look at the table) or when we could not determine gaze location. Coders overlapped on 20% of the sample and interobserver reliability reached an agreement of 85% or above for each infant. Such coding of looking measures from video recordings along with interobserver reliability is a standard procedure in infant studies (e.g., von Hofsten, 1982, 1984; Ruff and Rothbart, 1996; Clearfield and Mix, 1999; for a comprehensive review of visual attention measures). Looking measures are reported herein as the percent of trial duration spent looking to each area.

Kinematic Measures

A custom-made MATLAB program filtered the movement time series with a zero-phase, second-order Butterworth filter with a 6 Hz cut-off and transformed the time series into 3-D resultant hand-toy distance and velocity profiles for each hand. We focused our kinematic analyses on the preferred reaching hand during times when infants looked at the toy. We defined the preferred reaching hand as the hand used most frequently by infants in the post-intervention assessment phase of the study. If infants in the contingent and continuous groups did not perform enough contacts during that phase to use this criterion, we selected the hand that infants used most frequently during the sensory-motor intervention phase of the study. If infants in the control group did not perform enough contacts in the post-intervention assessment phase then we selected the hand with the lowest movement velocity during the reaching task as the preferred reaching hand. We used this velocity-based criterion as prior research indicates that as infants approach the emergence of reaching, velocity during reaching tasks tends to decline (Bhat et al., 2005).

To analyze toy-directed behavior, we analyzed the kinematic times series associated with time periods during which infants looked at the toy. To determine the portions of the time series corresponding to when infants looked at the toy, we synchronized the lateral reaching cameras, which contained the time-frame counter for the kinematics, with the gaze camera. Once synchronized, we recorded the kinematic time codes corresponding to periods when infants looked at the toy and entered these into the MATLAB program.

Kinematic computations included the mean time that the preferred reaching hand spent within 10 cm of the toy (Williams et al., 2015b), which we computed based on the resultant distance between the preferred hand position and the pre-determined toy position. Also, we computed the mean peak velocity of the preferred hand. The MATLAB program analyzed the velocity profile with a 3-point technique in order to determine peaks in the profile. Once the program identified the peaks, it divided the sum of all peak values by the total number of velocity peaks identified to produce a mean peak value.

RESULTS

Exposure Time

Due to sporadic fussiness not all infants in the contingent and continuous conditions completed 10 full trials each day. However, overall task exposure times, in total minutes, did not differ significantly between the contingent ($M = 103.45$, $SEM = 2.56$) and continuous [$M = 107.55$, $SEM = 13.74$, $t(20) = 0.840$, p (2-tailed) $= 0.411$, $d = 0.36$] groups.

Reaching

Total Contacts (Figure 2)

Separate Wilcoxon Signed-Ranks tests revealed that infants in the contingent ($M_{\text{Day 16}} = 27.64$, $SEM_{\text{Day 16}} = 11.17$), continuous ($M_{\text{Day 16}} = 7.91$, $SEM_{\text{Day 16}} = 2.81$), and control ($M_{\text{Day 16}} = 6.46$, $SEM_{\text{Day 16}} = 4.47$) groups exhibited significant increases in total contacts between pre- and post-intervention day [$Z = -2.675$, p (2-tailed) $= 0.007$, $r = 0.81$, $Z = -2.521$, p (2-tailed) $= 0.012$, $r = 0.76$, $Z = -2.032$, p (2-tailed) $= 0.042$, $r = 0.56$, respectively]. Further, curve estimation analyses over the 16-day period showed that the contingent and continuous groups displayed significant linear growth in total contacts [$F(1,14) = 65.514$, $p < 0.0001$, $R^2 = 0.82$, $F(1,14) = 16.918$, $p = 0.001$ $R^2 = 0.55$, respectively]. However, planned Mann–Whitney comparisons with the control group on post-intervention day values revealed that the continuous group did not display significantly more contacts relative to the control group [$U = 46.50$, $Z = -1.524$, p (2-tailed) $= 0.128$, $r = 0.31$], while the contingent group displayed significantly higher total contacts relative to the control group [$U = 38.00$, $Z = -2.017$, p (2-tailed) $= 0.044$, $r = 0.41$].

Visually Attended Target Contact Index (Figure 3)

The index of visually attended target contacts (z-score) provides (a) a single measure that captures the relative amount of visually attended and non-visually attended hand-target contacts performed over time and (b) a measure that allowed clear benchmarks for comparisons between the groups. **Figure 3** reveals that infants in the contingent and continuous groups displayed similar ratios of visually attended/non-visually attended target contacts during the first week of intervention but, from Day 8, the two groups began to diverge. Infants in the contingent group increased their number of visually attended hand-toy contacts relative to non-visually attended contacts as the study progressed, while the continuous group did not. **Figure 3** also shows that on all but 2 days after Day 8, infants in the contingent group had a visually attended target contact index that was greater than 1 standard deviation unit relative to the continuous group index, and on four of those days, the contingent group z-score values were above 1.65 (90% confidence level).

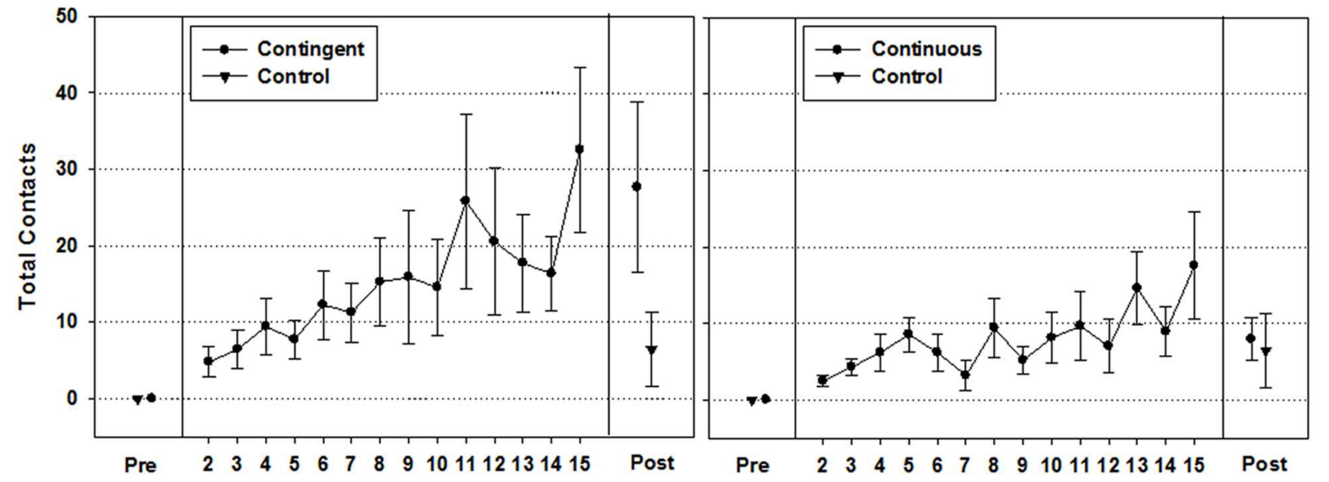

FIGURE 2 | Mean total contacts (±1 *SEM*) for the contingent (Left) and continuous (Right) groups by day. Control group values for pre- and post-test days are shown on each graph.

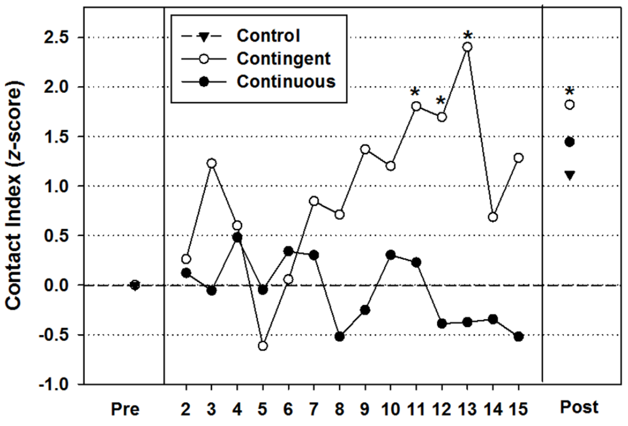

FIGURE 3 | Mean visually attended contact indices (*z*-scores) for each group by day. The dashed line at zero indicates no preference for visually attended or non-visually attended contacts. Points with an asterisk are index scores that are greater than $z > 1.65$, indicating performance level with a 90% confidence.

High versus Low Performers (Figure 4)

To gain more insights into these data, we examined whether the number of visually attended target contacts performed by the infants on the post-intervention day was an accurate reflection of the hand-toy contact history performed during the prior intervention days. This was relevant because there was much between subject variability on the last day performance and toy motion and sound were removed on post-test day. All of our three samples contained infants who did not produce any visually attended target hand-toy contacts on that last day despite the 14-day intervention (36% in the contingent group and 27% in the continuous group, compared to 69% in the control group). Some other infants produced as little as 1, 2, or 3 visually attended target contacts on the last day, and some contacted the toy quite often. Here we asked whether the infants with higher contact performance on the last day, were also the infants who most likely discovered the consequences of their actions through their contact history. Likewise, we asked whether the poor performers on the last day of the study were also the ones with a history of lower visually attended target contacts over the 14-day intervention. We anticipated that this analysis would shed further light on the respective impact our interventions on the process of discovering action consequences on learning to reach.

To examine this question, we used the group medians to split infants into high performers (those displaying hand-toy contacts above the group median) and low performers (those at and below the group median) based on the number of visually attended target contacts performed on the last day of the study. Then, we examined whether the last day performances were in line with the observed 14-day intervention progression. **Figure 4** presents the high versus low performers in the contingent group on the left panel and the high versus low performers in the continuous group in the right panel. A 2 (Performance Group) × 16 (Day)repeated measures ANOVA on the contingent group using a Greenhouse–Geisser adjustment for lack of sphericity revealed a significant main effect of Performance Group [$F(1,9) = 13.492$, $p = 0.005$, $\eta^2 = 0.600$], Day [$F(2.691,24.222) = 4.713$, $p = 0.012$, $\eta^2 = 0.344$], and Performance Group × Day interaction [$F(2.691,24.222) = 4.817$, $p = 0.011$, $\eta^2 = 0.349$]. The same analysis performed on the continuous group revealed no significant differences between Performance Groups, nor Days (all p-values > 0.154). This indicated that high versus low performance groups only differed in the contingent group. A last analysis, aimed at comparing high performers between intervention groups, revealed a main effect of Group [$F(1,8) = 7.429$, $p = 0.026$, $\eta^2 = 0.481$], and Day [$F(3.213,25.701) = 4.566$, $p = 0.010$, $\eta^2 = 0.363$], but no Group × Day interaction [$F(3.213,25.701) = 2.691$, $p = 0.064$, $\eta^2 = 0.252$]. Thus, in conclusion, when we split infants based on

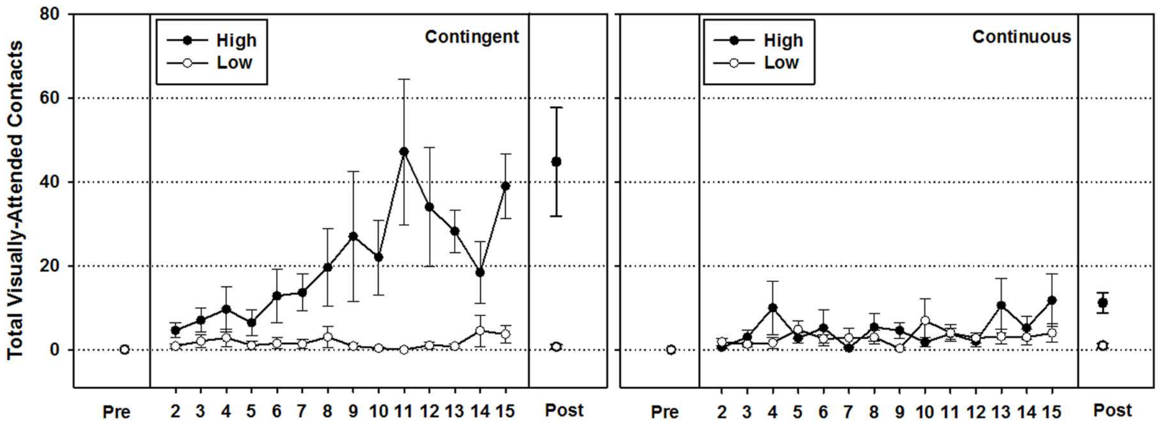

FIGURE 4 | Mean total visually attended contacts (±1 *SEM*) for high and low performers in the contingent (Left) and continuous (Right) groups.

the number of visually attended target contacts performed on the last day, we were able to show: (a) that the last-day performance accurately captured the history of contacts performed throughout the intervention period, and (b) that only the high-performing infants in the contingent group benefitted from the contact enhancement intervention by displaying a growing history of hand-toy contacts. No infants in the other performing groups did.

Looking

Day 1

To assess whether our intervention groups differed in their distribution of looking behavior at the start of the study, we performed a 3 (Group) × 5 (Look Area) repeated measures ANOVA on the Day 1 normalized looking durations. To adjust for a violation of sphericity we applied a Greenhouse–Geisser correction. There was no Group effect [$F(2,32) = 0.839$, $p = 0.441$, $\eta^2 = 0.05$] and no Group by Look Area interaction [$F(2.906,46.504) = 2.727$, $p = 0.056$, $\eta^2 = 0.146$]. However, there was a significant effect of Look Area [$F(1.453,46.504) = 59.370$, $p < 0.0001$, $\eta^2 = 0.65$]. Overall, infants looked at the toy the most (52.55%), then elsewhere (32.48%), then at the experimenter (12.73%), then at their left hand (2.52%), and least at their right hand (0.284%). All pairwise comparisons between the looking areas were significant at the $\alpha = 0.05$ level.

Day 16

To assess whether our intervention groups differed in their distribution of looking behavior at the end of the study, we performed a 3 (Group) × 5 (Look Area) repeated measures ANOVA on the Day 16 normalized looking durations. Again, we used a Greenhouse–Geisser adjustment for a sphericity violation. There was no Group effect [$F(2,32) = 0.550$, $p = 0.582$, $\eta^2 = 0.033$]. As on Day 1 we found a significant effect of Look Area [$F(1.420,45.427) = 131.895$, $p < 0.0001$, $\eta^2 = 0.805$]. Overall, infants looked at the toy the most (48.71%), then elsewhere (39.78%), then at the experimenter (8.59%), then at their left hand (1.82%), and least at their right hand (1.45%). Pairwise comparisons revealed that in the Contingent and Continuous groups, infant looked significantly more at the toy than all other look areas ($p < 0.05$) but showed equal looking elsewhere. The control group looked significantly more at the toy than all other look areas, including elsewhere ($p < 0.05$). Further, there was a significant Group by Look Area interaction [$F(2.839,45.427) = 4.626$, $p = 0.007$, $\eta^2 = 0.224$]. Within toy, experimenter, and left hand look areas, groups did not differ. Control infants looked significantly more at their right hand relative to continuous infants ($p = 0.042$). Also, control infants spent significantly less time than contingent infants ($p = 0.001$) and marginally less time than continuous infants ($p = 0.065$) looking elsewhere.

Over the Study Period

Figure 5 depicts the percent of trial duration that infants in the contingent and continuous groups looked to each area from pre- to post-intervention. To examine whether the distribution of looking behavior changed over time, we performed a 2(Group) × 5 (Look Area) × 16 (Day) repeated measures ANOVA, with a Greenhouse–Geisser correction. There were no main effects of Group [$F(1,20) = 1.000$, $p = 0.329$, $\eta^2 = 0.048$] nor Day [$F(1,20) = 1.885$, $p = 0.329$, $\eta^2 = 0.048$], but a main effect of Look Area [$(1.153,80) = 75.025$, $p < 0.0001$, $\eta^2 = 0.790$]. Overall, infants tended to look elsewhere the most (45.18%), then at the toy (44.49%), then at the experimenter (8.73%), then at their left hand (1.13%), and least at their right hand (0.42%). There was also a Look Area by Day interaction [$F(9.038, 20) = 3.945$, $p < 0.0001$, $\eta^2 = 0.165$] indicating a change in looking behavior over time in some Look Areas, but not all. Follow-up testing confirmed that in both intervention groups, infants decreased their amount of looking at the toy over time, while they increased their amount of looking elsewhere [$F(7.245,20) = 4.866$, $p < 0.0001$, $\eta^2 = 0.196$]. These trends in looking behavior did not differ between high and low performers in either intervention groups.

Kinematics

Figure 6 (left) reports the mean peak velocity of the preferred reaching hand on the pre- and post-test days of the study for

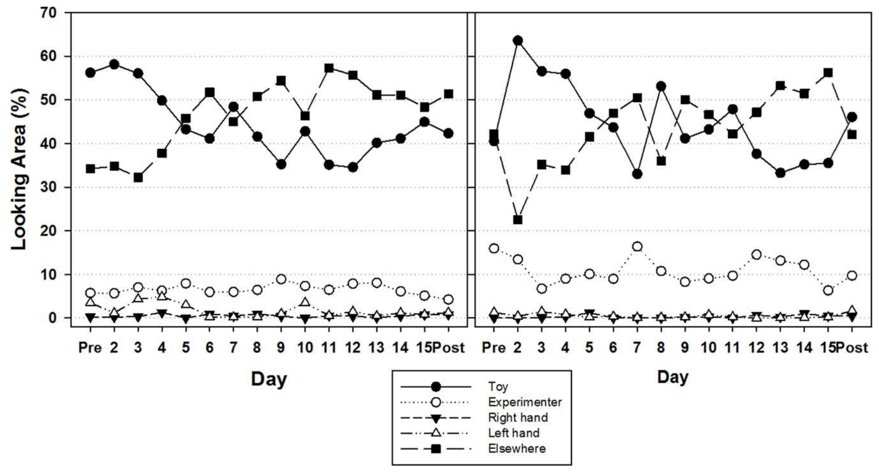

FIGURE 5 | Mean percent trial of looking duration by Look Area for infants in the contingent (Left) and continuous (Right) groups.

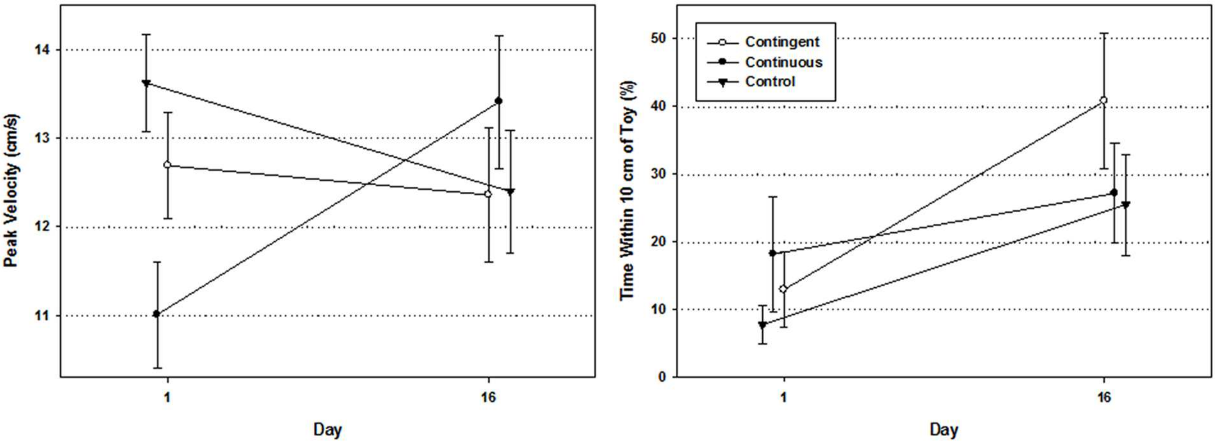

FIGURE 6 | (Left) Mean peak velocity of the preferred reaching hand by group. **(Right)** Mean percent of time that preferred reaching hand was within 10 cm of the toy.

all three groups. A 3 (Group) × 2 (Day) repeated measures ANOVA revealed no significant effect of Group [$F(2,32) = 0.668$, $p = 0.520$, $\eta^2 = 0.04$] nor of day [$F(1,32) = 0.314$, $p = 0.579$, $\eta^2 = 0.01$] but, there was a significant Group by Day interaction [$F(2,32) = 4.785$, $p = 0.015$, $\eta^2 = 0.23$]. *Post hoc* analyses indicated that while the contingent and control groups showed no significant change in peak velocity, the continuous group displayed a significant increase in peak velocity between pre- and post-test day ($p = 0.011$).

Figure 6 (right) displays the mean percent of time infants had the preferred reaching hand within 10 cm of the toy between pre- and post-test days of the study. Separate Wilcoxon Signed-Ranks tests revealed that only the contingent group exhibited a significant increase in the time spent within 10 cm of the toy [$Z = -2.490$, p (2-tailed) $= 0.013$, $r = 0.75$]. The increases displayed in the continuous and control groups were not significant [$Z = -1.156$, p (2-tailed) $= 0.248$, $r = 0.35$, $Z = -1.642$, p (2-tailed) $= 0.101$, $r = 0.46$, respectively].

DISCUSSION

In this study, we examined the impact that hand-toy contact consequences had on the developmental trajectories of infant reaching behavior. Specifically, we manipulated the context in which toy sound and motion would be activated to examine how such context enhancements could augment infants' persistence at reaching for the toys. A critical difference between intervention groups was that while one group (contingent) experienced such enhancement solely during successful hand-toy contacts, the other group (continuous) was able to experience such enhancement continuously whether attempting to reach or not and independently from successful hand-toy contacts. Using tenets drawn from Dynamic Systems Theory, the TNGS, and Approximate Optimal Control, on the one hand, and the Intersensory Redundancy Hypothesis on the other, we predicted that if the toy manipulations served to enhance the action-perception cycle, then infants in both intervention groups would increase the frequency of hand-toy contact with the moving and sounding toy, compared to the non-intervention control group which had visually attractive, yet still and silent toys. Such findings would support the interpretation that those infants, in each intervention group, followed different routes to discover and select effective arm movements for the reaching task. But, our results revealed that infants in the contingent group were the ones who benefitted the most from their intervention.

With regard to the amount of total hand-toy contacts, both intervention groups showed significant gains in reaching from the first to the last day of the study, but only the contingent group produced hand-toy contact amounts that were significantly greater than those produced by the control group (**Figure 2**). Furthermore, the visually attended target contact index indicated that infants in the contingent group began to diverge from the continuous group about half way through the study by performing more visually attended target contacts relative to non-visually attended target contacts (**Figure 3**). To gain a better sense of the immediate impact that the varied experiences available to the contingent and continuous conditions had on the development of reaching behavior, we focused in on the variability in infants' performances on the post-intervention day and traced it back to the history of hand-toy contact observed during the intervention. When doing so, results revealed that only higher performing infants in the contingent group showed significant gains in contacts over time while infants in the continuous group did not (**Figure 4**).

Generally speaking, the observed increase in visually attended target contacts is consistent with prior research in that repeated opportunities to actively attempt reaching behaviors and perceive the behavioral consequences may be enough to drive the reaching selection process (Bojczyk and Corbetta, 2004; Lobo et al., 2004; Williams et al., 2015b). Theoretically, infants in both intervention groups were able to explore the reaching task, perform various reaching movements, experience direct hand-toy contact, and gradually select those movements that met task demands based on the developing value function. However, interestingly, our intervention groups indicated that only infants in the contingent condition, where toy motion and sound occurred only in response to their successful action, made significant progress over time. Those infants presumably discovered the association between making contact with the toy and eliciting toy motion and sound as a direct consequence of their movement. In the continuous group, infants could experience toy motion and sound, but it was independent of their action. Consistent with the above mentioned theoretical frameworks, interactions with a responsive toy contributed to highlight a successful reaching movement, which, in turn, spurred the action-perception cycle, permitting further refinement of the developing value function and allowing infants to more effectively select reaching movements that met the immediate task demands (Jennings et al., 1979; Edelman, 1987; Thelen and Smith, 1998; Berthier et al., 2005; Williams et al., 2015a). Further support may be seen in the visually attended target contact index analyses where infants in the contingent group began to display many more visually attended to non-visually attended target contacts over time relative to the continuous group. Based on these results, we believe that the contingent infants were more effectively, and efficiently, selecting the successful reaching movements over time through the creation, refinement, and use of a specific value function.

The looking analyses revealed no differences between intervention groups with regard to visual attention allocation. At the start of the study, all three groups demonstrated equal distributions of looking patterns toward the different looking categories (toy, experimenter, right hand, left hand, elsewhere). All infants spent significantly more time looking at the toy and elsewhere relative to the other categories. Over the course of the 16-day study, however, visual attention to the toy declined despite remaining overall relatively high compared to the other looking categories. Conversely, the direction of visual attention to elsewhere increased over time (**Figure 5**). This change in visual attention allocation did not affect the rate of toy contact, since it continued to increase over time (see Williams et al., 2015b for similar findings). More surprising, however, was the fact that we did not find differences in looking behavior between intervention groups. We designed the toy for the continuous group based on work in the area of intersensory redundancy (Bahrick and Lickliter, 2000; Bahrick et al., 2004). As stated in the introduction, we expected the autonomously activated, moving, and sounding toy to capture infants' visual attention more and subsequently drive higher amounts of persistence in trying to touch the moving and sounding toy. Our looking analyses clearly revealed that this did not occur. A possible explanation for these results is that looking time and level of attention are distinctly different. For instance, psychophysiological work has shown that infants shift their level of information processing during single looks toward stimuli. Through measures of heart rate variability, infants shift from stimulus orienting, to sustained attention (active information processing), and attention termination all within the same look to a stimulus (Richards, 1997; Reynolds and Richards, 2008). It is possible that the monotony of the toy motion did not serve to attract visual attention and maintain sustained attention to the toy as much as we thought it would in this group. Another possibility is that the low amount of hand-toy contacts in the continuous group compared to looking times that are equivalent to those of the contingent group, reflect a different attention-action ratio than the one present in the contingent group. We can speculate that infants in the continuous group may have spent more time processing the synchronous, multimodal event in an attempt to map those perceptual characteristics to their movements to meet task demands. The kinematic results, which we discuss below, may provide an indirect assessment of such an ongoing process.

The kinematic analyses on the first and final days of the study revealed that infants in the continuous group modulated their arm movements presumably to match immediate task demands, while infants in the contingent and control group did not. Specifically, infants in the continuous groups displayed a significant increase in peak speed over the course of the study (**Figure 6**, left). These results may indicate that these young infants capitalized on their respective sensory-motor experiences to select different kinds of movements with particular motor control characteristics to match the varying task demands. In the typical reaching situation, with stationary toys, lower peak movement speeds are associated with better reaching control while higher peak speeds typically indicate less control (Thelen et al., 1993, 1996; Bhat et al., 2005). However, the infants in the continuous group may have learned, through their particular sensory-motor experience, that if they selected more rapid reaching movements, they would increase their chances of contacting the moving target. von Hofsten and Lindhagen (1979) showed that infants at the initial transition to reaching for stationary objects are also capable of reaching for moving ones. We can infer from their results that infants modified their reaching speeds to accomplish their task but in our study we explicitly showed the kinematic changes. Theoretically, infants' value functions built up through their respective sensory-motor experiences in such a way as to drive the selection of movements, even at the kinematic level, to meet task demands.

As hinted above, the peak speed results for infants in the continuous group may also potentially be related to their visual attention. It is possible that the synchronous, multimodal event (toy motion and sound) truly drove their attention and allowed them to perceive and extract specific characteristics of the multimodal event such as rate and rhythm. Specifically, the continuous infants may have spent more time sustaining their attention to process the characteristics of such a multimodal event (Bahrick and Lickliter, 2000; Bahrick et al., 2004; Reynolds and Richards, 2008). Consequently, those infants may have also been slower at mapping their motor behavior onto the moving toy pattern to make contact and one strategy available for success would be to increase movement speed.

Also, our kinematic analysis showed that the contingent group was the only group to show a significant increase in the amount of time spent with the preferred reaching hand near the toy. We know that infants gradually move their arms closer to midline (White et al., 1964; von Hofsten, 1984; Spencer and Thelen, 2000) and this is true of our results as well. All infants did show an increase in the amount of time spent with the preferred reaching hand near the toy. However, only the contingent group's increase reached statistical significance. Again, we believe that over the course of the study, having been exposed to the contingently activated link between reaching movements and successful outcome, the contingent infants developed a more precise value function which allowed them to select movements that would increase the likelihood of success in the reaching situation.

A potential limitation of this study may be a focus only on short-term consequences of the sensory-motor intervention. Indeed, many of the more recent investigations into the impact of early sensory-motor interventions have focused on reaching movements in 6-month-old or younger infants (Needham et al., 2002; Lobo et al., 2004; Lobo and Galloway, 2008, 2013; Libertus and Needham, 2010; Lee and Newell, 2013; Williams et al., 2015b). Based on prior research, we know that various types of early sensory-motor experiences have immediate short-term consequences on early infant reaching and exploratory behavior. However, with the prediction made by many studies that the emergence of reaching has an impact on all domains of development (Fogel et al., 1992; Bushnell and Boudreau, 1993; Fogel, 1997; Thelen and Smith, 1998; Eppler, 1995; Corbetta and Snapp-Childs, 2009) it is important for future research to go beyond just investigating the short-term consequences of early sensory-motor experience. Rather, after examining the emergent developmental trajectories of reaching behavior as a function of early sensory-motor experience, researchers should examine how such experiences could lead to distinct cascadic effects over developmental time. As reviewed in the introduction, reach onset entails a number of behavioral ramifications at multiple levels. Understanding how these ramifications could be tied to specific early perpetual-motor experiences is an important developmental question.

Another potential limitation may be the fact that the control group on days 1 and 16 was presented with different toys than the infants in the contingent and continuous conditions. Thus, it could be possible that the observed differences in reaching behavior between our intervention conditions and the control group resulted from using different toys. These toy differences could have captured infants' attention differentially, and in turn, affected the amount of reaching behavior produced, particularly on day 16. While it is true that we discovered differences in reaching behavior, we did not find such differences to be related to differences in looking behavior. Our analysis of day 16 looking behavior revealed that infants in the contingent, continuous, and control groups spent equal amounts of time visually attending the toys. Also, the control infants were the only group to allocate significantly more time looking to the toy than the other four look areas, including elsewhere. If infants in the control group had lacked interest in the toys, we would have seen less looking at the toy relative to both the other conditions and look areas. Thus, despite these between group toy differences, it does not appear that looking results on the final day may have driven the observed differences in reaching behavior

Finally, another limitation of this study may concern the lack of a continuous control group receiving daily exposure with toys that are not sounding nor moving. Such a control group could have provided a better baseline to estimate the added impact of our contingent and continuous intervention conditions on reaching development. The reason we did not collect such a basic repeated task exposure group as part of this study is because we already had tested a group similar to that condition in our prior study (Williams et al., 2015b). If we compare results from that prior study with results from the present study, we find that the contingent group displayed the steepest reaching progress over time, followed next by the repeated exposure group (Williams et al., 2015b), and finally followed by the continuous group with the less steep progress.

We contend that our results are in agreement with tenets of the Dynamic Systems Theory, TNGS, and Approximate Optimal Control perspectives. However, a potential alternative theoretical account, especially for the results presented here, is straightforward operant conditioning. Indeed, the notion of contingency as it impacts the control and selection of behavior is central to that perspective (Skinner, 1974, 1981). However, a growing amount of research in the fields of neuroscience, perceptual, motor, emotional, and cognitive development, among others, indicates that even seemingly simple behaviors, such as that of reaching for and contacting a toy, is actually quite complex (Smith, 2005; Winkielman et al., 2015). Specifically with regard to reaching, contemporary research indicates that many subsystems contribute cooperatively to the performance of such a behavior (Thelen and Smith, 1994, 1998; Spencer et al., 2000; Clearfield and Thelen, 2001; Corbetta, 2009; Cunha et al., 2015). Among the factors underlying the learning of such a behavior, we do not discount the contribution of operant learning principles. On the contrary, such principles are at play in the learning-to-reach process, as evidenced by the centrality of reinforcement learning mechanisms aiding the development of the value function that aids the selection of reaching movements in Approximate Optimal Control perspectives (Barto, 2002; Berthier et al., 2005). However, an explanation based on operant conditioning alone falls short, in our opinion, in capturing all the factors and behavioral complexity tied to the emergence and subsequent development of new skills. In that sense, we see the combination of Dynamic Systems Theory, TNGS, and Approximate Optimal Control as complementing one another in accounting how brain, motor, perception, and experience all contribute to different extents to our understanding of the behavioral learning process observed.

In closing, contemporary theoretical perspectives such as Dynamic Systems Theory, TNGS, and Approximate Optimal Control argue that reaching behavior emerges gradually through repeated self-generated activity during the reaching task. Repeated exposure to the reaching situation offers infants opportunities to engage in continuous action-perception cycles during which they discover the consequences of various reaching movements, create and develop a value function from perception of such consequences, and subsequently use the value function to select those reaching movements that lead to the more positive outcomes (Edelman, 1987; Thelen and Smith, 1998; Berthier et al., 2005; Williams et al., 2015a). The notion that repeated task exposure, without external guidance, is enough to drive the emergence of reaching behavior has support across multiple types of reaching situations (Bojczyk and Corbetta, 2004; Lobo et al., 2004; Lobo and Galloway, 2008; Williams et al., 2015b). Furthermore, based on Schlesinger and Parisi's (2001) work, it appears that early in the reaching process, the movement consequence of hand-toy contact and haptic feedback received, carries a high value and sparks the action-perception cycle to drive a more efficient selective process (Corbetta et al., 2015; Williams et al., 2015b). In this study, we capitalized on adding further consequences to the hand-toy contact event by providing infants with responsive toys, which moved and sounded only upon contact. Based on the results, we infer that the contingently activated toy highlighted the movement consequence of hand-toy contact, which increased the repetition of action-perception cycles. This repetition of action and perception drove the creation of a precise value function that allowed infants in the contingent condition to more efficiently discover and select reaching movements adaptive to the task-at-hand.

AUTHOR CONTRIBUTIONS

JW designed study, collected the data, did most of the analyses, and wrote the first draft of the manuscript. DC contributed to design of the study, helped complete data collection, performed additional analyses, and contributed to writing and revising of first draft provided by JW.

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Atypical object exploration in infants at-risk for autism during the first year of life

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Autism Spectrum Disorder (ASD) is a neurodevelopmental disorder usually diagnosed by the end of the second year of life. Early signs of ASD within the first year of life are still unclear. The main purpose of the present study was to compare object exploration skills between infants at-risk for ASD and typically developing (TD) infants to determine early markers for autism within the first year of life. Sixteen at-risk infants and 16 TD infants were longitudinally followed from 6 to 15 months of age during an object exploration task involving three objects with distinct size, shape, and texture, i.e., a long rattle, a rigid circular ball, and a soft circular koosh ball. All sessions were videotaped for coding of manual exploration (grasping and dropping), oral exploration (mouthing), and visual exploration (looking). We also obtained follow-up outcomes using various developmental questionnaires at 18 months and email follow-up on developmental delays/ASD diagnosis after the infants' second birthdays. Our results showed object-based differences in exploration patterns that extended across both groups. We also noticed context-dependent group differences for various exploratory behaviors across objects and ages. Specifically, at 6 months, at-risk infants showed less grasping of the rigid ball as well as less mouthing and greater looking at the rattle compared to TD infants. At 9 and 12 months, at-risk infants demonstrated significantly lower levels of purposeful dropping of all objects and greater looking at the rattle. Lastly, at 15 months, at-risk infants showed persistent mouthing of the rigid ball and rattle compared to TD infants. In addition, 10 out of 16 at-risk infants developed various motor, social, and language delays or ASD diagnosis at follow-up. Taken together, early context-dependent delays/abnormalities in object exploration could be markers for future developmental delays in infants at-risk for autism. Moreover, promoting early object experiences through socially embedded, free and structured play could have significant implications for multisystem development including perceptuo-motor, social communication, and cognitive development in at-risk infants.

Keywords: autism, object exploration, infants, motor, social, communication, development

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Introduction

Autism Spectrum Disorder (ASD) is a neurodevelopmental disorder characterized by impairments in social communication development such as lack of reciprocity during social interactions, reduced use of communicative gestures, and a complete lack of or delay in language development, as well as by the presence of restricted and repetitive behaviors such as hand flapping and preoccupation with objects (Mitchell et al., 2006; Sullivan et al., 2007; Eigsti et al., 2011; Leekam et al., 2011; American Psychiatric Association, 2013). The current prevalence of ASD is 1 in 68 children (Centers for Disease Control and Prevention, 2014) with diagnostic confirmation usually by the second year of life (Robins et al., 2001; Shattuck et al., 2009). Early detection in the second year of life gives families access to appropriate behavioral interventions and is known to improve future outcomes (Osterling and Dawson, 1994; Rogers, 1998; Fein et al., 2013). Early detection studies have typically reported retrospective data on infants who later developed ASD as well as prospective data in infant siblings of children with ASD or AU sibs. Although diagnostic features of autism are within the social communication domains, some of the early signs of autism within the first year have been observed in the perceptuo-motor domains (Teitelbaum et al., 1998; Gernsbacher et al., 2008; Ozonoff et al., 2008b). Retrospective reports suggested that early signs of autism include motor delays (Teitelbaum et al., 1998; Gernsbacher et al., 2008; Ozonoff et al., 2008b) as well as excessive visual exploration of objects (Maestro et al., 2002, 2005; Bhat et al., 2010). However, recent prospective studies have identified subtle atypicalities specific to autism as early as the first year of life. During free exploration of objects, AU sibs showed reduced mouthing and grasping as well as excessive looking at 6 and 9 months of age (Koterba et al., 2012; Libertus et al., 2014). Therefore, the present study builds on the current literature by conducting a prospective longitudinal study comparing object exploration skills between at-risk infants and age-matched, typically developing (TD) infants from 6 to 15 months of age with developmental questionnaire follow-up at 18 months.

Object exploration refers to infants' exploration of toys and objects using oral (i.e., mouthing), manual (i.e., grasping, fingering, shaking, banging, rotating), and visual (i.e., looking) modalities (Ruff, 1984; Palmer, 1989). In order to explore objects in different ways, infants require substantial fine motor and gross motor skills. For example, manual modes of exploration such as fingering, shaking, transferring, and rotating objects require considerable hand and finger control (Needham et al., 2002; Barrett et al., 2008). Similarly, good trunk control is critical for proficient use of arms while exploring objects (Rochat and Goubet, 1995; Lobo and Galloway, 2008). In fact three weeks of enhanced postural training led to improved reaching, mouthing, and fingering of objects in 2- to 5-month-old TD infants (Lobo and Galloway, 2008). Moreover, object exploration skills have implications for other forms of development such as perceptual (Needham, 2000; Bhat and Galloway, 2006; Lobo and Galloway, 2008; Koterba et al., 2012), social communication (Meltzoff, 1995; Fagan and Iverson, 2007; Iverson et al., 2007), and cognitive development (Caruso, 1993; Bourgeois et al., 2005; Fontenelle et al., 2007). In terms of perceptual development, infants learn various object properties such as texture, shape, size, color, and sound while exploring objects (Ruff, 1984, 1986; Palmer, 1989; Rochat, 1989). For example, 3- to 4-month-old infants who spent more time exploring objects had better perception of object properties such as the boundaries of two closely placed objects compared to infants who spent less time exploring objects (Needham, 2000). Infants' experience with objects improves their object knowledge and directly affects their performance in various cognitive tasks (Caruso, 1993; Bourgeois et al., 2005). When infants were asked to retrieve a toy from a container, their success directly correlated with their object exploration abilities. Specifically, infants who spent majority of their time exploring objects were more successful and used different strategies to retrieve the toy from the container (Caruso, 1993). Lastly, object play promotes both non-verbal communication skills such as showing and pointing (Iverson and Goldin-Meadow, 2005) as well as verbal communication skills such as vocalizations produced while exploring objects (Fagan and Iverson, 2007; Iverson et al., 2007) and labeling of objects (Baldwin and Markman, 1989). Specifically, rhythmic shaking of the rattle was closely related to babble onset in 4- to 9-month-old infants (Iverson et al., 2007) and mouthing of objects was closely associated with consonant production in 6- to 9-month-olds (Fagan and Iverson, 2007). Overall, object exploration could be a valuable paradigm to examine various forms of development in the first year of life. Next, we will be discussing the current literature on developmental trends in object exploration skills in TD infants and infants at-risk for autism.

Infants show substantial improvements in object exploration skills from birth to the end of the first year of life. Several factors including advancing age, improvements in motor skills, novelty of objects, as well as object properties influence infants' exploratory behaviors. Even newborn infants show differential oral and manual responses to objects of varying texture and rigidity (Rochat, 1987). However, active object exploration emerges around 3- to 6-months of age with the onset of reaching and grasping (Ruff, 1984; Rochat, 1989; Lobo and Galloway, 2008). At 6 months of age, infants spent the majority of their time mouthing and grasping objects and this sharply declined around 12- to 15-months of age with concurrent improvements in complex manual exploratory behaviors such as fingering, transferring, and rotating objects (Belsky and Most, 1981; Ruff, 1984). These improved fine motor skills may allow infants to perceive additional structural details of objects. In terms of visual exploration, early on, infants engaged in looking behaviors in isolation; however, older infants looked at objects while simultaneously fingering, turning, or rotating them (Ruff, 1986; Ruff et al., 1992). Looking accompanied with manual exploration provides infants with greater information about object properties than looking alone. Moreover, older infants showed preferential looking toward novel objects than familiar objects (Ruff, 1986). In the current study, we were interested in comparing the developmental trajectories for visual, oral, and manual exploratory behaviors in TD and at-risk infants over the first 15 months of life.

Exploratory behaviors are also influenced by object properties including size, shape, texture, and weight of objects, often called object affordances or natural opportunities for actions on objects (Newell et al., 1989, 1993; van Hof et al., 2002; Bourgeois et al., 2005; Barrett et al., 2008; Corbetta and Snapp-Childs, 2009; Libertus et al., 2013). For example, infants showed greater grasping of smaller objects whereas they looked more at larger, perceivable objects (Rochat, 1989). In addition, 9- to 12-month-old infants explored object properties such as shape, size, and texture by rotating, fingering, and transferring objects, whereas they explored properties such as weight, sound, and rigidity by banging and shaking objects (Ruff, 1984). Infants' grasping patterns depended on object size such that smaller objects were grasped unimanually and larger objects were grasped bimanually. Similarly, infants squeezed non-rigid objects more compared to rigid objects (Newell et al., 1989, 1993; Barrett et al., 2008). Given the interactions between object affordances and exploratory strategies of TD infants, we were interested in examining whether at-risk infants suitably and flexibly adapted their exploratory strategies to different object affordances over the first 2 years of life.

Unusual object exploration in the first year of life has been reported in retrospective studies in infants who later developed ASD as well as prospective studies comparing infants at-risk for autism and TD infants. Some abnormalities include excessive mouthing (Baranek, 1999; Bhat et al., 2009; Koterba et al., 2012), excessive visual fixation (Maestro et al., 2002; Zwaigenbaum et al., 2005; Bhat et al., 2010; Koterba et al., 2012; Chawarska et al., 2013), and repetitive use of objects (Ozonoff et al., 2008a). During the first year of life, AU sibs showed distinct mouthing patterns such as less mouthing of objects as early as 6 months (Bhat et al., 2009; Koterba et al., 2012). In contrast, excessive mouthing was reported at 9- and 12-months in infants who later developed ASD (Baranek, 1999). This developmental trajectory for mouthing differs compared to TD infants who predominantly use oral exploration at 6 months but transition to more advanced forms of manual exploration at 9 months with a concurrent decrease in oral exploration (Belsky and Most, 1981; Ruff, 1984). In terms of visual exploration in the first year of life, there is converging evidence from retrospective and prospective studies that infants at-risk for autism show greater visual fixation on objects (Zwaigenbaum et al., 2005; Koterba et al., 2012) and less attention toward social stimuli including caregivers and experimenters compared to TD infants (Maestro et al., 2002; Bhat et al., 2010; Chawarska et al., 2013). These unusual visual attention patterns continue from infancy into early childhood (Swettenham et al., 1998; Mottron et al., 2007; Shic et al., 2011; Chawarska et al., 2012). Lastly, several studies have also reported repetitive use of objects including less functional play between 9 and 12 months (Baranek et al., 2005) and excessive spinning of objects at 12 months (Ozonoff et al., 2008a) in AU sibs and infants who eventually developed ASD. Overall, there is considerable evidence supporting the presence of delayed and atypical object exploration skills in at-risk infants within the first year.

In spite of the unequivocal nature of the evidence supporting the early atypical nature of object exploration in infants at-risk for autism, there are several gaps in this literature. Specifically, studies have restricted their examination of at-risk infants to specific ages or to specific types of exploration. For instance, Ozonoff et al. (2008a) compared the object exploratory skills of at-risk infants who eventually developed ASD with those of TD infants at 12 months of age. Similarly, other studies restricted their examination of object exploration skills of infants to only two time-points within the first year (Baranek et al., 2005; Bhat et al., 2009; Koterba et al., 2012; Libertus et al., 2014). Along the same lines, the majority of the studies have evaluated a single type of skill such as manual, oral, or visual exploration in isolation (Maestro et al., 2002; Baranek et al., 2005; Bhat et al., 2010; Libertus et al., 2014). A comprehensive understanding of the developmental trajectory of object exploration skills in at-risk infants would require studying different forms of exploration in conjunction over the course of development. Moreover, given that exploratory strategies employed by infants are influenced by object affordances, it would be critical to consider object properties while studying exploratory behaviors. For instance, group differences in object exploration may be highly context-dependent; in other words, they may be revealed only during specific types of exploration involving specific objects at specific time points in development. Therefore, it would be important to assess different forms of exploration over the course of development with objects providing a variety of affordances. In the current longitudinal study, we aimed to concurrently and systematically examine different forms of object exploration including oral, visual, and manual behaviors as infants explored three objects of varying sizes, shapes, and textures, namely a rattle, a rigid ball, and a koosh ball from 6 to 15 months of age. We think that this design will allow us to better understand the context-dependency of group differences between TD and at-risk infants. This in turn will have significant implications for screening and identification of delays in at-risk infants within the first year of life. In the present study, we compared the manual (grasping and dropping), oral (mouthing), and visual (looking) exploration skills of TD and at-risk infants as they explored three different objects – a rattle, a rigid ball, and a koosh ball at 6, 9, 12, and 15 months of age.

Our first aim was to assess <u>object-related differences</u> or differences in how infants' explored the specific object affordances. We hypothesized that both TD and at-risk infants would perceive object affordances and adapt their actions on objects accordingly. For example, infants would demonstrate greater grasping and mouthing of the easily graspable rattle, greater dropping of the sounding rigid ball, and greater looking at the novel koosh ball. Our second aim was to examine <u>group differences</u> in object exploration skills between at-risk and TD infants from 6 to 15 months of age. We hypothesized that at-risk infants would show delays in age-appropriate exploration of objects compared to TD infants. Specifically, they would demonstrate context-dependent differences such as less grasping and mouthing at an early age, as well as less purposeful dropping, greater looking, and persistent mouthing at an older age. Lastly, we were interested in examining any shifts/delays in the developmental trajectories for different forms of exploration in at-risk infants compared to TD infants. We hypothesized that TD infants would replace immature exploratory behaviors such as mouthing with more advanced forms of information-gathering behaviors such as grasping and dropping from 6 to 15 months of age. In contrast, we expected at-risk infants to show a delayed developmental transition from immature to more advanced forms of object exploration.

Materials and Methods

Participants

Sixteen infants at-risk for autism (14 AU sibs and two preterm infants who later developed ASD) and 16 TD full term infants with no significant birth history or family history of ASD were observed over four visits at 6, 9, 12, and 15 months of age (see **Table 1**) within the object exploration paradigm. In terms of socioeconomic status, all families belonged to the upper–middle or upper class (Hollingshead, 1975, see details in Table 1). Participants were recruited through local day care centers, autism service providers such as clinics and schools, web postings, and word of mouth. We excluded infants with significant birth history including low birth weight, head injury, birth trauma, any known genetic disorder, hearing or vision impairment, or any orthopedic or other medical diagnoses that could affect participation. The older siblings of all 14 AU sibs met diagnostic criteria for ASD based on the Autism Diagnostic Interview-Revised (ADI-R; Lord et al., 1994), expert clinical judgment, and/or medical records. Two preterm twins were enrolled in the study with no specific diagnoses as our research protocol was broader and included multiple at-risk populations. Both preterm infants were diagnosed with ASD in the second year of life based on the aforementioned criteria; hence, we have included their data within the group of at-risk infants. All parents signed the formal parental permission form approved by the University of Connecticut's Review Board before participating in the study.

Future Outcomes of At-Risk Infants

We obtained developmental outcomes for infants in both groups at 18 months using parent questionnaires, the Ages and Stages Questionnaire-third edition (ASQ-3; Squires et al., 1999) and the Modified Checklist for Autism in Toddlers (M-CHAT; Robins et al., 1999, 2001). The ASQ-3 has multiple developmental domains of personal–social, communication, gross and fine motor, and problem solving/cognitive abilities (Squires et al., 1999). A developmental delay was defined as a total score $\leq$1SD below the mean standard score. M-CHAT is a 23-item yes/no checklist for the screening of ASD and a failure on any three items or two critical items indicates higher risk to develop ASD (Robins et al., 1999, 2001). Fifteen out of 16 parents of TD infants and 14 out of 16 parents of at-risk infants filled out the 18-month questionnaires (see details in **Table 2**). None of the TD infants reported significant delays on the ASQ-3 and M-CHAT. Among at-risk infants, eight reported delays on one or more domains of the ASQ-3 and six failed on the M-CHAT (see **Table 2**). We also conducted follow-up email inquiries with parents after the toddler's second birthday regarding any developmental delays, diagnoses, and services received. None of the TD infants received developmental diagnoses at 2 years whereas eight at-risk infants developed delays/ASD diagnosis, specifically, five at-risk infants had language delays and three received an ASD diagnosis. In terms of services received, six of the eight at-risk infants with formal diagnoses/delays were receiving early intervention services based on parent emails (see **Table 2**). Taken together, 10 AU sibs received poor outcomes; of those six AU sibs failed on the M-CHAT, demonstrated delays on the ASQ-3 and parents reported developmental delays/ASD diagnosis during email follow-up. The parents of the preterm twins did not complete the 18-month questionnaire but reported ASD diagnosis during email follow-up. Lastly, two other AU sibs reported multiple delays on the ASQ-3 but did not follow-up via email. These findings clearly distinguish the group of at-risk infants from the TD group; but due to small sample sizes we will not be distinguishing the performance of toddlers who developed future delays/diagnoses from those who did

TABLE 1 | Participant characteristics.

Group	*n*, Gender F:M	Ethnicity C, AA/M	SES Mean ± SD	Age in months (Mean ± SD)			
				6	9	12	15
Typically developing (TD)	16, 6:10	15 C, 1 AA	55.32 ± 9.22	6.93 ± 0.60	10.02 ± 0.46	12.98 ± 0.69	15.86 ± 0.46
At-risk	16, 3:13	15 C, 1 M	52.03 ± 12.66	6.83 ± 0.60	9.70 ± 0.55	12.97 ± 0.89	15.62 ± 1.13
ps	ns	ns	ns	ns	ns	ns	ns

N, total number of participants in each group; F:M, total number of females and males in each group; SES, socioeconomic status; C, Caucasian; AA, African American; M, Mixed; ns, p-values not significant (i.e., ps > 0.05).

TABLE 2 | Future outcomes of at-risk infants.

Group	ASQ-3 (18 months)			M-CHAT (18 months)	Emails – ASD Diagnosis/ Delays	Emails –Receiving Services
	Personal social and communication	Gross and fine motor	Problem solving			
At-risk	6/14	3/14	2/14	6/14	8/14	6/14

not report any delays. However, individual data have been reported for the at-risk group in the results section (see **Figures 7A–D**).

Experimental Set Up

Infants were seated upright in a booster seat with the tester on one side (see **Figure 1A**). A long rattle, circular rigid ball, and circular koosh ball were presented one at a time at the center of the tabletop within the infant's reach (see **Figure 1B**). These objects were chosen as they varied in size, shape, and texture and hence afforded different types of exploratory behaviors. For example, the rattle afforded shaking and grasping, the sounding rigid ball afforded dropping/throwing, and the novel koosh ball afforded looking and holding. The presentation was in a fixed order – the rattle, the rigid ball, and then the koosh ball. The tester demonstrated the properties of objects, i.e., shaking of the rattle and the rigid ball or pulling strings of the koosh ball before presenting the object. The infant was allowed to freely explore the object for about one minute. If the object was dropped on the floor, it was presented again to the infant. Each session was videotaped for further coding. In terms of missing data, TD infants missed their visits as follows – 0/16 at 6 months, 2/16 at 9 months, 0/16 at 12 months, and 4/16 at 15 months. Similarly at-risk infants missed visits as follows - 3/16 at 6 months, 1/16 at 9 months, 0/16 at 12 months, and 1/16 at 15 months. The visits were missing due to later recruitment, illnesses, and/or scheduling conflicts.

Behavioral Coding

A custom coding scheme was used to code the duration of each exploratory behavior using frame-by-frame analysis. Grasping was any form of manual contact with the object including higher level behaviors such as holding, shaking, banging, and fingering but excluding low level behaviors such as touching. Dropping was coded when the object was out of the infant's hand including instances of accidental slips and purposeful drops. Mouthing was coded when the object was in contact with the infant's mouth; this required infants to grasp the object and bring it to their mouth. Looking was visual fixation on the object when it was on the table or grasped. The percent duration of each behavior was calculated for each object presentation. Intra-class correlations (ICCs) were used to determine intra- and inter-rater reliability using 36 min of the dataset for each behavior. Intra- and inter-rater reliability scores were greater than 85% for the various exploratory behaviors based on ICC coefficients (grasping ≥ 0.88, dropping ≥ 0.93, mouthing ≥ 0.99, and looking ≥ 0.95).

Statistical Analysis

We conducted a single Pillai's Trace Multivariate Analysis of Variance (ANOVA) with behavior (grasping, dropping, mouthing, looking), age (6, 9, 12, 15 months) and object (rattle, rigid, koosh) as within-subjects factors and group (TD group, at-risk group) as the between-subjects factor. As mentioned previously, an important aim of our study was to compare group differences in object exploration skills between at-risk and TD infants. Hence, we conducted two types of planned comparisons: (a) group differences at each age were examined using independent *t*-tests and (b) developmental changes in exploratory behaviors were examined using dependent *t*-tests within each group. We will report group differences as early (at 6 months), mid (at 9 and 12 months), and late (at 15 months) differences. Similarly, we will report on developmental changes in exploratory behaviors as early (from 6 to 9 months), mid (from 9 to 12 months), and late (from 12 to 15 months) changes. We considered $p \leq 0.05$ as significant for all the comparisons. The missing values were replaced with the average of the group for any given visit.

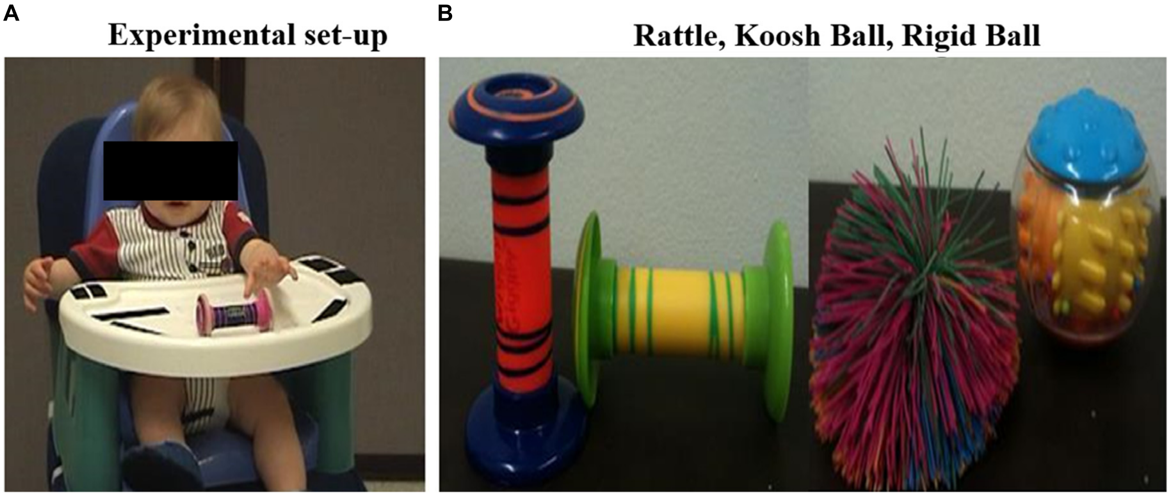

FIGURE 1 | The experimental set up with an infant sitting in a booster seat (A) and the objects presented – a rattle, a koosh ball, and a rigid ball (B).

Results

Object-Based Differences in Exploratory Behaviors in TD and At-Risk Infants

Both TD and at-risk infants clearly demonstrated differential exploration of the rattle, rigid ball, and the koosh ball suggesting that both groups perceived object affordances. Specifically, infants demonstrated greater grasping of the rattle (see **Figure 2A**) compared to other objects. There was more dropping of the sounding rigid ball compared to the other objects (see **Figure 2B**). Similarly, both TD and at-risk infants demonstrated greater mouthing of the rattle compared to the other objects (see **Figure 2C**). Lastly, there was more time spent looking at the koosh ball compared to the rattle and rigid ball (see **Figure 2D**). In terms of individual data, 12–16 out of the 16 TD infants and 9–6 out of the 16 at-risk infants followed their respective group trends.

Group Differences and Differences in Development of Object Exploration in TD and At-Risk Infants

The multivariate analysis showed a significant main effect of behavior [Pillai's Trace = 0.96, $F(3,28) = 208.92$, $p < 0.05$, $\eta_p^2 = 0.96$] and several interactions with behavior as a factor, including, behavior × object [Pillai's Trace = 0.94, $F(6,25) = 65.76$, $p < 0.05$, $\eta_p^2 = 0.94$], behavior × age [Pillai's Trace = 0.80, $F(9,22) = 9.62$, $p < 0.05$, $\eta_p^2 = 0.80$], behavior × age × group [Pillai's Trace = 0.65, $F(9,22) = 4.61$, $p < 0.05$, $\eta_p^2 = 0.65$], and behavior × object × age [Pillai's Trace = 0.86, $F(18,13) = 4.44$, $p < 0.05$, $\eta_p^2 = 0.86$]. Hence, we conducted separate ANOVAs for each behavior. Based on our planned comparisons, we analyzed the three-way or two-way interactions for each of the four exploratory behaviors to report group differences at each age and developmental changes in each group.

Grasping

The ANOVA for duration of grasping showed significant main effects of object [$F(2,30) = 66.23$, $p < 0.05$, $\eta_p^2 = 0.69$] and age [$F(3,30) = 4.54$, $p < 0.05$, $\eta_p^2 = 0.13$], as well as interaction effects of object × age [$F(6,30) = 6.01$, $p < 0.05$, $\eta_p^2 = 0.17$] and object × age × group [$F(6,30) = 4.60$, $p < 0.05$, $\eta_p^2 = 0.13$].

Group differences for grasping

Early group differences were observed for grasping with at-risk infants showing less grasping of the rigid ball at 6 months compared to TD infants (see **Figure 3B**; **Table 3**). No other group differences were observed for grasping behaviors.

Developmental changes in grasping

In terms of *early changes*, TD infants showed reduced grasping of the rigid ball between 6 and 9 months (see **Figure 3B**; **Table 4**) with no clear changes for the rattle and koosh ball. In contrast, at-risk infants significantly increased the grasping of the rattle and the rigid ball with no changes for the koosh ball (see **Figures 3A,B**; **Table 4**). In terms of *mid changes*, TD infants increased grasping of the rattle and at-risk infants increased grasping of the koosh ball between 9 and 12 months (see **Figures 3A,C**; **Table 4**). No late changes were observed for both groups.

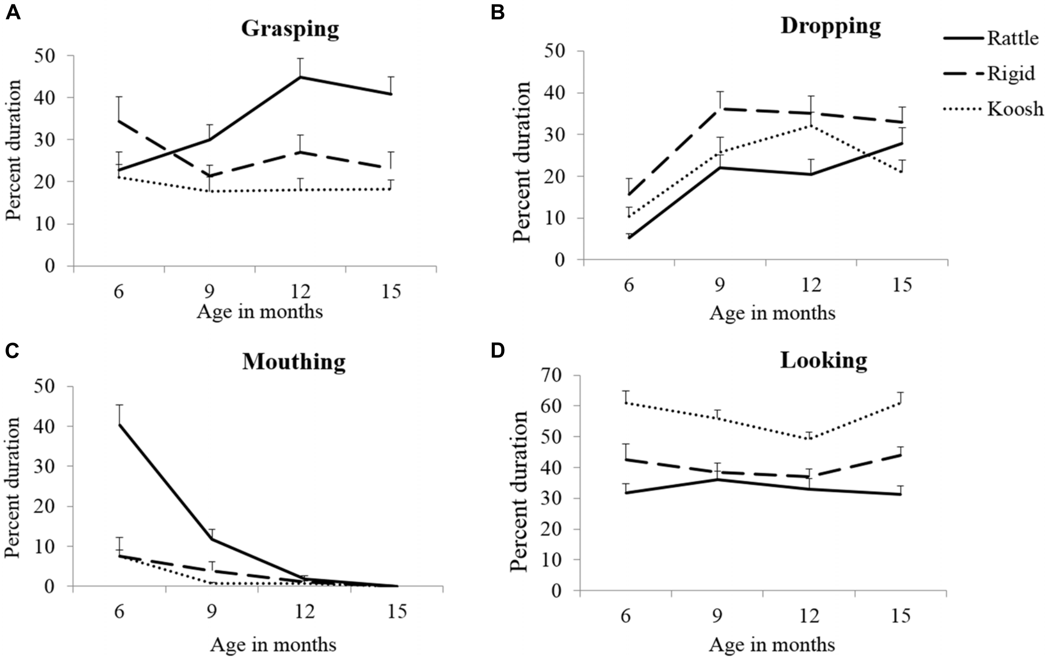

FIGURE 2 | Object-based differences in grasping (A), dropping (B), mouthing (C), and looking (D) in typically developing infants.

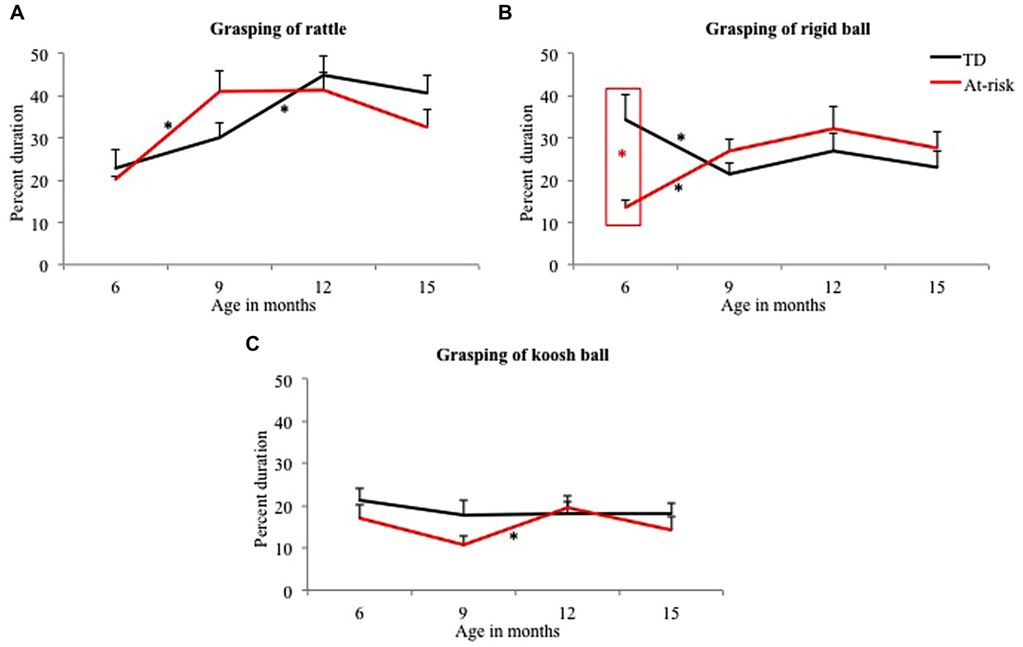

FIGURE 3 | Group differences and developmental trends for grasping of rattle (A), rigid ball (B), and koosh ball (C) in typically developing and at-risk infants. *indicates $p < 0.05$. The red * within a red box indicates a group difference and black * indicates a developmental change between the two ages for the group indicated.

TABLE 3 | *P*-values for group differences in object exploration between TD and at-risk infants.

Behavior	Age (in months)			
	6	9	12	15
Grasping	<0.01 (RB)	ns	ns	ns
Dropping	0.03 (A)	<0.01 (A)	<0.01 (A)	ns
Mouthing	0.02 (R)	ns	ns	<0.01 (R) 0.05 (RB)
Looking	0.02 (R)	ns	<0.01 (KB)	ns

R, Rattle; RB, Rigid Ball; KB, Koosh Ball; A, All objects; ns, p-values not significant.

Dropping

The ANOVA for duration of dropping indicated main effects of object $[F(2,30) = 19.36, p < 0.05, \eta_p^2 = 0.39]$ and age $[F(3,30) = 12.92, p < 0.05, \eta_p^2 = 0.30]$, as well as an age × group interaction $[F(3,30) = 5.81, p < 0.05, \eta_p^2 = 0.16]$.

Group differences for dropping

Significant early and mid group differences emerged for dropping behaviors. Specifically, at-risk infants engaged in greater dropping of objects at 6 months but lower levels of dropping at 9 and 12 months compared to TD infants (see **Figure 4**; **Table 3**).

Development changes in dropping

Typically developing infants showed an early increase in dropping of objects from 6 to 9 months whereas at-risk infants showed a delayed increase in dropping of objects from 12 to 15 months (see **Figure 4**; **Table 4**).

Mouthing

The ANOVA for mouthing duration indicated significant main effects of object $[F(2,30) = 29.42, p < 0.05, \eta_p^2 = 0.50]$ and age $[F(3,30) = 40.36, p < 0.05, \eta_p^2 = 0.57]$ as well as interaction

TABLE 4 | *P*-values for developmental changes in object exploration in TD and at-risk infants.

Behavior	Early (6–9 months)		Mid (9–12 months)		Late (12–15 months)	
	TD	At-risk	TD	At-risk	TD	At-risk
Grasping	0.02 (RB)	<0.01 (R,RB)	0.02 (R)	0.03 (KB)	ns	ns
Dropping	<0.01 (A)	ns	ns	ns	ns	<0.01 (A)
Mouthing	<0.01 (R)	<0.01 (R) 0.02 (KB)	<0.01 (R)	ns	0.05 (R)	ns
Looking	ns	ns	ns	ns	<0.01 (KB)	ns

R, Rattle; RB, Rigid Ball; KB, Koosh Ball; A, All objects; ns, p-values not significant.

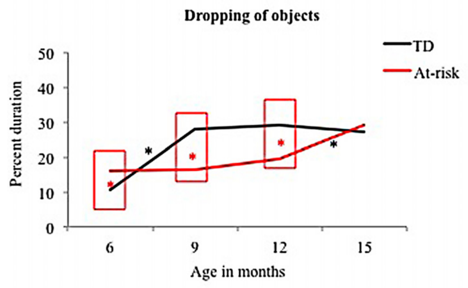

FIGURE 4 | Group differences and developmental trends for dropping of objects in typically developing and at-risk infants. *indicates a $p < 0.05$. The red * within a red box indicates a group difference and black * indicates a developmental change between the two ages for the group indicated.

effects of object × age [$F(6{,}30) = 17.81$, $p < 0.05$, $\eta_p^2 = 0.37$] and object × age × group [$F(6{,}30) = 4.47$, $p < 0.05$, $\eta_p^2 = 0.13$].

Group differences for mouthing

Significant early and late group differences were seen for mouthing behaviors. At-risk infants showed less mouthing of the rattle at 6 months (see **Figure 5A**; **Table 3**) and greater mouthing of the rattle and rigid ball at 15 months of age compared to TD infants (see **Figures 5A,B**; **Table 3**).

Development changes in mouthing

In terms of *early changes*, both TD and at-risk infants significantly decreased mouthing of the rattle from 6 to 9 months (see **Figure 5A**; **Table 4**). At-risk infants also decreased mouthing of the koosh ball from 6 to 9 months (see **Figure 5C**; **Table 4**). In terms of *mid and late changes*, TD infants continued to reduce mouthing of the rattle whereas no significant reductions in mouthing were observed in at-risk infants (see **Figure 5A**; **Table 4**).

Looking

The ANOVA for looking duration showed a main effect of object [$F(2{,}30) = 88.11$, $p < 0.05$, $\eta_p^2 = 0.74$] and a significant object × age × group interaction [$F(6{,}30) = 3.20$, $p < 0.05$, $\eta_p^2 = 0.10$].

Group differences for looking

Significant early and mid group differences were observed for looking behaviors. At-risk infants spent greater time looking at the rattle at 6 months (see **Figure 6A**; **Table 3**) and at the koosh ball at 12 months (see **Figure 6C**; **Table 3**) compared to TD infants.

Developmental changes in looking

In terms of early, mid, and late changes, both groups showed no major changes in looking patterns (see **Figures 6A–C**; **Table 4**) except increased looking at the koosh ball in TD infants between 12 and 15 months (see **Figure 6C**; **Table 4**).

In summary, early group differences observed included less grasping of the rigid ball, less mouthing of the rattle, greater looking at the rattle, and greater dropping of all three objects in at-risk infants compared to TD infants. The only mid group differences observed were lower levels of purposeful dropping at 9 and 12 months and greater looking at the koosh ball at 12 months

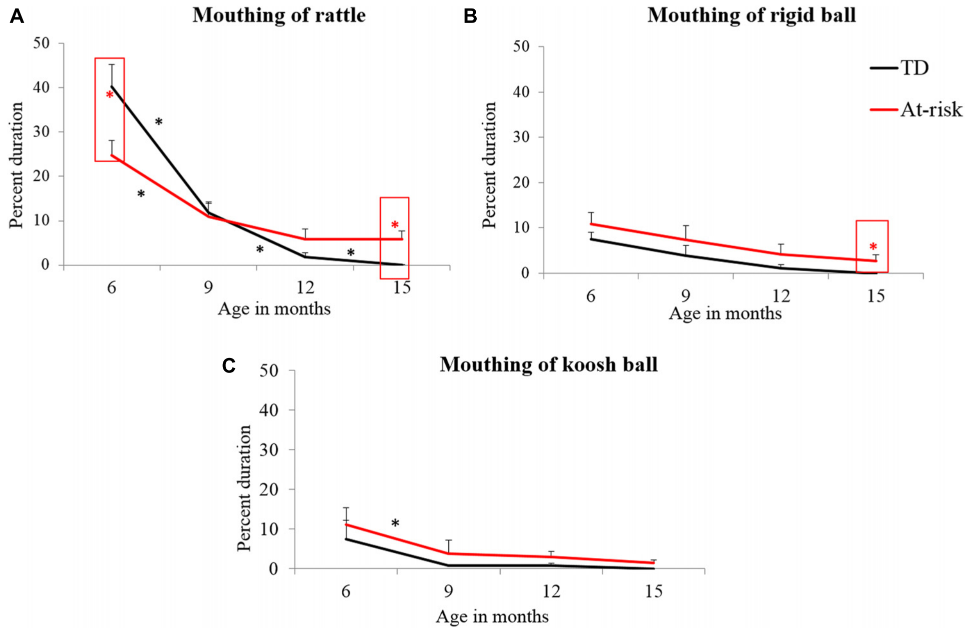

FIGURE 5 | Group differences and developmental trends for mouthing of rattle (A), rigid ball (B), and koosh ball (C) in typically developing and at-risk infants. *indicates a $p < 0.05$. The red * within a red box indicates a group difference and black * indicates a developmental change between the two ages for the group indicated.

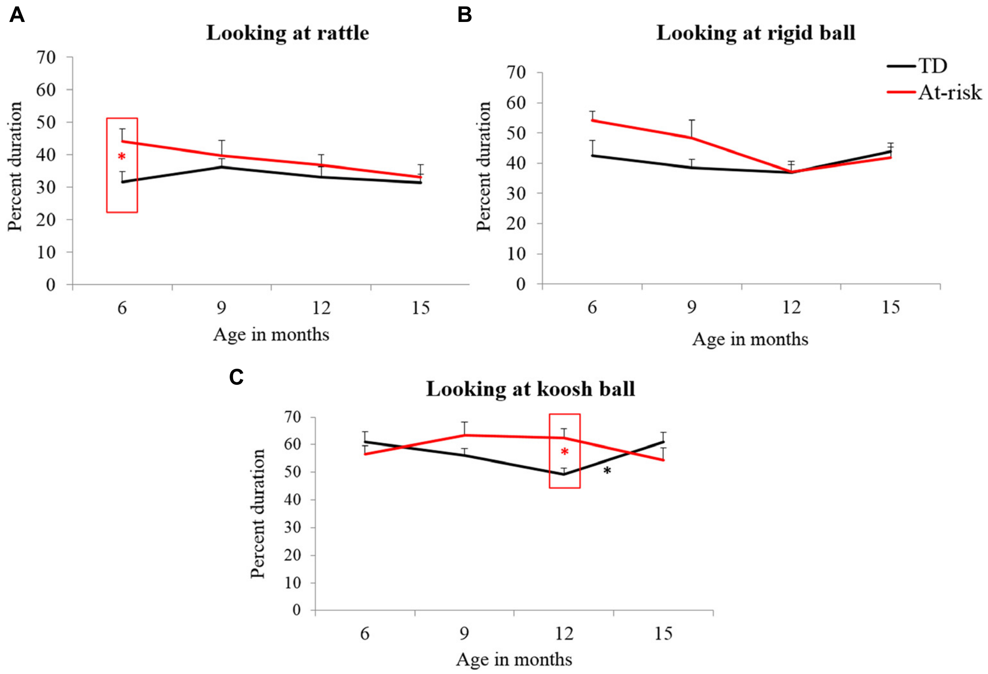

FIGURE 6 | Group differences and developmental trends for looking at rattle (A), rigid ball (B), and koosh ball (C) in typically developing and at-risk infants. *indicates a $p < 0.05$. The red * within a red box indicates a group difference and black * indicates a developmental change between the two ages for the group indicated.

in at-risk infants compared to the TD group. Lastly, in terms of late group differences, at-risk infants demonstrated persistent mouthing of the rattle and rigid ball compared to TD infants. In terms of individual data, 10–16 of the 16 at-risk infants always performed poorly compared to the TD group's average values (see **Figures 7A–D**).

In terms of developmental changes, early changes for TD infants included reduced grasping with concurrent increases in purposeful dropping of multiple objects. In contrast, at-risk infants increased grasping early on and showed delays in the onset of purposeful dropping behaviors. Both TD and at-risk infants showed an early decrease in mouthing of objects. Mid changes for TD and at-risk infants included increased grasping of multiple objects. TD infants also continued to show a reduction in mouthing behaviors with the rattle, although similar changes were not observed in at-risk infants. At-risk infants began to develop purposeful dropping behaviors between 12 and 15 months. Late changes for TD infants included further reduction in mouthing behaviors and an increase in looking at the koosh ball. At-risk infants did not show any developmental changes in exploratory behaviors from 12 to 15 months. In terms of individual data, 12–16 out of the 16 TD infants and 12–15 out of the 16 at-risk infants followed their respective group trends.

Individual Data for At-Risk Infants

Individual data from the at-risk infants are compared to the at-risk and TD group averages in **Figures 7A–D**. The 10 at-risk infants with future delays/ASD diagnosis have been highlighted in the figures as red dotted lines, the at-risk group's average is a red solid line, and the TD group average is a black solid line. As discussed in the section "Group Differences and Differences in Development of Object Exploration in TD and At-Risk Infants," at-risk infants showed poor grasping of the rigid ball at 6 months compared to the TD group average (see **Figure 7A**). In terms of dropping, the majority of the at-risk infants showed less dropping of the rigid ball than the TD group average at 9 months (see **Figure 7B**). In terms of mouthing, the majority of the at-risk infants showed less mouthing of the rattle at 6 months and persistently greater mouthing at 15 months than the TD group average (see in **Figure 7C**). Lastly, most of the at-risk infants showed greater looking at the koosh ball at 12 months compared to the TD group average. Moreover, looking periods appeared to be consistently higher in the at-risk infants across visits compared to the TD group average (see **Figure 7D**). It should be noted that the majority of the at-risk infants including at-risk infants without delays performed poorly compared to the TD average.

Discussion

Summary of Results

To our knowledge, this is the first study to longitudinally compare the developmental changes in visual, oral, and manual exploration using three different objects between TD and at-risk infants from 6 to 15 months of age. Both groups adapted their exploration to the unique properties of objects by demonstrating greater grasping and mouthing of the easily-graspable rattle,

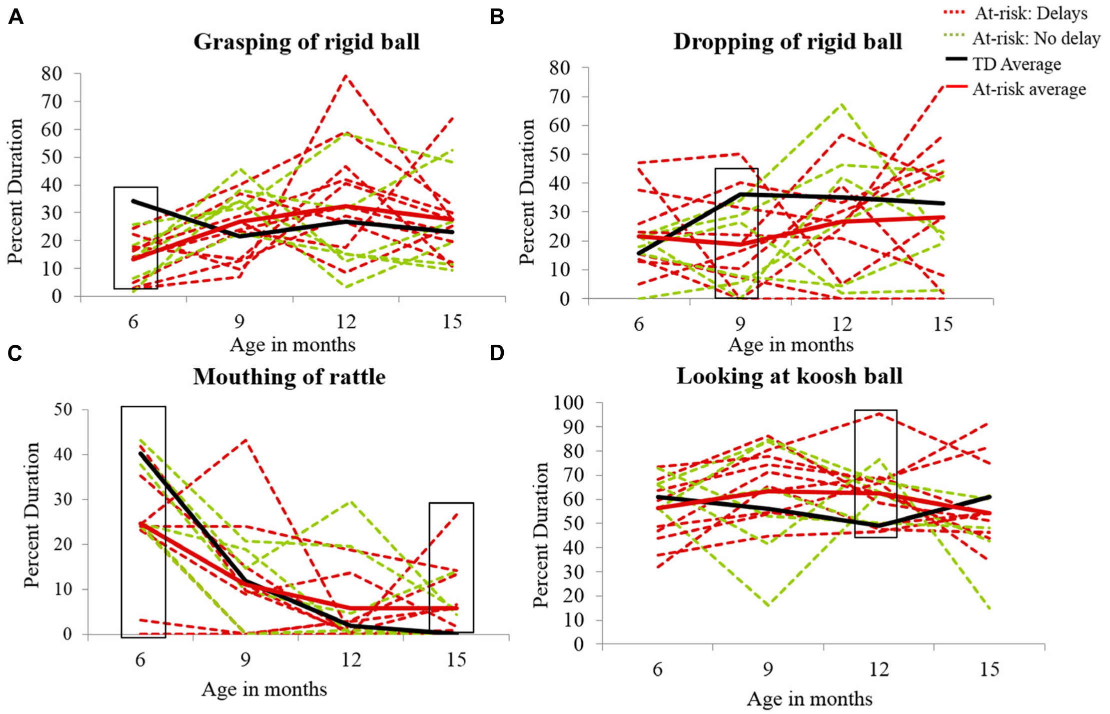

FIGURE 7 | Individual data for grasping of the rigid ball (A), dropping of the rigid ball (B), mouthing of the rattle (C), and looking at the koosh ball (D) in at-risk infants. The solid black line represents the average of the typically developing group and the solid red line represents the average of the at-risk group. The red dotted lines represent the 10 at-risk infants with future delays/ASD diagnosis, and the green dotted lines represent the at-risk infants without any future delays. The black boxes highlight the group differences with the majority of the at-risk infants performing worse than the typically developing group average.

greater dropping of the sounding rigid ball, and greater looking at the novel koosh ball compared to the other objects (see section Object-Based Differences in Object Exploratory Behaviors in TD and At-Risk Infants and **Figures 2A–D**).

In terms of group differences in grasping, at-risk infants showed deficient grasping of the rigid ball at 6 months (see **Figures 3–6**). In addition, they showed deficient functional dropping of objects at 9 and 12 months compared to TD infants. In terms of mouthing, at-risk infants showed reduced mouthing of the rattle at 6 months but demonstrated persistent mouthing of the rattle and rigid ball at 15 months compared to TD infants. Lastly, at-risk infants showed greater looking at the rattle at 6 months as well as at the koosh ball at 12 months compared to TD infants.

In terms of developmental changes, we examined early (between 6 and 9 months), mid (between 9 and 12 months), and late (between 9 and 15 months) changes in object exploration of TD and at-risk infants (see section Group Differences and Differences in Development of Object Exploration in TD and At-Risk Infants and **Figures 3–6**). In terms of early changes for grasping and dropping, TD infants showed reduced grasping of the rigid ball with a concurrent increase in dropping. In contrast, at-risk infants showed increased grasping of the rattle and rigid ball with no onset of dropping. Mid changes for the TD and at-risk infants included increased grasping of various objects. In terms of late changes at-risk infants increased dropping of objects from 12 to 15 months. In terms of mouthing, TD infants showed high levels of mouthing early on but reduced mouthing behaviors over development whereas at-risk infants showed lower levels of mouthing early on with persistent mouthing at 15 months. Looking patterns did not change with development for both groups except for some increase in exploratory looking at the koosh ball in TD infants between 12 and 15 months.

Object-Based Differences in Exploration

In the current study, infants were presented with three perceptually distinct objects that varied in terms of their shapes, sizes, and textures. Infants demonstrated greater grasping and mouthing of the rattle, greater dropping of the rigid ball, and greater looking at the koosh ball. These object-based differences in exploratory strategies could be due to salient differences in properties and affordances of objects as well as infants' prior experiences with similar objects. For example, in terms of object properties, the cylindrical rattle allowed for a relatively easy hook grasp compared to the circular rigid ball that required a larger bimanual palmar grasp or the koosh ball that required more advanced coordination using a multi-digit pincer grip. Previous studies have also demonstrated variations in infants' grasping patterns based on object structure, such as bimanual palmar grasps for larger objects and pincer grips for smaller and softer objects (Newell et al., 1989, 1993; Newman et al., 2001; Barrett et al., 2008). Similarly, infants in both groups seemed to have perceived specific object affordances and adapted their actions accordingly. Other studies have also shown that infants between 6 and 12 months typically perceive object affordances such as shaking, banging, and dropping (Ruff, 1986; Loucks and Sommerville, 2013). Along these lines, the rattle might have afforded grasping and shaking to produce a sound and the sounding rigid ball might have afforded throwing or dropping. Moreover, since mouthing behaviors are dependent on infants' ability to grasp objects (Whyte et al., 1994), infants might have demonstrated greater mouthing and grasping of the rattle compared to other objects. Additionally, the narrow, cylindrical structure of the rattle makes it relatively easier to mouth compared to the wide and circular rigid ball or the filamentous koosh ball. Lastly, since the koosh ball is a relatively novel toy that is typically not a part of infants' natural environment, it might have evoked greater visual fixation in both groups. In fact, early on, infants hesitated to grasp the koosh ball as they were unsure of its affordances and instead looked at it longer. Overall, there were several interesting object-based differences in exploration observed in both groups.

Group Differences and Developmental Changes in At-Risk and TD Infants

In terms of group differences for grasping, at-risk infants showed less grasping of the rigid ball compared to TD infants at 6 months (see **Figure 3B**). Along these lines, grasping delays have been reported in AU sibs at 6 months of age within an object exploration task as well as on a standardized motor assessment, the fine motor sub-test of the Mullen Scales of Early Learning (Libertus et al., 2014). Grasping delays in at-risk infants in our study could be attributed to specific object properties of the rigid ball as well as to the postural and fine motor delays seen in at-risk infants. Specifically, the rigid ball used in our study was harder to grasp compared to the rattle and the koosh ball due to its large size, thereby requiring good bimanual control. Moreover, postural instability as well as poor fine motor control may have contributed to grasping delays in at-risk infants (Teitelbaum et al., 1998; Landa and Garrett-Mayer, 2006; Ozonoff et al., 2008b; Bhat et al., 2011; Nickel et al., 2013). For example, some of the early gross motor delays in at-risk infants include postural asymmetries as well as delayed acquisition of postures such as rolling, sitting, crawling, and walking (Teitelbaum et al., 1998; Ozonoff et al., 2008b; Nickel et al., 2013). Postural instability can lead an unstable base of support, which in turn can impair infants' reaching and fine motor skills (Spencer et al., 2000). Moreover, infants who later developed ASD demonstrated poor fine manual control including delays in the onset of grasping, reaching, and pointing skills (Landa and Garett-Mayer, 2006; Gernsbacher et al., 2008). Overall, poor gross and fine motor control can significantly impair manual exploration skills of infants at-risk for ASD.

In terms of developmental changes in grasping, at-risk infants increased grasping of the rigid ball and rattle from 6 to 9 months and of the koosh ball from 9 to 12 months, whereas TD infants increased grasping of the rattle between 9 and 12 months. Infants are known to improve their grasping abilities between 6 and 15 months of age with a transition from ulnar grasps to radial palmar grasps (Butterworth et al., 1997). Similarly, 12- to 14-month-old infants' showed appropriate, anticipatory changes in grasp formation based on object shape and size compared to 5- to 6-month-old infants (Fagard, 2000; Barrett et al., 2008). Along the same lines, we observed that infants began to engage in more sophisticated forms of manual exploration including fingering, shaking, banging, and rotating objects that could have contributed to an increase in grasping from 9 to 15 months. Currently, we are coding for more refined and sophisticated forms of manual exploration in both groups of infants.

In terms of group differences for dropping, at-risk infants spent greater time dropping objects at 6 months of age but demonstrated lower levels of functional dropping at 9 and 12 months compared to TD infants (see **Figure 4**). The greater dropping at 6 months in at-risk infants may be due to their fine motor delays leading to difficulties in grasping objects and unintentional slips while attempting to grasp toys. The reduced dropping at 9 and 12 months in at-risk infants may be an early indicator of poor functional and object-appropriate play in at-risk infants. A few other studies have also shown delayed functional play in AU sibs and infants later diagnosed with ASD during the first year of life (Baranek et al., 2005; Ozonoff et al., 2008a). Specifically, AU sibs showed non-functional use of objects such as excessive spinning and rotating of toys at 12 months of age (Ozonoff et al., 2008a).

In terms of development trends in dropping, at-risk infants demonstrated delayed emergence of functional dropping behaviors compared to TD infants. Dropping behaviors typically emerge between 9 and 12 months and increase with development (Ruff, 1986; Ruff et al., 1992). In our study, we observed that several TD infants engaged in dropping behaviors early on due to the specific sounding properties of rigid objects and to initiate social games with caregivers. Infants were seated in a high chair and dropping toys on the floor or on the table produced sounds that infants found appealing. Infants also used such behaviors as an opportunity to initiate interactions with caregivers as they checked back with them after purposefully dropping toys. Therefore, we think that dropping behaviors in TD infants were a form of early functional play. Along these lines, other research also suggests that TD infants manipulate sounding objects more often compared to non-sounding objects within the first year, suggesting that infants recognize object properties and engage in functionally appropriate actions (Palmer, 1989).

In terms of group differences in oral exploration of objects, at-risk infants' demonstrated reduced mouthing of the rattle at 6 months and excessive mouthing of the rattle and rigid ball at 15 months compared to TD infants (see **Figures 5A,B**). Note, that the koosh ball was the least mouthed object due to its novel texture/appearance. Early delays in mouthing could be a function of poor grasping abilities. There is evidence to suggest that early on, oral exploration of objects is closely related to the manual exploratory skills of infants (Whyte et al., 1994) with better grasping allowing for easier mouthing. Given the early grasping delays observed among at-risk infants, it was not surprising that they also engaged in less mouthing at 6 months compared to TD infants. Similar delays in early mouthing abilities of AU sibs have been observed at 6 months of age in other studies (Bhat et al., 2009; Koterba et al., 2012).

In terms of developmental changes in mouthing, TD infants reduced mouthing of the rattle from 6 to 9 and 9 to 15 months (see **Figure 5A**); such an early decrease in mouthing fits with what is known in the literature (Belsky and Most, 1981; Ruff, 1984; Rochat, 1989). Mouthing is a predominant form of exploration at 6 months of age and is known to reduce after the onset of more refined forms of manual exploration (Belsky and Most, 1981; Ruff, 1984; Rochat, 1989). At-risk infants showed an early reduction in mouthing, however, they failed to reduce mouthing from 9 to 15 months resulting in persistent mouthing at 15 months. Excessive mouthing of objects has also been reported in infants later diagnosed with ASD between 9 and 12 months of age (Baranek, 1999). This unusual persistence of oral exploration in at-risk infants could be due to infants seeking additional sources of sensory input by mouthing or chewing inedible objects (Dunn et al., 2002; Baranek et al., 2006; Tomchek and Dunn, 2007). Tomchek and Dunn (2007) reported that 95% of their study sample of children with ASD between 3 and 6 years had a sensory processing dysfunction including an over- or under-responsiveness to different sensations (Tomchek and Dunn, 2007).

Lastly, in terms of visual exploration, both TD and at-risk infants demonstrated greater looking at the novel koosh ball at 6 months suggesting that both groups were equally enamored by this unfamiliar object. However, at-risk infants additionally showed excessive looking at the rattle at 6 months and at the koosh ball at 12 months compared to TD infants (see **Figures 6A,C**). Moreover, individual data in **Figure 7D** show a general trend for excessive visual exploration of objects in at-risk infants compared to TD infants. It is worth emphasizing that at-risk infants demonstrated excessive visual exploration irrespective of the novelty of objects used. For example, they looked more even at the relatively familiar rattle. Various studies have reported unusual visual fixation on objects in AU sibs (Ozonoff et al., 2008a; Bhat et al., 2010; Koterba et al., 2012) and their inability to disengage visual attention during the first year of life (Zwaigenbaum et al., 2005). Such excessive object fixation in AU sibs usually co-occurred with reduced attention to social partners and could directly contribute to the delayed social development in infants who eventually develop autism (Maestro et al., 2002, 2005; Bhat et al., 2010; Chawarska et al., 2013).

In terms of developmental changes in visual exploration, both at-risk and TD infants showed no changes in looking patterns except for increased looking at the koosh ball in TD infants from 12 to 15 months (see **Figure 6C**). This could be due to the development of more refined forms of manual exploration in TD infants requiring focused attention at the koosh ball while manipulating it in sophisticated ways. Our findings fit with those of another study where infants showed no clear changes in looking duration from 7 to 12 months during a free play-based task involving presentation of a variety of objects with distinct properties (Ruff, 1986).

Taken together, our longitudinal study comparing object exploration skills in TD and at-risk infants revealed that group differences in object exploration are highly context-dependent; delays in exploratory behaviors in at-risk infants are evident at different time points in development for specific objects with distinct affordances. Our study suggested that TD infants showed several advances in their strategies for object exploration from 6 to 15 months of age as a result of improvements in fine motor control as well as improved perception of object affordances. At-risk infants showed similar but delayed developmental trajectories in exploratory behaviors. For example, at-risk infants demonstrated grasping delays as well as a delayed emergence of functional dropping behaviors. In addition, they showed a reverse developmental trend for oral exploration, i.e., reduced early mouthing and persistent mouthing at later ages.

Implications for Early Diagnosis and Treatment

The current study is unique in its approach of longitudinally studying various forms of object exploration concurrently in the context of objects with varying affordances in TD and at-risk infants within the first 15 months of life. We observed significant group differences in object exploration skills of at-risk infants from 6 to 15 months. Importantly, our study adds to the current literature by suggesting that group differences in exploratory behaviors are highly context-dependent such that delays in specific exploratory strategies are observed for specific objects and/or at specific ages. This has important implications for early screening as well as planning of object-based interventions for at-risk infants. Specifically, caregivers and clinicians should observe object play of infants within natural and structured settings for identifying early signs of autism risk. The set of objects used during exploratory play will play a crucial role in uncovering delays/atypicalities in object exploration skills in at-risk infants at different ages. Specific red flags for atypical object exploration during the first half of the first year include reduced oral and manual object exploration as well as increased visual regard for objects and other non-social stimuli. During the second half of the first year, a lack of age-appropriate and object-appropriate functional play such as shaking of sounding objects, dropping of ball-like objects, and fingering of soft objects could be signs of increased risk. In addition, at-risk infants may show persistent mouthing and unusually greater oral hyposensitivity.

Reduced and atypical object exploration could impact various forms of development in at-risk infants. Specifically, object exploration abilities are directly related to the development of cognitive skills such as object knowledge (Caruso, 1993; Bourgeois et al., 2005), non-verbal, and verbal communication skills such as the use of gestures and words within a social context (Fagan and Iverson, 2007; Iverson and Wozniak, 2007), as well as social skills such as imitation, joint attention, and pretend play (Bruckner and Yoder, 2007; McDuffie et al., 2012). Promoting object interactions within a social context will enhance multisystem development of infants at-risk for developing ASD. The use of object-based interventions can advance social skills such as turn taking and shared attention with caregivers as well as non-verbal and verbal communication skills such as showing and pointing to objects and object labeling (McDuffie et al., 2012). Object-based interventions could be implemented as early as 3 months to improve specific motor skills such as grasping and reaching in TD infants as well as AU sibs (Needham et al., 2002; Lobo and Galloway, 2008). Libertus and Landa (2014) reported enhancements in grasping following two weeks of active training with sticky mittens to facilitate object exploration in infants at-risk for autism. However, the same study did not find strong correlations between improved grasping performance and social attention in infants at-risk for autism suggesting that there are significant social delays in this population which may need substantial training to impact social attention at a young age as well as in the future (Libertus and Landa, 2014). It would be important to further investigate caregiver-training approaches to effectively use triadic interactions between at-risk infants and their caregivers within object exploration contexts to facilitate social interactions. Such forms of socially embedded object play also termed joint attention interventions are often used in preschool-based early intervention settings for children with autism (Kasari et al., 2010). For example, during the second half of the first year, caregivers could consider offering periods of free exploration and problem solving, model appropriate functional actions on objects, as well as engage in object sharing and pretend play with their infants. Caregivers must carefully select multiple objects with varying affordances to model actions, including everyday tools for pretend play and toys that promote sharing and cooperative play. Overall, object play could be a useful tool for early identification and treatment of infants at-risk for ASD and must be incorporated within early identification and intervention scenarios.

Study Limitations

One of the limitations of our study was the slightly diverse at-risk group with the inclusion of two preterm twins. Preterm infants are a known population at-risk for ASD (Limperopoulos et al., 2008) and the two preterm infants included in our study received an ASD diagnosis after their second birthday. Another study limitation was the loss of data due to delayed recruitment, illnesses, and scheduling conflicts as is expected in longitudinal studies. However, the majority of the data were retained across all ages for both groups and did not appear to affect the overall group trends. The blocked presentation of objects may have influenced infants' exploratory behaviors; however, the object-based differences appear to be meaningful and specific to the affordances of objects. Lastly, we clearly need to replicate our study results using larger sample sizes.

Conclusion

The goal of the present study was to compare the early development of object exploration skills in infants at-risk for ASD and TD infants during the first 15 months of age along with follow-up at 18 and 24 months. While none of the TD infants developed delays or diagnoses in the future, several at-risk infants had multiple developmental delays or an ASD diagnosis. Our results indicate that at-risk infants demonstrated clear delays or abnormalities in object exploration such as early delays in grasping and mouthing, excessive visual exploration, reduced or delayed functional exploration of objects, and persistent mouthing later in life. Our study offers evidence to support the use of object exploration as a paradigm for early identification of perceptuo-motor delays and as an intervention context to promote motor, cognitive, and social communication skills in infants at-risk for developing autism.

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METHODS
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fNIRS: An Emergent Method to Document Functional Cortical Activity during Infant Movements

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The neural basis underlying the emergence of goal-directed actions in infants has been severely understudied, with minimal empirical evidence for hypotheses proposed. This was largely due to the technological constraints of traditional neuroimaging techniques. Recently, functional near-infrared spectroscopy (fNIRS) technology has emerged as a tool developmental scientists are finding useful to examine cortical activity, particularly in young children and infants due to its greater tolerance to movements than other neuroimaging techniques. fNIRS provides an opportunity to finally begin to examine the neural underpinnings as infants develop goal-directed actions. In this methodological paper, I will outline the utility, challenges, and outcomes of using fNIRS to measure the changes in cortical activity as infants reach for an object. I will describe the advantages and limitations of the technology, the setup I used to study primary motor cortex activity during infant reaching, and example steps in the analyses processes. I will present exemplar data to illustrate the feasibility of this technique to quantify changes in hemodynamic activity as infants move. The viability of this research method opens the door to expanding studies of the development of neural activity related to goal-directed actions in infants. I encourage others to share details of techniques used, as well, including analyticals, to help this neuroimaging technology grow as others, such as EEG and fMRI have.

Keywords: fNIRS, motor development, goal-directed actions, infant reaching, neuroimaging methods

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The depth and range of specific foci in this Research Topic section illustrate that the ontogeny of reaching has been an important area of research in both developmental movement science and psychology. However, the neural basis underlying an infant's production of goal-directed actions has yet to be determined. Scientists in motor development have been yearning for empirical evidence of infant brain activation patterns that support the kinematic and kinetic patterns of functional motor skills. Over the past two decades, functional near-infrared spectroscopy (fNIRS) has emerged as a neuroimaging technique that promises to enable studies of the brain activation patterns in infants. The goal of this paper is to elucidate the utility of fNIRS in the context of goal-directed infant reaching. The first section outlines the knowledge gap in our understanding of neuromotor development and the need to examine brain activation patterns in this field. The following section highlights traditional neuroimaging techniques and how they compare to fNIRS, followed by a brief history and the basic physics of the fNIRS technology. The next section focuses on the processing stream of data that shows the changes in hemodynamic activity of the primary motor cortex as infants reach for an object. Here, the challenges of the processing and analysis data are highlighted. The final section of this paper contains research questions for future studies that will help build broader empirical bases for understanding the central nervous system's (CNS) contributions to the emergence of goal-directed actions.

THE KNOWLEDGE GAP IN NEUROMOTOR DEVELOPMENT

How can the direct examination of brain activity during infants' reaching validate or challenge our theories about the emergence of functional motor skills? Theory and data suggest that multiple subsystems contribute to the emergence of first reaches (Thelen et al., 1993; Clearfield and Thelen, 2001). As infants gain sufficient muscle strength, eye-hand visual perception, and self-initiated practice moving their arms, reaching patterns manifest as babies attempt to make hand contact with objects. Further, each of these subsystems has its own developmental trajectory. For example, initially more muscles are activated than "needed," and infants co-activate muscles to reach for an object (Thelen et al., 1993, 1996). With practice, these movements become smoother and muscle activation patterns become more efficient (Thelen et al., 1993, 1996).

At the CNS level, the theory of neuronal group selection (Edelman, 1987; Sporns and Edelman, 1993) and dynamic neural field theory (Schöner et al., 1997) hypothesize that the brain becomes organized to contribute to the production of successful goal-directed task (Byrge et al., 2014). We do not know, however, how the brain areas associated with goal-directed actions evolve as infants are developing reaching patterns that lead to consistent, sequential, and efficient patterns. The investigation of this unexplored frontier would yield insight onto the ontogeny of brain activation patterns that parallel the development of both the novel skills and improvements in control over these behaviors. Ultimately, such findings are critical to provide foundational understanding and optimize development in those with motor deficits and delays.

Extensive research provides the basis for an adult model of the CNS activity during motor learning and the initiation and control of motor actions. Specific regions, such as the primary motor cortex (M1), prefrontal cortex (pFC), and cerebellum (Crbl) play complimentary and unique roles during different stages of learning (Doyon and Benali, 2005; Halsband and Lange, 2006). The M1 drives neural activations of muscles for voluntary limb movements, the pFC increases activity during the early phases of learning when there are high number of errors, and the Crbl, through feedback processing, adaptively controls the limb movement and trajectory. Adult brains, unlike infants', have years of experience and practice learning to perform new behaviors. Thus, it would be difficult to claim that tasks commonly used in adult brain-imaging studies are truly novel and not simply adaptive. However, we do not know if these same CNS areas play the same roles as infants learn to produce goal-directed actions. We have the technology to verify that infants visually engage with and explore attractive toys prior to reaching (Corbetta et al., 2012), but we do not have evidence of specific brain regions that are activated, or in what sequence they contribute to early and ultimately skilled and adaptive behavior.

COMPARISON OF TECHNIQUES

Traditional neuroimaging techniques such as functional magnetic resonance imaging (fMRI) and electroencephalography (EEG) have provided rich information regarding the specific functions and temporal processing of brain regions that underlie motor learning and control. The external validity of these studies can be limited by technical constraints. For example, studies of upper limb motor control in the fMRI scanning environment often involve button presses or reaches with limited degrees of freedom. This limitation is imposed both by the tight space of the scanning environment and the need to reduce noise resulting from head movement. Further, the requirement to lay supine during data acquisition may introduce differential cognitive demands or visuospatial relationships that would not be present in the normative environment. While many adults can cope with environmental and technical constraints the unfamiliarity and noise of the fMRI scanning environment can be unsettling for young children and infants who are required to stay awake and alert during data acquisition. Additionally, infants seldom remain still for extended periods of time and may not have developed the abilities to overcome increased cognitive demands associated with mirrored visual displays or altered visuospatial requirements.

While EEG removes some of the cognitive and visuospatial issues associated with laying supine, degrees of freedom are often still limited to avoid muscular artifacts, ocular artifacts and/or large-scale drifts in the data that result from electromagnetic noise. Strict thresholds for various artifacts result in discarded data during the analyses of infant samples (Stets et al., 2012) leading to the need for high number of trials. Advances in active electrode technology and data analyses have provided some promising results in adult behaviors, such as walking (Gwin et al., 2010) however, these techniques still need improvement (Kline et al., 2015). Set-up times of 1–2 h to prepare the required number of channels place unrealistic expectations on the tolerance of the infant even before any data has been collected. Moreover, the low tolerance to movements across populations in fMRI or EEG limits the type of motor skills that can be investigated. Such technological constraints have held back the field of neuromotor development from making significant progress acquiring the empirical data to confirm hypotheses regarding the neural basis of early motor skill acquisition. Interestingly, however, two studies (Bell and Fox, 1996; Corbetta et al., 2014) have measured EEG coherence, or change in synaptogenesis, and cortical reorganization as infants gained experience with a new motor skill (e.g., crawling or walking). Such studies demonstrate that efforts have been made using EEG to capture developmental changes of the CNS as infants acquire motor skills.

Recently, fNIRS has become a popular tool among developmental scientists to investigate the cortical activation patterns of young children and infants (Vanderwert and Nelson, 2014). fNIRS is a non-invasive neuroimaging technique, which makes it safe to use with infants and can be used repeatedly and for long periods of time. The fNIRS technology and setup allows for larger body movement compared to traditional techniques, making it a particularly effective neuroimaging tool in pediatric research. Furthermore, fNIRS offers improved temporal resolution compared to fMRI and spatial resolution compared to EEG. Moreover, the spatial resolution of fNIRS, although inferior to that of fMRI, affords the ability to localize patterns of activity to specific cortical regions. Such information is critical when investigating the rapidly developing brain of young infants and children.

As a result, the number of researchers using fNIRS to study behaviors and populations that were difficult or nearly impossible with traditional neuroimaging techniques (e.g., fMRI and EEG) have increased substantially (Boas et al., 2014) over the past two decades. Moreover, studies focused on young children and infants have shown the largest increase (Lloyd-Fox et al., 2010; Aslin et al., 2015; Wilcox and Biondi, 2015).

EMERGENCE OF fNIRS

fNIRS was first used as an assessment to monitor the adequate delivery of nutrition and oxygen of the brain in preterm infants receiving intensive care (Brazy et al., 1985). This technique then evolved into clinical studies using single-channel measurements. In 1993, Hoshi and colleagues successfully measured and described neural activity in different areas of the cortex by using five single-channel measurement points (Hoshi and Tamura, 1993). From then, the fNIRS technology developed rapidly and successfully employed multi-channel systems that have provided three-dimensional images (Ferrari and Quaresima, 2012). Specifically, over the past decade, the technique has flourished into a reliable and effective tool to quantify changes in cortical oxygenation in participants across the lifespan.

How Does fNIRS Work and What Does It Measure?

The generation and transmission of electrical activity in neurons is an energy intensive process. When a population of neurons is active, there is an increased metabolic demand. Initially, oxygen supply to the area of neuronal activity lags demand. As oxygen concentration decreases vasoactive agents trigger dilation of local arterioles to increase oxygen rich cerebral blood flow. The influx of oxygen rich blood exceeds oxygen demand such that the local concentration of oxygenated hemoglobin (HbO) increases. At the same time as HbO concentration increases, the local increase in blood flow results in a slight decrease in deoxygenated hemoglobin (HbR). This sequence of events is often portrayed in the form of the canonical hemodynamic response function (HRF, **Figure 1**). It is this relative difference in HbO and HbR that is quantified to infer changes in neural activity. Unlike fMRI in which concentrations are inferred based upon the different magnetic properties of HbO (diamagnetic) and HbR (paramagnetic), fNIRS takes advantage of differences in light absorption spectra between HbO and HbR.

With fNIRS, near-infrared light is directed via source optodes at the scalp, traveling through the scalp, skull, cerebrospinal fluid, and into the cortical tissue. Light that passes through the cortex is reflected back toward the scalp and is then collected by detector optodes (**Figure 2**, Villringer and Chance, 1997). Within the near infrared light window (650–1000 nm) of the electromagnetic spectrum, biological tissue is transparent. The light that enters the cortical tissue is predominantly absorbed by hemoglobin. fNIRS utilizes two different wavelengths, each to be sensitive to HbO and HbR. That is, the lower wavelength (650–700 nm), is predominantly absorbed by HbR, while the higher wavelength (800–850 nm) is predominantly absorbed by HbO. The use of two wavelengths allows the calculation of changes in total hemoglobin (HbT). Thus, fNIRS uses the changes in concentration of HbO and HbR as markers of blood flow in the brain to determine function of the area under investigation.

Overview and Setup of fNIRS

The near-infrared light is delivered via fiber optic cables that terminate into a specialized headgear. The optodes can be embedded into the headgear before it is placed on the participant's head, allowing for a much quicker and smoother process to precisely position the cap. This becomes particularly useful when working with infants because repositioning the headgear multiple times can increase the chances of the infant becoming fussy. Once the headgear is in position the fiber optic cables are often bundled or tied into a position that does not interfere with or touch the participant. It is worth mentioning that movement of the fiber optic cables does not introduce artifacts or drifts in the data, which often troubles EEG/ERP studies with young children and infants. Thus, participants can move their head without the introduction of artifacts in the data. This element is particularly useful when measuring infant brain responses, as participants at this age rarely stay still. Energetic and sudden head movements can cause the optodes to move and lose contact with the scalp, leading to artifacts in the data.

The fNIRS technology and setup have limitations as well. The amount and quality of near-infrared light that passes through into the cortex can be affected by large amounts of hair or dark-colored hair that come between the optodes and the scalp. This often leads researchers to devise tightly-fitting caps to ensure the tip of the optodes are as close as possible to the scalp. Alternatively, the hair can be combed away to provide a clear path for the light to pass through the scalp. This issue is a smaller concern with infants as they have not fully developed high volumes of hair.

The use of light and the setup in fNIRS makes it a well-suited tool to investigate the brain activation patterns of infants. fNIRS tolerates perhaps the largest degrees of movement across any neuroimaging technique which invites developmental movement researchers to examine the underlying neural bases of emerging goal-directed actions. To date, however, most studies that use fNIRS with infants and young children investigate visual object processing (Wilcox et al., 2012, 2014) and auditory processing (Gervain et al., 2008; Nakano et al., 2009). There are a few studies that used fNIRS to investigate the motor system as infants observed others performing an action (Lloyd-Fox et al.,

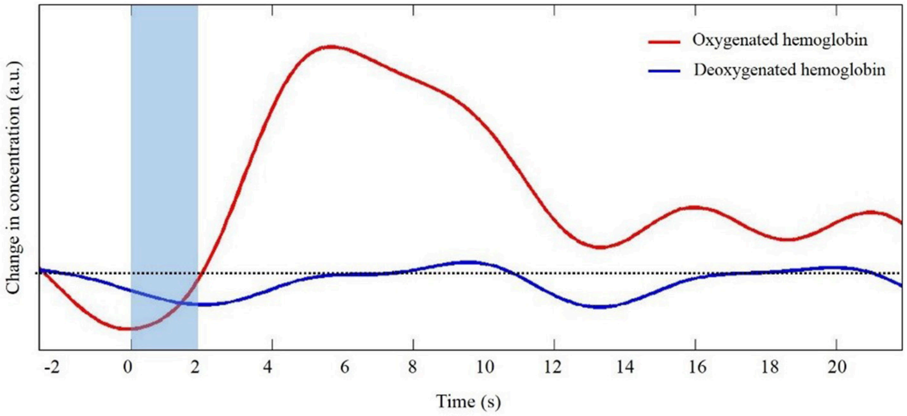

FIGURE 1 | Representative trace of the canonical hemodynamic response function (HRF). Shaded region indicates the time of task. Dotted line indicates zero changes in concentration (i.e., baseline values).

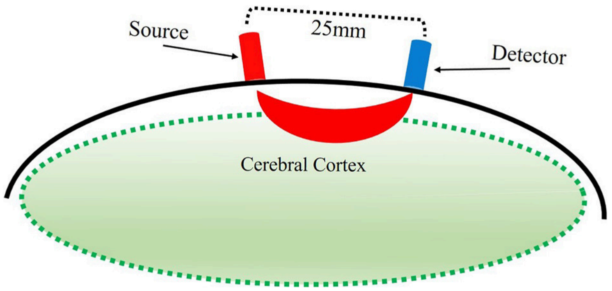

FIGURE 2 | Illustration of estimated path of near-infrared light between source and detector optodes.


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FIGURE 3 | Picture of lab setup. Curtain in front of monitor is closed during presentation of toy and reopens after infant reaches for toy during rest phase.

2013; Southgate et al., 2014). These studies demonstrate the presence of some form of ability to understand the actions of others. However, these studies do not examine emergent brain activity associated with the inherent control of their own actions requiring online evaluation of sensory feedback and updating of motor plans. Thus, we do not fully understand how the underlying brain activation patterns emerge as infants acquire new functional motor skills. In the next section, the study I will introduce builds on the rich behavioral findings about the ontogeny of reaching and is grounded in strong theoretical framework.

fNIRS IN THE CONTEXT OF GOAL-DIRECTED REACHING

Lab Setup

This section presents methodology and unpublished data from a study in the lab, where we measured changes in M1 activity as infants reached for a toy (Nishiyori et al., in press). Briefly, infants were secured in a traditional testing seat used to study infant reaching, with a soft chest wrap to provide security and reduce trunk movement. The seat was on a table so the infant was near the researchers' eye-level (**Figure 3**). We positioned the headgear, with the optodes already embedded, so that the center of our probe array was directly over the center of the infant's head (Cz, International 10–20 system). The cables extended upward over the infant's head and were held by a research assistant. We positioned a monitor in front of infants who watched calming videos before and after each test trial for no less than 20 s, which allowed us to collect rest-phase values. The experimenter introduced toys within arm reach at midline, and helped keep the infant calm in between test trials.

Probe Array

We used four source and six detector optodes, ∼25 mm apart, creating 12 channels that covered the bilateral motor cortex (**Figure 4A**). Each optode terminated into a grommet, a plastic button-like piece that was secured into our headgear (**Figures 4B,C**). We created our array this way so we could detect hemispheric differences in activity in addition to any bilateral activity. The current adult-based model suggests that contralateral M1 activity drives unilateral limb movements, while bilateral M1 activity drives bilateral limb movements (Nishiyori et al., 2016). Our main question focused on the developmental changes of M1 activity as infants developed functional motor

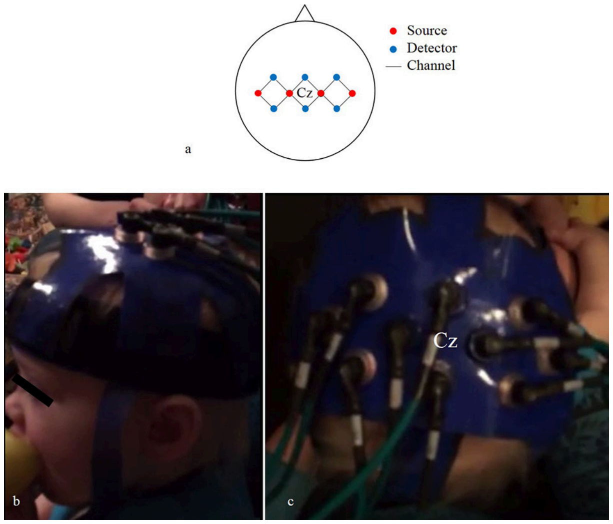

FIGURE 4 | Probe array (A) of channels (black lines) that connect sources (red circles) and detectors (blue circles). Lateral **(B)** and superior **(C)** views of the headgear on an infant's head.

skills. Thus, we wanted to be able to detect patterns of change within the M1 between distinct levels of skill. After several pilot sessions, we decided that 10 optodes (four sources and six detectors) provided the best spatial resolution while bearing the least weight on the infant's head.

Pre-Processing

The data pre-processing stream begins by removing physiological noise (e.g., heart pulsations), slow drifts, and motion artifacts from the optical signal. Low-pass and high-pass filtering are common methods to remove both the physiological noise and slow drifts, respectively. Motion artifacts, on the other hand, are sudden and intense changes in signal and can be removed or corrected using different algorithms. Additionally, we used a digital video recorder to identify different types of behavior offline and during the pre-processing stream.

We synchronized our video data with our fNIRS data. This enabled us to identify the time of onset of each reach and to determine the amount of movement of uninvolved body segments (e.g., head and legs). There were two types of movements that we were concerned about. The first type was arm and leg movements during the rest phase that could affect our measures. We could then identify and eliminate segments in our fNIRS data that could be affected by these type of movements. The second type are head movements that directly jitter or affect the contact between the tip of the optode and the scalp (**Figure 5**). When an optode moves and the path of the light is interrupted or redirected momentarily, spikes in the data can be observed. Following a spike, the system may take a few seconds to stabilize. Spikes have high frequencies which are unlike that of biological signals such as hemodynamic responses, and can be easily identified and eliminated in the time series. We were particularly cautious regarding head movements, especially when it was within 2–3 s from the time of onset of reach. The large spikes caused by head movements could influence the amount and intensity of the NIRS measurements. After the noises are removed, the optical signal is converted into concentrations of HbO and HbR using the modified Beer-Lambert Law (Cope et al., 1988).

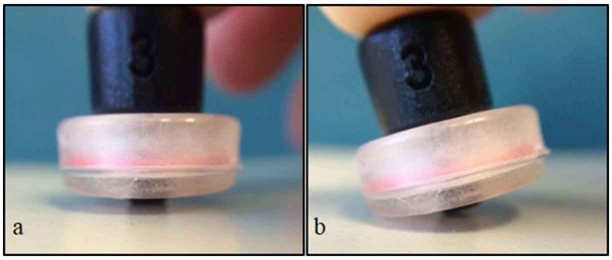

FIGURE 5 | Simulation of optode position and contact with surface. Full contact of optode perpendicular to surface **(A)**, and tilt or "jittered" optode caused by movement **(B)**.

We visually examined the time series to accurately determine the changes in concentration of both HbO and HbR in the M1 as infants reached for a toy while eliminating any data contaminated by significant motion artifacts. **Figures 6**, **7** display portions of the time series from a single channel extracted from the dataset. Each time series represents changes in concentration of HbO and HbR from a single channel. **Figure 6A** displays a section of the time series that is very clean and in which the expected increase in HbO is easy to identify and clearly timed with the onset of the reach movement. **Figure 6B** displays a slightly messy time series for a similar reach. The changes in concentration are timed with the onset of the reach, but during the rest-phase, some similar scale increases can be seen. In addition, the increase in HbO also contains small spikes that are caused by extraneous body segment movement, verified through our synchronized video data. This type and frequency of motion-artifacts were the most commonly observed in our dataset (Nishiyori et al., in press). Finally, **Figure 6C** displays a time series for another reach clearly observed in the video but for which the data would not be considered for further analyses, because most of the time series is contaminated with artifacts caused by jerky head movements. The goal at this stage in pre-processing the data is to eliminate noise, any spontaneous fluctuations, and brain activity that is not tied to the task. The next step is to clean up the data by using, if necessary, motion-correction algorithms to retain trials that may contain a reasonable amount of motion-related artifacts.

The primary goal of motion-correction is to retain as many trials that would otherwise be rejected when it contains motion artifacts. Several approaches have been proposed to assist the filtering process. For example, Virtanen et al. (2011) used an accelerometer to quantify the magnitude of movements to correct for motion artifacts in the fNIRS data. However, additional equipment on an infant's head is not ideal, especially when they already are wearing a cap. Alternatively, most researchers have relied on the changes in the amplitude of the data that is unique to motion-artifacts. This approach can be applied at the post-processing stage by filtering out the motion artifacts.

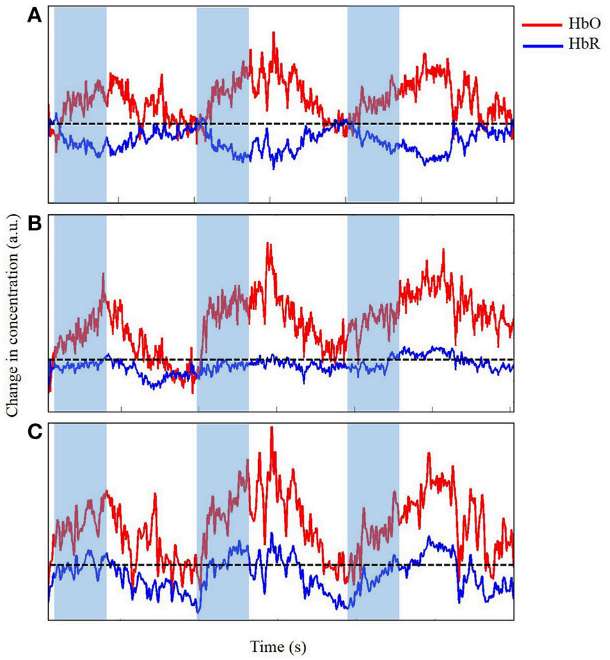

FIGURE 6 | Time series of change in concentration of Hbo and HbR, unfiltered (A), acceptable (B), and unacceptable (C) data in arbitrary units (a.u.). Shaded region indicates time during reach. Dotted line indicates zero changes in concentration.

Brigadoi et al. (2014) compared five different algorithms, freely-available, to real functional fNIRS data to correct for motion artifacts. They concluded that correction for artifacts with any of the algorithms retained more trials than simply rejecting trials that contained motion artifacts. Furthermore, the researchers suggested that among the five algorithms they tested, the wavelet filtering (Molavi and Dumont, 2012) retained the most number of trials, making it the most promising technique to correct for motion artifacts (Brigadoi et al., 2014).

In our study, we applied wavelet filtering to best correct our motion-related artifacts. **Figure 7** displays the slight improvements of the time series from **Figure 6**. The time series displayed in **Figure 7A** shows minimal improvements from **Figure 6A** because the time series was already clean with minimal artifacts. **Figure 7B** displays a modest improvement from the slightly messy time series of **Figure 6B**. The wavelet-filtering proves to be the most effective and useful in this type of time series. Finally, in **Figure 7C**, the times series has generously improved from **Figure 6C**. In this case, the motion-correction algorithm is "over-correcting" noise or artifacts in what may be observed as task-related changes in brain oxygenation, and was not considered for further analyses. Particularly for our study, we wanted to distinguish between desired movements (e.g., reaching for the toy) and undesired movements of the leg, trunk, and/or head. Infants reached for a toy, which at times, made them move their bodies and lower limbs. In addition, infants often moved their heads by looking in different directions, which was most likely related to the artifacts we saw in our fNIRS data. Unrelated to the task, fussy infants would move their heads energetically, which introduced the largest artifacts to the data. Thus, during our study, keeping infants content and engaged by funneling their attention to the videos or our research assistants was a crucial step to minimize the number of movement-related artifacts. When infants became fussy briefly, we ran additional trials once the infants calmed down and were relatively content. Sometimes, when infants were looking around the room too often, we extended the rest-phase to ensure a minimum of 30 s in which the infants moved minimally and were relatively calm. These approaches were the product of several pilot sessions that proved to be the most effective while collecting the necessary measures.

Time series similar to that of **Figures 7A,B** were considered for further analysis. The time series were then epoched, consisting of 3 s prior to and 10 s post-onset of reach. Epochs were then average for each channel and baseline corrected to the pre-movement period (rest). We then compared the changes in HbO and HbR between the two phases, rest and task, to determine significant task-related activity. The location and number of channels, among the 12, that detected task-related activity determined the area or distribution of motor cortex activity during reaching.

Together, with well-designed and piloted equipment set up and motion-correction algorithms, most of the trials from the sessions can be retained. Such movements, both task-related and extraneous, would not be tolerated in most other neuroimaging techniques, but we are able to demonstrate that the fNIRS data is certainly usable and can generate important findings. There are additional challenges that users must be aware of and, we trust will reduce and be eliminated as the technology and software continue to evolve. In the next section, I will touch on a few of these challenges.

CHALLENGES

"Rest-Phase"

A unique challenge to neuroimaging studies that investigate neuromotor behaviors in infants relates to the need to compare tasks or conditions in order to identify brain activity specifically associated with the test task. Most neuroimaging studies in other domains with infants utilize a large number of trials to calculate the average hemodynamic response for a specific task. For goal-directed actions, however, it is difficult to obtain a high number of trials because infants often do not tolerate repeating the same movement or goal as they express their boredom by failing to attend to the test task. As a result, researchers must determine the number of trials infants will tolerate while also achieving the necessary power to test for significance in task-related change in brain activity. Similarly, the rest phase that precedes the task must also be carefully controlled in order to have a meaningful (usable) trial.

The goal of the rest phase in neuroimaging studies is to allow brain activity to return to baseline or near-baseline. The values measured during the rest phase are often compared with values during the task phase to detect any significant brain activity above baseline. In this setup, the rest phase is important to control in order to detect the task-related changes in brain activity.

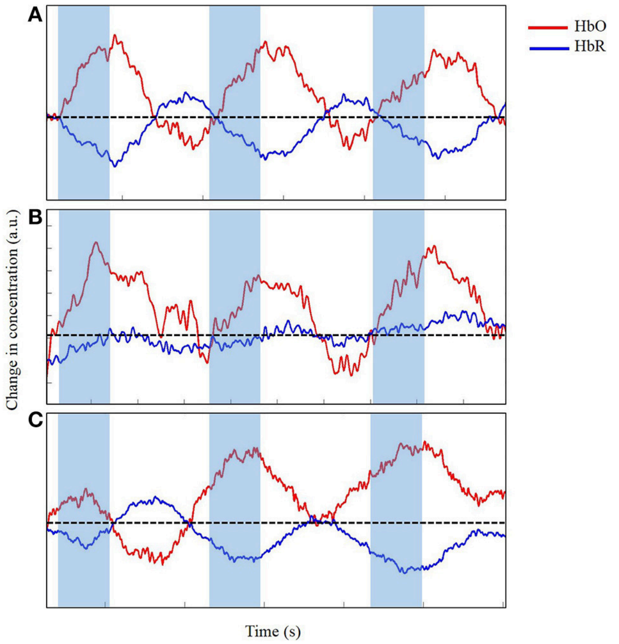

FIGURE 7 | Time series of change in concentration of HbO and HbR, after wavelet-filtering, optimal (A), acceptable (B) and unacceptable (C) data in arbitrary units (a.u.). Shaded region indicates time during reach. Dotted line indicates zero changes in concentration.

When rest-phase values contain artifacts or are higher than the task-phase values due to uncontrollable infant behaviors, the comparisons would not allow detection of significant task-related activity. Specifically in our study (Nishiyori et al., in press), we needed infants to be alert while minimally moving any limbs to reduce M1 activity during the rest phase. Our rest-phases consisted of infants watching videos that would keep them alert and minimally engaged. We chose videos that were calming and did not provoke energetic movements.

An alternative approach is to use a control stimulus or task. In this approach, the goal is similar to the static rest-phase, but the values measured during the control task can be used to provide a contrast in brain activity between the experimental task and the control task. Moreover, the control task must be known or hypothesized, a priori, to elicit less brain activity than what is expected of the target brain region during the experimental task. Most often in studies focused on cognitive development, these control tasks are small deviations from the experimental task to target the unique feature inherent to the study or research question (e.g., biological vs. non-biological movement of objects). The challenge becomes finding the best control task for goal-directed actions. For example, the experimenter could present a toy sufficiently out of reach that the infant would only be able to visually explore and not attempt to reach for it. The data acquired during these trials would examine brain activity associated with the observation of the toy and/or the planning of the reaching movement, which should generate additional brain activity. Future users should carefully consider the design of the control task or the use of a static rest-phase to ensure the maximum retention of trials. Ultimately, the control task needs to serve as a comparison/contrast to delineate brain activity associated with the goal-directed action.

An emerging approach that eliminates the need, analytically, for a rest phase involves the examination of differences between HbO and HbR concentrations. This approach, known as correlation based signal improvement (CBSI), is a tool to improve signal quality and delineate functional neural activation. Cui et al. (2010) have suggested using the negative correlation between HbO and HbR to classify the degree of functional neural activation.

The negative correlation is simplistic in design, does not require baseline correction, and is blind to the experimental design, which could improve the signal quality (Cui et al., 2010). CBSI would be able to detect significant activity without the bias of a rest-phase or a control task and has been demonstrated to be effective in functional data with children (Buss et al., 2014) as a method to classify a robust task-related neural response in the underlying cortical regions. CBSI relies on the basic assumption of the canonical hemodynamic response function, in which there is an increase in HbO concentration coupled with a slight decrease in HbR concentration. The correlation, however, may not be as reliable when HbO and/or HbR concentrations asymptote to or overshoot the baseline (Cui et al., 2010).

Headgear

As most users of the fNIRS technology would agree, the headgear is one of the most essential and crucial pieces of the technology used to acquire a quality set of data. Select fNIRS systems, such as Hitach's ETG-4000 and earlier models, have headgears with pre-determined configurations with set distances (3 cm for adults, 2–2.7 cm for neonates and infants) between source and detector optodes. Other fNIRS systems, such TechEn's CW6 and earlier models, come with free-hanging bundled fiber optic cables. Thus, users can construct the configuration of the optodes. This configuration can be designed, first, by using freely-available software (e.g., SDgui of the AtlasViewer package, Aasted et al., 2015) to precisely map out the positions of each source and detector and how they are interconnected (see Aasted et al., 2015). This enables the user to configure the array into specific shapes with selected distances between sources and detectors depending on the region of interest (ROI) and target population (see Wijeakumar et al., 2015). Furthermore, researchers are establishing methods to digitally register the NIRS probes on an infant MRI template (Lloyd-Fox et al., 2014; Aasted et al., 2015; Emberson et al., 2015). Ultimately, this will allow users to simulate their probe array superimposed on the cortical template to determine if probes cover the intended region(s) of the brain. Next, users must re-create the configuration onto the headgear.

The selection of the headgear's material should be guided by what the target population can tolerate. In most adult studies, headgear is often tight or snug to ensure the tip of the optodes are as close as possible to the scalp. Although this would maximize the likelihood of acquiring data with the fewest motion artifacts, for young children and infants, however, this is often not well tolerated. Thus, users need to choose materials that are infant-friendly but firm enough to hold the optodes in their respective positions. Additionally, the headgear should be easy to fit onto an infant's head to quickly and accurately position it over the ROI, but then be adjustable to assure a snug fit without slippage of optodes away from the intended position.

We found that more traditional fabric or spandex-type caps were too stressful for infants to have put on them and remain on. We also found that using a traditional cap, like a beanie, often left the top, near the vertex, with excess space or creases, which were not desirable for our ROI in the previously mentioned study. The cap, however, may be feasible for measuring other areas such as the frontal and temporal regions. Thus, we used a thin layer of Dycem, a non-slip rubber-like material often used in physical therapy sessions to enhance grip. This material can conform to the different shapes of heads, easy to cut, and rigid enough to hold the grommets. We constructed a two-piece headgear made of Dycem that consisted of a headband and a panel embedded with grommet-pieces for the optodes. The headband had Velcro on the outside and the panel had legs with Velcro pieces on the inside. This allowed us to secure the position of the panel by latching the legs onto the headband. Our headgear proved to be effective, primarily because we only measured motor cortex activity. Studies that investigate multiple areas, especially if the areas are not next to each other, will require several pieces that are connected together.

The goal of the headgear is to secure the optodes in the desired position on the head and to keep the near-infrared light directed at the scalp. Ultimately, the security of optodes will determine how much motion can be tolerated before artifacts are introduced. As a result, users should invest a substantial amount of time designing, constructing, and piloting the headgear.

The two challenges I have outlined here are those that our group has particularly grappled with at the beginning of our study, but also are critical pieces to any new study using the fNIRS technology. There is a community of researchers working together to share the progress in using and processing data, and novel methods. This information is collectively shared at annual workshops and biennial conferences (The Society for Functional Near-Infrared Spectroscopy., 2015). New users can access free resources, such as Homer2 (Huppert et al., 2009) the Matlab based package to preprocess fNIRS data and other tools on the Neuroimaging Informatics Tools and Resources Clearinghouse (NITRC) website as a helpful guide to understand and effectively incorporate fNIRS to answer their research questions.

FUTURE APPLICATIONS

To the best of our knowledge, we are one of the first groups to explore and examine motor cortex activity in infants as they performed goal-directed actions. The aim was to begin to construct a body of empirical evidence by directly investigating the development of brain activity during functional movements in order to better understand the emergence of and improvement in control of functional motor skills. We began this journey to dig deeper in our understanding of how skills emerge from basic science and theoretical perspective and to provide foundational knowledge that will have clinical applications to optimize development in those with disabilities. To build on this base, we encourage future research to focus on quantifying activity of multiple regions of the brain, sequential activity among regions, longitudinal designs, and assessing the effects of interventions.

Multiple Regions/Sequential Activity

Goal-directed actions involve volition, planning, and execution, including adapting and correcting, during the movement. For each of these contributions to the behavioral outcome, there are respective brain region(s) involved, each of which develops as the skill emerges over time (Twardosz, 2012; Byrge et al., 2014). Moreover, the amount each region contributes to the action may also fluctuate depending on the level of skill as well as other subsystems that are developing (e.g., executive functions). Future research is needed to determine the changes in neural contributions of different brain regions that underlie goal-directed actions. In addition, the sequence in which each brain region activates leading up to the onset of reach would reveal the unique pattern of activity during early neuromotor control. Such investigations would explore the variability in the way the neural contributions emerge and change across individuals. While the order and contribution of multiple cortical areas in well-practiced skills performed by adults are established, the variability observe during early development, both behaviorally and in the neural data to date, makes a strong case for the theoretical concept, at least in early life, that motor behaviors are softly assembled in response to the demands of the task.

Elicited vs. Voluntary—Effects of Practice on Elicited vs. Self-Initiated Movement

Goal-directed actions are voluntary, but there are many behaviors that can be elicited from an infant. For example, stepping while supported on a treadmill is an elicited behavior that allows researchers to understand behaviors infants can produce without practice (Thelen and Ulrich, 1991). These elicited patterns demonstrate the plasticity and adaptability of the control systems for movement, early in life. Moreover, we know that the CNS in infants undergo significant changes and organization as infants explore and practice ways to control their movements. We do not know, however, which areas or how much each area of the brain changes as the control of movement improves or when or why, from a neural perspective, infants are able to perform elicited patterns such as supported treadmill stepping.

By creating a context in which infants are engaged to practice elicited behaviors, we may help them induce changes at the neural level. These may be distinct from those generated by self-initiated movements. For example, many researchers have constructed unique and clever experiments to address how infants' actions are influenced by their prior experiences. Specifically, Needham and colleagues provided infants ∼1 month prior to the onset of reaching, with "sticky mittens" to simulate prehension. The enriched experience showed that infants who gained early experience increased their object engagement and demonstrated more sophisticated object exploration strategies compared to infants with no experience.

Until recently, it was thought that the adhesiveness of the sticky mittens simulated successful grasps, and through repeated experience, goal-directed behaviors were formed (Needham et al., 2002). Williams et al. (2015), however, showed that repeated task exposure with active, reaching-specific experience enhanced formation of goal-directed behaviors compared to grasping simulation through sticky mittens. The later study showed that the task-specific exposure and practice improved goal-directed behaviors more than the simulation of successful reach-and-grasp by sticky-mittens. Comparison of brain organization between task-specific and simulated movements would provide insight to the plasticity of our CNS and how the type or specificity of experience can influence the functional behavior. fNIRS would be a useful tool to shed light on the emerging brain activation patterns as a function of the specific types of experiences.

Longitudinal Designs

To date, most studies investigating brain activity with young children and infants are cross-sectional. In order to understand the organization and reorganization of brain activity, and individual differences in development trajectories, longitudinal designs are necessary. Such designs would provide a better understanding of the reciprocal influences between changes in brain organization and behavioral changes and skill acquisition and control. For example, future researchers can investigate changes in brain activity in the months leading up to and/or months following the onset of successful reaches to determine the changes of motor areas as new functional motor skills emerge.

Role of the Cerebellum

Studies using fNIRS have only been able to successfully quantify cerebral cortex activity; subcortical regions are out of range for the near-infrared light to detect changes in activity because light can only travel a few centimeters through the skull and into the brain tissues (Gervain et al., 2011; Quaresima et al., 2012). The cerebellum (Crbl) is a unique brain structure that is not as deep as subcortical structures such as the amygdala or hippocampus, but in adults the shape of the skull and the cerebellum's position relative to surrounding tissues and neck muscles obstruct the near-infrared light from reaching it for precise measurements. In infants, because the skull's shape is still more rounded and tissues surrounding the cerebellum are much thinner, there is strong reason to believe that the fNIRS technology can be positioned correctly to detect and quantify Crbl activity.

The cerebellum is known for its role in adaptive control and online error correction of targeted movements in adults (Buckner, 2013; Koziol et al., 2014). In infants, the contribution of the cerebellum to motor behavior has been explored minimally. Most hypotheses stem from either theoretical frameworks or data regarding structure and neurophysiology of the cerebellum. In adults, fMRI data show that the cerebellum plays a critical role during the early stages of learning a new skill (Doyon et al., 2002; Halsband and Lange, 2006). Skills that have been tested using fMRI technology, however, are generally deviations or modifications of already well-learned and practiced skills (e.g., finger sequence learning or visual-motor adaptation of manipulandum movement). In other words, the cerebellum needs only to correct or adapt an already-learned motor action. In infants, reaching for a toy is a nascent skill. Infants have been working toward achieving this goal through repeated general movements of the arms often in the direction toward a desired toy, but the "skill" is not yet stable nor functional.

The theory of neuronal group selection (TNGS) proposed by Gerald Edelman suggests that the cerebellum receives sensory inputs and enhances/reinforces successful actions (i.e., the outcome, such as the contact with or grasp of an object) initiated by the motor cortex (Sporns and Edelman, 1993). During development, as infants repeat cycles of acting and perceiving the consequences and persistently try to solve the problem of controlling their limbs, cerebellar activity is hypothesized to be high. The increased activity is later reduced as the accuracy in movement (e.g., arms toward object) improves (Sporns and Edelman, 1993). This hypothesis, is derived from neuroembryology and postnatal neural development data and has been supported via models tested with computer simulations (e.g., Darwin III); it has been further supported via neural monitoring during reaching by monkeys (Georgopoulos et al., 1981), but has yet to be tested directly by measuring cortical activity of human infants. With the emergence of fNIRS, we can measure cerebellar activity during motor learning and test the compatibility between traditional adult studies and infant data to begin to construct an evidence based model of the development of neuromotor control.

CONCLUSION

In summary, I have outlined the utility of the fNIRS technology in the context of goal-directed actions. The technology has advantages and limitations; however, it possesses great potential to move the field of neuromotor development forward. fNIRS opens the door to the investigation of brain activity as infants perform motor skills in less-constricted and naturalistic environments. This type of investigation enables researchers to understand the real-time brain activity and its changes over time, as infants improve the control of motor skills. As we continue to identify more clever ways to investigate the development of goal-directed actions, we can expand our knowledge of the brain-behavior link and how it evolves by using the fNIRS technology in future studies. Future users can utilize the information provided here to devise and improve designs to investigate the neural underpinnings of goal-directed actions in infants. Over time, new findings will emerge and we can successfully build the body of empirical evidence that delineates the developmental model, and not infer from the adult-based models of neuromotor control and learning.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and approved it for publication.

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Not Just Being Lifted: Infants are Sensitive to Delay During a Pick-Up Routine

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In the present study we observed whether infants show online adjustments to the mother's incipient action by looking at their sensitivity to changes as the pick-up unfolded. Twenty-three 3-month-old infants and their mothers were observed in the lab, where mothers were instructed (1) to pick-up their infants as they usually did (normal pick-up), and then (2) to delay the pick-up for 6 s after placing their hands on the infants' waist (delayed pick-up). In both Normal and Delayed conditions infant's body tension, affective displays and gaze shifts were coded during three phases: Approach, Contact, and Lift. Additionally, a measure of infants' head support in terms of head lag at the beginning and end of Lift was computed. Results showed that during normal pick-up infants tensed up their body during the Approach phase and increased their tension during contact, maintaining it through Lift; their head was also supported and in line with their body during Lift. When the pick-up was delayed, infants also tensed their body during Approach, yet this tension did not increase during the Contact phase and was significantly lower at Lift. Their head support was also lower in the Delayed condition and they shifted their gazes away from their mothers' face more often than in the Normal condition. These results suggest that infants are sensitive to changes of the timing of the pick-up sequence, which in turn may have affected their contribution to the interaction.

Keywords: pick-up, early routines, body tension, violations, cooperation, action understanding

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INTRODUCTION

From their very 1st days of life, infants are involved in sequential and repeated activities or routines, such as having a diaper changed (Nomikou and Rohlfing, 2011), being fed (Kochukhova and Gredebäck, 2010), playing social games (Ratner and Bruner, 1978; Bruner and Sherwood, 1983; Fantasia et al., 2014b), or being picked up (Service, 1984; Lamb and Malkin, 1986; Reddy et al., 2013). Because of their predictability, these routines support infants' ability to understand and take part in others' goal-directed actions, for instance by learning to anticipate the caregivers' behavior (Gredebäck and Melinder, 2010) and respond to affective and interactive temporal contingencies (Gratier, 2003; Hilbrink et al., 2015). The goal of the present study was to examine infants' contribution to the caregiver's pick-up behaviors by studying their sensitivity to changes in the pick-up timing.

Routines as Contexts of Co-Operation

Being involved in and directly addressed as recipients of others' actions is a crucial experience for infants in the 1st year of life (Reddy and Uithol, 2015). Unlike the free and spontaneous interactions caregivers may engage in with infants, routines are usually organized around a structured activity (Fantasia et al., 2014b). Routines provide infants with early opportunities to take part in a shared activity, and also allow them to become gradually more coordinated and collaborative with others. Previous research suggests that being involved in joint activities is critical for children's development of memory (Sommerville and Hammond, 2007), planning and problem-solving skills (Radziszewska and Rogoff, 1988), and also more mature cooperative abilities (e.g., Brownell and Carriger, 1990; Ashley and Tomasello, 1998; Warneken et al., 2006, 2012).

However, being involved and participating in routine joint activities are two different aspects of interacting. For example, Henderson et al. (2013) have suggested that 10-month-olds understand collaborative goals of a shared activity only after having actively experienced that activity. Participating requires that a person assumes a more active role in an interaction. Do infants participate – in the sense of collaboratively engage – in shared routines? Research examining the development of collaboration and cooperative behaviors has primarily focused on children from 1 year of age, while evidence from developmental studies on infants' early participation in joint, cooperative activities is scarce and controversial. Hubley and Trevarthen (1979, p. 58) were the first to define early mother–infant interactions as cooperative, in a way that "each of the subjects is taking account of the other's interests and objectives in some relation to the extrapersonal context, and is acting to complement the other's response". They presented evidence of early cooperative understanding during early communicative interactions between young infants and their mothers, by showing that from 8 to 12 month infants increased their ability to integrate expressions of interpersonal communication with cooperative praxic acts (Hubley and Trevarthen, 1979). On the other hand, Keitel et al. (2014) cautiously proposed that infant perception of joint actions develops starting at 9 month and differs from their perception of individual actions; in other words, before 9 month they are not expected to cooperate.

One way to address the controversy about the development of shared intentionality and joint action (see Tollefsen and Dale, 2012, for a review) is to investigate infants' contribution to the building up of a shared activity with others, by observing how they complement others' actions with movements. That is, looking at infants' motor behaviors during routines may shed light on infants' awareness of others' situated and goal-directed actions. As Smitsman and Corbetta (2010) have suggested, studying action development is fundamental to understanding how and what infants learn about their environment. Action anticipation (or prediction), for instance, has been extensively studied in the last two decades as a measure of infants' developing understanding of the goals and intentions of others' actions (Gredebäck and Melinder, 2010; Kanakogi and Itakura, 2010; see Hunnius and Bekkering, 2014, for a review). Moreover, Reddy et al. (2013) have suggested that infants' anticipatory motor adjustments to being picked up may reveal their ability to understand and adjust to the incipient action by the mother in a participatory way. However, anticipating the other's action in order to facilitate the onset of an activity is only part of the story. Supporting and dynamically coordinating with the other while the action unfolds also seems a crucial contribution for the action success.

Another way to explore whether infants have an understanding of a shared, familiar activity is to look at changes in infants' responses to unexpected behaviors by the adult (e.g., infant's reaction to maternal breach in engagement, or withdrawal from an ongoing interaction). Experimental paradigms based on such violations have been successfully used to investigate infants' expectations in a range of different domains from very early on (Murray and Trevarthen, 1986; Baillargeon, 1994; Nadel et al., 1999). For example, previous research has shown that infants tend to look longer at their partner or shift their gaze frequently in response to unexpected behaviors (Phillips et al., 1992; Bertin and Striano, 2006). Looking at changes in infants' behavior during a modified version of a routine activity may thus reveal infants' expectations about or understanding of how that very activity should be performed, and consequently, tell us something about infant awareness of others' intentions-in-action.

In the present study both these aspects – examining motor behaviors as means of complementing the other's action, and observing behavioral changes in response to violations of a routine – have been used to look at infants' contribution to being picked up.

Being Picked Up

Previous research has shown that 4- to 5-month-old infants have expectations to be picked up when crying after waking up, showing signs of distress if the adult fails to do so (Lamb and Malkin, 1986). At around 6 to 7 months of age infants request to be picked up by lifting their arms up in response to mothers' approach (Lock, 1984), although this response is strongly affected by the mother's style of picking up and communication with the infant (Service, 1984). Recent evidence showed that being picked up also seems to involve a fair amount of postural and kinematic coordination by the infant. Reddy et al. (2013) found that when the caregivers' approach was clear and visible, even 2-month-old infants made appropriate anticipatory adjustments to the mother's pick-up action. Specifically, the authors found that infants increased the rigidity of their bodies, while general thrashing was reduced, and moved their extremities to create space for the mother to hold them comfortably, by widening or raising their arms. Interestingly, the authors also noticed a rotation of the head when infants were just about to be lifted, which may have served to increase stiffening in the neck muscles, thus reducing the lag of the head during the lift. This finding is in line with current literature on motor development showing that head control, already present around 3 months of age, is critical for a range of early behaviors, including those related to postural stability, motility and vision. In turn, this may support the argument about infants' gradual involvement in social exchanges (for a review see Adolph et al., 2009).

The Present Study

In light of these findings, in the present study we observed 3-month-old infants' contribution to their mother's movements over the entire duration of a pick-up episode when this was performed at a usual pace and with a delay before the lift. Reddy et al.'s (2013) study showed that at 2 months all anticipatory adjustments to approaching pick-up were in place, but the process was not yet as fluent as at 3 months. From 4 months infants began to be interested in the mother's hands, which sometimes served to distract the infant from the pick-up itself; this distraction became very pronounced at 5 months and later. Thus, 3 months was the ideal age for studying infant responses to delays during a pick-up episode.

We chose to frame infants' contribution in terms of their motor behavior, following preliminary observations of changes in their movements and limbs tension during a pilot study. A measure of Body Tension was thus created, and we hypothesized that this tension would increase over the course of a normal pick-up episode to reach its peak during lift. In contrast, we expected that infants' Body Tension will decrease when the pick-up is delayed.

Following the observations by Reddy et al. (2013) on infants' neck adjustment just before being lifted, we measured infants' head sustain (i.e., Head Lag) as an additional measure of being prepared (or unprepared) to being lifted. If in a normal pick-up episode infants would keep their head in line with their body to sustain the mother's lifting action, we hypothesized that a delay in the pick-up sequence would then leave infants unprepared to being lifted, showing a floppy head and thus a larger Head Leg.

Since our design involved a delay or violation from the usual experience infants have of the pick-up sequence, we also added two measures that have been extensively used in previous research on violation of expectations in infancy, namely shifts in gaze (Phillips et al., 1992) and affect displays (Legerstee and Markova, 2007).

MATERIALS AND METHODS

Participants

Twenty-three 3-month-old infants (10 girls, $M_{\text{age}} = 96.04$ days, $SD = 3.92$ days) participated in the study. All infants were healthy at birth, Caucasian, and from lower to middle class families, as determined by parental reports on years of education. Maternal age at time of birth ranged from 26 to 37 years ($M_{\text{age}} = 31$ years, $SD = 3.17$ years). Volunteer parents were recruited through family centers, nurseries, and pre/antenatal classes in town. Ethical approval was obtained from the University Ethics Committee (University of Portsmouth) and informed consent was obtained from parents. Two dyads were excluded from the original sample of 25 infants due to the infants' fussiness and lack of interest during the observations.

Materials and Procedure

Mother–infant dyads were observed in a quiet, spacious room at a University Infant laboratory. Prior to the start of the testing session, mothers were asked whether their infants appeared to be showing any anticipation of their actions in general and, more specifically, of impending picks-up in various situations. Then the experimenter and the infant played for approximately 3–5 min to familiarize the infant with the new environment. The *Bayley Scales of Infant Development* – Second Edition (BSID-II; Bayley, 1993) were then administered to control for infants' motor maturity, cognitive skills and equivalent developmental age. One infant scored lower than one percentile under the average on the Mental Scale (Mental Index score = 82). However, this infant's behavioral responses were not different from the average responses of the other infants, thus this infant was included in the final sample. The BSID-II average assessment length was 12 min. Following the BSID-II assessment, infants were laid down on a mat (47 cm × 47 cm) placed on a low table (36 cm off the floor). Interactions were filmed with a digital camera that focused on the infant (recording at 30 frames per second).

All dyads were observed in two conditions: (1) Normal and (2) Delayed. In order to prevent changes in mothers' usual pick-up routines, the normal pick-up always preceded the delayed pick-up. To observe a normal pick-up episode, mothers were instructed to chat with their infants and pick them up a few times during the interaction whenever they felt infants were comfortable and attentive, ensuring that the infants could see their arms as they approached to pick them up. Mothers attempted between two and four pick-up episodes overall. To choose one normal pick-up episode to be coded in this condition, three criteria were used by two independent judges to ensure their usability (see also Reddy et al., 2013): (i) the mother's arms were approaching frontally and were therefore potentially visible to the infant; (ii) the infant's gaze was directed toward the mother; and (iii) the episode was preceded by a period of engagement, increasing the likelihood of the infant wanting to be picked up. If more than one episode met these criteria, the first good episode was chosen. There was disagreement about the criteria in two cases, which was resolved following re-viewing of the video material.

To observe a delayed pick-up, mothers were asked to repeat the same procedure, but hold their hands on the infants' waist for approximately 6 s before lifting. The end of the 6 s delay was signaled by the experimenter. Because our aim was to evaluate the effects of a breach in infants' expectations, the Delayed condition was only observed once for each dyad. In one case, however, the mother had to repeat the delayed pick-up procedure due to the infant's fussiness.

Measures

Identifying Phases Within Pick-Up Episodes

Each normal and delayed pick-up episodes was divided into three phases: (1) Approach: beginning from the onset of the mother's arms starting to approach the infant until Contact; (2) Contact: beginning from the onset of the mother's hands contacting the infant's waist until the onset of Lift; (3) Lift: beginning from the movements of mother's hands on the infant's waist until the infant's body was completely detached from the mat.

One coder viewed and identified the frame points for the onset of Approach and Contact, and onset and offset of Lift for all infants in both conditions (Normal and Delayed). A second coder independently viewed 25% of the video material in both conditions. The coders disagreed on two pick-up episodes out of 24 (within 10 video frames, i.e., at 30 fps, 1/3 of a sec). Coefficients of agreement for each phase are presented in **Table 1**.

Mean durations for each of these three phases were as follows: Approach = 2.49 s, Contact = 2.05 s and Lift = 1.54 s in the Normal condition, and Approach = 1.55 s, Contact = 8.32 s, and Lift = 1.48 s in the Delayed condition. As expected, the duration of the Contact phase was significantly longer for the Delayed than the Normal condition, $F(1,22) = 195.93$, $p < 0.00$, $\eta^2 = 0.899$, 95% *CI* [5.34, 7.2], confirming that mothers were following our instructions. However, while there was no significant difference in the duration of the Lift phase between conditions ($p = 0.566$), the Approach phase was significantly longer in the normal compared to the delayed pick-up, $F(1,22) = 5.279$, $p = 0.031$, $\eta^2 = 0.194$, 95% *CI* [0.09, 1.789]. The difference in Approach duration in the two conditions may be due the procedure order. Since the Delayed condition was always presented after at least one normal episode, mothers may have acquired familiarity with the procedure so that the delayed episode was generally quicker than the normal one(s).

Behavioral Coding

The following infant behaviors were coded in all three phases in both conditions: Body Tension, Head Lag, Gaze Shifts, and Positive and Negative Affect displays. The duration (relative to the duration of each phase in each condition for each infant) of *Body Tension* was measured as the onset and offset of simultaneous movements of arms and legs in any of the following combinations: *Arms* stretched out, widening out to the side, raising up, or stretching toward the mother; and *Legs* extending flat and raising slightly upward, or tucking up.

To assess infants' stiffening of the neck when lifted, we measured their Head Lag during the Lift phase in both normal and delayed pick-ups. Using the video software Dartfish, we created this measure by calculating the angle between chin, chest and neck border for each infant at two points: (a) beginning of Lift, corresponding to the onset of the Lift phase, which was used as a baseline to control for each infant's individual angle when the head was leaning on the mat; and (b) halfway through Lift, operationalized as the midpoint in time of the Lift phase, which was adjusted to account for individual variations in the Lift phase duration. If the infant's head dropped backward while being lifted, then this resulted in an increase of the measured angle (i.e., decreased head-neck strength) at the midpoint of the Lift phase.

Infants' *Gaze* was coded when directed to the mother's *face,* the mother's *body*, or *away* from the mother. We then measured how many times infants shifted their gaze from the mother's face to away and from the mother's face to the mother's body during the Approach and Contact phases in both conditions.

Finally, the frequency of Positive and Negative Affect displays was coded and adjusted to the duration of each phase in each condition for each infant (i.e., frequency*mean/actual duration of the phase). *Positive Affect* displays were defined as smiles (i.e., raised cheeks and corner of lips turned up with mouth open or closed) or laughs (i.e., raised cheeks, mouth open, lower, and upper gum visible, eyes open, or winked, possibly accompanied by some vocalizations), whereas *Negative Affect* displays were defined as frowns (i.e., furrowed brow and downturned mouth) or sad expressions (i.e., mouth, eye brows, and cheeks turned down) (see also Legerstee and Markova, 2007).

Infants' behaviors were coded by one observer blind to the rationale of the study. Episodes were watched at least twice: initially at normal speed to identify relevant behaviors, and then frame by frame to identify onset and offset points of each behavior. A second observer (also blind to the rationale of the study) independently coded 25% of the video material in both conditions. Inter-observer reliability was assessed using the Intraclass Correlation Coefficient, and values ranged from 0.861 to 1 (see **Table 1**).

TABLE 1 | Inter-Rater Reliability (calculated as Intra-Class Correlations; ICC) for all Measures used in the Present Study.

Measure		ICC
Phases	Approach	1
	Contact	0.999
	Lift	0.998
Body Tension		0.97
Gaze	Mother's Face	0.967
	Mother's Body	0.861
	Away from Mother	0.913
Affect	Positive	0.906
	Negative	1
Head Lag	Beginning Lift	0.996
	Midpoint Lift	0.998

RESULTS

Means and standard deviations for all measures are presented in **Table 2**. Repeated-measures ANOVAs were computed separately for each infant behavior. Pairwise comparisons were adjusted with a Bonferroni correction.

A repeated-measures ANOVA for Body Tension with condition (Normal, Delayed) and phase (Approach, Contact, Lift) as the within-subjects variables, showed a significant main effect of condition, $F(1,22) = 24.48$, $p < 0.001$, $\eta^2 = 0.527$, 95% *CI* [0.120, 0.294], and a significant interaction between condition and phase, $F(2,44) = 8.828$, $p = 0.001$, $\eta^2 = 0.286$. Simple contrasts revealed that the total duration (in terms of ms) of time were infants had their body tensed increased from Approach to Contact in the Normal condition ($p = 0.016$, 95% *CI* [−0.397, −0.035]), but decrease from Approach to Lift ($p = 0.012$, 95% *CI* [0.055, 0.513]) as well as from Contact to Lift ($p = 0.004$, 95% *CI* [0.065, 0.381]) in the Delayed condition (**Figure 1**).

To compare Head Lag before and during Lift in the two conditions, a repeated-measures ANOVA was computed with condition (Normal, Delayed) and time (beginning lift, midway

TABLE 2 | Descriptive Statistics for all Measures in Both Conditions and All Phases.

Measure	Normal		Delayed	
	M	***SD***	***M***	***SD***
Body Tension (relative duration in ms)				
Approach	0.39	0.30	0.46	0.34
Contact	0.61	0.22	0.40	0.17
Lift	0.65	0.33	0.17	0.18
Head Lag (angle)				
Beginning Lift	76.63	13.45	79.14	13.78
Midpoint Lift	89.08	13.92	105.43	12.78
Positive Affect (relative frequency)				
Approach	1.33	1.92	0.82	1.14
Contact	1.39	1.61	0.75	0.85
Lift	0.27	0.62	0.02	0.10
Negative Affect (relative frequency)				
Approach	0.19	0.79	0.35	1.13
Contact	0.01	0.06	0.76	0.83
Lift	0.16	0.46	0.40	0.58
Gaze Shifts from Mothers' Face to Away (relative frequency)				
Approach	0.43	0.66	0.48	0.51
Contact	0.3	0.47	1.26	0.69
Gaze Shifts from Mothers' Face to Mothers' Body (relative frequency)				
Approach	0.26	0.45	0.74	0.69
Contact	0.35	0.49	1.18	0.89

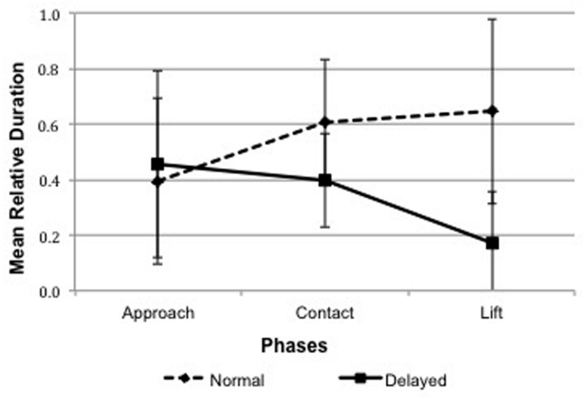

FIGURE 1 | Mean relative durations of Body Tension across the three phases in Normal and Delayed Pick-Up episodes.

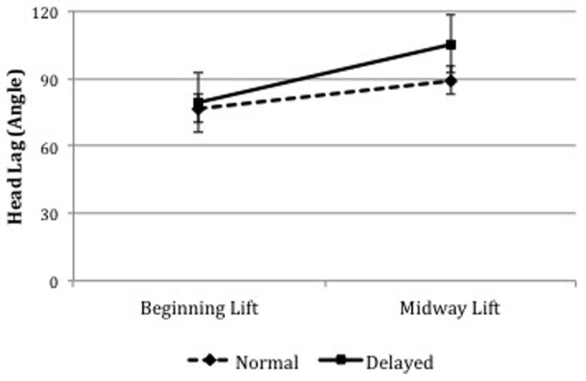

FIGURE 2 | Mean Head Lag angles at the beginning and midpoint of Lift in Normal and Delayed Pick-Up episodes.

lift) as the within-subjects factors. Results revealed a significant main effect of condition, $F(1,22) = 17.94$, $p < 0.001$, $\eta^2 = 0.449$, 95% *CI* [4.81, 14.04], and time, $F(1,22) = 126.58$, $p < 0.001$, $\eta^2 = 0.852$, 95% *CI* [15.80, 22.94], as well as a significant interaction between condition and time, $F(1,22) = 26.32$, $p < 0.001$, $\eta^2 = 0.545$ (**Figure 2**). While there was no difference between the conditions at the beginning of the Lift ($p = 0.291$, 95% *CI* [−7.32, 2.30]), simple contrasts showed that halfway through the Lift Head Lag was significantly higher in the delayed than in the normal pick-up, $F(1,22) = 32.73$, $p < 0.001$, $\eta^2 = 0.598$, 95% *CI* [−22.28, −10.42], suggesting that infants' neck had lost its tension and the head was not aligned with the rest of the body when the child was lifted after a delay.

A repeated-measures ANOVA on the frequency of Gaze Shifts with direction (face-to-mother's body, and face-to-away), condition (Normal, Delayed), and phase (Approach, Contact) as the within-subjects factors, showed a significant main effect of condition, $F(1,22) = 42.73$, $p < 0.001$, $\eta^2 = 0.66$, 95% *CI* [0.39, 0.76], and phase, $F(1,22) = 15.39$, $p = 0.001$, $\eta^2 = 0.412$, 95% *CI* [0.14, 0.45], as well as a significant interaction between phase and condition, $F(1,22) = 16.61$, $p = 0.001$, $\eta^2 = 0.43$. Simple contrasts indicated that in the Delayed condition Gaze Shifts were significantly more frequent during Contact than during Approach, $F(1,22) = 37.66$, $p < 0.001$, $\eta^2 = 0.631$, 95% *CI* [−1.63, −0.81], while in the Normal condition there was no difference in Gaze Shifts between Approach and Contact ($p = 0.852$, 95% *CI* [−0.44, −0.52]). The direction of the shifts (i.e., from mother's face to mother's body vs. away) was not significant.

Finally, repeated-measures ANOVAs on affect displays with condition (Normal, Delayed) and phase (Approach, Contact, Lift) as the within-subjects variables, revealed a significant main effect of condition for Positive Affect, $F(1,22) = 4.957$, $p = 0.037$ $\eta^2 = 0.184$, 95% *CI* [0.03, 0.89], and Negative Affect, $F(1,22) = 6.583$, $p = 0.018$, $\eta^2 = 0.23$, 95% *CI* [0.66, 0.07], indicating a higher frequency of Positive Affect displays in the Normal ($M = 0.996$) than in the Delayed ($M = 0.533$) pick-up, and a higher frequency of Negative Affect displays in the Delayed ($M = 0.504$) than in the Normal ($M = 0.122$) pick-up. Moreover, there was a significant main effect of phase for Positive Affect, $F(2,44) = 6.235$, $p = 0.004$, $\eta^2 = 0.221$, showing that, in both conditions, infants displayed significantly less positive affect during Lift ($M = 0.148$) compared to Approach ($M = 1.073$, $p = 0.016$, 95% *CI* [0.15, 1.71]) and Contact ($M = 1.071$, $p < 0.001$, 95% *CI* [0.43, 1.42]).

DISCUSSION

The goal of the present study was to provide evidence for the argument that cooperating with the caregiver's action is embedded in the embodied participation in joint routines. To this end, we observed 3-month-old infants' behaviors during a natural interaction, when mothers either picked up the infant normally or they delayed the pick-up sequence. Our results indicated that when the pick-up interaction unfolded normally infants tensed up their body, stiffened their neck (i.e., decreasing the lag between the chin and the chest) and displayed more positive affect than when the pick-up was delayed. In other words, when Contact was not followed by a lift within the usual time frame, infants released their arms and legs as well as their neck tension and displayed more negative affect.

We observed a typical constellation of gaze, affective displays and body movements, which varied in the two conditions. During Approach in both Normal and Delayed conditions, infants showed a tendency to look attentively at their mothers, smile or laugh, and thrust their legs or/and arms. When the pick-up sequence progressed normally, after Contact infants continued looking at their mothers – often maintaining their positive affect – and increased their body movements into a more regular pattern that was here coded as Body Tension. As the sequence turned into Lift, Body Tension peaked and most infants kept gazing at the mother, strengthening their neck with their head in a frontal position. Few infants turned their head sideways, which may represent another strategy to support their head to prevent a head lag, as suggested by Reddy et al. (2013). In contrast, when the pick-up was delayed after Contact, most of the infants began to display negative affects after approximately 3.5 s while mothers were keeping their hands on infants' waist; some infants shifted their gaze back and forth from the mother's face to her hands or away, and the majority of them decreased their body tension. These behavioral changes then continued during delayed Lift, where infants' eye contact with their mothers continued to be fluctuating and they motor behavior weakened: the body tension dropped to the lowest point, and most of the infants manifested a loss of tension in the neck resulting in an increased head lag.

These results hold implications for our understanding of infants' participation in shared actions that go beyond infants' ability to adjust to or anticipate the mother's action. Specifically, our findings suggest a particular sensitivity to the timing and sequence of the pick-up action as it unfolds, and possibly about the duration of each of its phases. Infants showed a similar motor response and gaze focus on the mother's face during Approach in both conditions, which may be considered a "preliminary" phase signaling the beginning of the pick-up sequence. In the following phase, marked by the mothers' contact with the infants' waist, the increase in body tension and positive affect highlighted that infants gained most of their tension and then maintained it steadily throughout the lift. On the contrary, when the pick-up was delayed, infants lost their preparatory tension, indicating their sensitivity to the timing and sequence in which the pick-up action generally progressed – with the mother's hands first on the waist and then moving down for lifting the infant's up.

What does this suggest in terms of infants' participation in a normal pick-up routine? Infants seem to invest their bodily and affective energy not only in anticipation to, but also contingently adjusting to the mother's behavior during the entire unfolding of the action. The release of tension during the Delayed condition seems to support this argument. While an interpretation of infants' participatory behaviors as either co-operative or based on simple associations remains to be addressed by future research, our findings indicate that infants supported and adjusted to their mothers' timing of pick-up behaviors.

The increase of gaze shifts from Approach to Contact during the delayed pick-up, could be interpreted as an attempt to disambiguate the mother's behavior, as previous research has reported (Phillips et al., 1992; Behne et al., 2005). Yet, since these shifts were equally distributed between gaze away and to the mother's body, it is difficult to specify their exact function. Most mothers did not show any affective expressions during the delay of the pick-up, while few of them smiled or vocalized to the infant when she or he looked at them. One possible explanation could be that infants disengaged from the interaction to avoid distress, as suggested by studies using the Still-Face Face paradigms (Tronick et al., 1978; Adamson and Frick, 2003). Alternatively, gaze shifts may be an attempt to grasp and share the mother's attention in an ambiguous situation (Amano et al., 2004), and thus allow infants to track their mothers' action and try to make sense of it.

Some limitations of the present study need to be addressed in future research. First, the fact that the Normal pick-up was always performed first may have influenced infants' responses to the subsequent delay in the pick-up sequence by, for example, increasing the infants' attention to the violation of the usual way they are picked up; counterbalancing the two conditions may have helped to have a clearer effect of the delay on the infant's behavior. At the same time, asking mothers to introduce a delay in their natural pick-up routine before picking up their infants may have disturbed their naturally occurring behaviors. Future studies exploring the pick-up routine need to consider these two aspects and their implications seriously. Second, being picked up twice within a relatively short period of time might have overstretched infants' attentiveness, resulting in the overall decrease of participation showed by infants in the delayed pick-up episode. However, our results indicate that infant behaviors were comparable in the approach phase of both conditions, and only during contact did the infants begin to realize that 'something is not quite right'. Despite these findings, our study design did not allow us to determine the precise point in which infants detected the violation in the pick-up flow and changed their behavior. This is problematic, conceptually as well as practically, because infants could make allowances for the delay by expecting to be picked up for some time and thus behaving as if the pick-up was not delayed. Yet, it could be argued that by analyzing the whole contact phase, where the change occurred, and not the specific time where the infant would have normally been picked up until it eventually was, we accounted for these individual allowances, and thus consider this a conservative approach. Finally, being picked up was de-contextualized and not related to any previous activity nor functional to the following one, as is usually the case. This may have affected the infants' natural behavior. Future research aiming to investigate infants' participation in daily, familiar practices (not only a pick-up routine) would strongly benefit from observing mothers and infants interacting in their natural environment, such as at home. We believe that such a change in setting may reveal aspects of infants' participation as rich and functional, which cannot be observed in other, more artificial contexts.

CONCLUSION

Our study suggests that, when being picked up, infants are not passive recipients of actions performed on them, but alert and active participants behaving according to the emergent features of the activity. Early signs of co-operative participation can be found in the way infants supported and responded to their mothers' timing of movements, facilitating or adjusting to the pick-up action as it unfolded. This is in line with a more dynamic and developmental approach to the study of cooperation that takes into account the role of infants' daily experience with shared practices (see also Fantasia et al., 2014a). Indeed, by participating in early routines infants take part in a process of "conventionalization" of social practices, which integrates affective, cognitive, communicative and kinetic aspects. What makes behaviors predictable for infants may lie in the experience of moving together, lived through a multiplicity of sensory modality, including proprioception. As Fogel and Thelen (1987) have proposed, social behavior is not behavior *toward,* but mostly behavior *with* others. Of course, should an adult decide to pick-up an infant against her or his will, she would easily succeed without much effort. Yet, the motivation and pleasure achieved through a pick-up interaction might probably not be the same, as infant responsiveness and engagement during the pick-up is arguably crucial in its potential for motivating the caregiver and fostering the intersubjective exchange.

AUTHOR CONTRIBUTIONS

VR has made a substantial contribution during the preliminary phases of the study conception, design, and theoretical building up of the arguments. She also made an important contribution to the interpretation of data.

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What Does It Take for an Infant to Learn How to Use a Tool by Observation?

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Observational learning is probably one of the most powerful factors determining progress during child development. When learning a new skill, infants rely on their own exploration; but they also frequently benefit from an adult's verbal support or from demonstration by an adult modeling the action. At what age and under what conditions does adult demonstration really help the infant to learn a novel behavior? In this review, we summarize recently published work we have conducted on the acquisition of tool use during the second year of life. In particular, we consider under what conditions and to what extent seeing a demonstration from an adult advances an infant's understanding of how to use a tool to obtain an out-of-reach object. Our results show that classic demonstration starts being helpful at 18 months of age. When adults explicitly show their intention prior to demonstration, even 16-month-old infants learn from the demonstration. On the other hand, providing an explicit demonstration ("look at how I do it") is not very useful before infants are ready to succeed by themselves anyway. In contrast, repeated observations of the required action in a social context, without explicit reference to this action, considerably advances the age of success and the usefulness of providing a demonstration. We also show that the effect of demonstration can be enhanced if the demonstration makes the baby laugh. Taken together, the results from this series of studies on observational learning of tool use in infants suggest, first, that when observing a demonstration, infants do not know what to pay attention to: demonstration must be accompanied by rich social cues to be effective; second, infants' attention is inhibited rather than enhanced by an explicit demand of "look at what I do"; and finally a humorous situation considerably helps infants understand the demonstration.

Keywords: observational learning, demonstration, tool use, social cues, infants

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INTRODUCTION

Infants are avid explorers of the environment: their intrinsic motivation drives them to constantly look for new experiences which, in turn, increases their knowledge of the environment and allows them ultimately to display typically human behaviors such as tool use. In particular, it has been hypothesized that the "origins of tool use in humans can be found [. . .] in the perception-action routines that infants repeatedly display as they explore their environments." (Lockman, 2000, p. 137). But whereas such a mechanism of discovery is undoubtedly an important factor in development, another, more economical, but less studied mechanism also exists, namely observational learning.

Observational learning can be defined as the process whereby an adult or a child "attempts to imitate another person executing a new motor skill" (Hayes et al., 2008, p. 407). Imitation is a rapid and efficient means to learn a new skill, allowing the learner to avoid painstaking trial-and-error learning. Whereas some imitation can be observed from birth, for instance for mouth opening, and whereas as early as 6 months infants can repeat the manual action an adult makes in front of him, such as squeezing a duck (Abravanel et al., 1976), true observational learning appears much later, not before the second year (Meltzoff, 1988; Elsner and Aschersleben, 2003; Elsner et al., 2007; Esseily et al., 2010).

In this paper, after a short reminder of what is known about observational learning during early development, the conditions leading to successful imitation, and after briefly presenting the tool-use problem and the spontaneous behavior of 12–22 month-old infants confronted with this problem, we will review studies we have been performing in our laboratory which investigate possible reasons for the late appearance of observational learning in our tool-use task. One issue we will consider is whether it is possible to advance the age of observational learning and in which conditions of context and of demonstration.

OBSERVATIONAL LEARNING

As said above, observational learning is a special case of imitation, in which the action to be imitated is not part of the child's existing repertoire of actions or which is failed without prior demonstration. Thus, whereas imitation of simple actions can be observed as early as 6 months of age (for reviews see Poulson et al., 1989; Elsner, 2007; Elsner et al., 2007), this cannot be considered to be observational learning, because these simple actions are already in the infant's motor repertoire. Observational learning of a new skill has been less studied, at least in infants and toddlers (see Ashford et al., 2007's meta-analysis for children and adult studies). In one study it was shown that at 12 months, infants can learn by observation how to bimanually manipulate a rolling drum to produce music (Fagard and Lockman, 2009). At 14–15 months they can learn by observation to push a button to produce music (Meltzoff, 1988; Elsner and Aschersleben, 2003). In the latter study they are surprised if the effect they produce is not similar to that produced by the adult. In another study it appeared that at 15 months, children can learn by observation how to turn a bottle upside down to retrieve a small peg inserted in it (Esseily et al., 2010).

Observational learning seems to occur later for tool use. For instance, Chen and Siegler (2000) showed that even well after 18 months, infants may still be unable to learn how to use a tool through observation. Between 18 and 35 months, some infants used the tool appropriately to retrieve a toy after observation, but others still used indirect strategies such as trying to reach with their hands, asking for their mother's help or simply staring at the toy without trying to reach for it. In the pilot testing of their Nagell et al. (1993) study, also noticed that the three 18-month-olds they observed were unable to use a rake to get a toy out of a cage after demonstration from the experimenter. In contrast, in the 1993 study itself, some 2-year-olds showed occasional successes, more so in the groups which had been shown the action first ($2\frac{1}{2}$ successes out of 10) than in the no-model group (less than 1/10 success). Thus, learning a complex multiple-step skill by observing an adult is difficult before the end of the second year of life. Before considering tool use as part of the larger category of two-step or "means-end" actions acquired during early childhood, we will briefly review the studies in which manipulating the modeling conditions impacted on infants' success in reproducing the modeled action.

FACTORS INFLUENCING THE REPRODUCTION OF MODELED ACTIONS IN YOUNG CHILDREN

Many studies have been devoted to understanding how infants and young children reproduce the action modeled by an adult. It has been traditionally said that, as opposed to non-human primates, young infants tend to imitate not only the goal of the demonstrated action (emulation) but also the means used by the model to reach this goal (Nagell et al., 1993), sometimes even over-imitating irrelevant means (Whiten et al., 2009; McGuigan and Robertson, 2015). A growing body of research has tried to understand the factors leading infants to either imitate the means or else to only emulate the goal.

These studies have revealed several factors. Young children predominantly imitate the means when the set-up makes the goal of the action less clear (e.g., reaching toward the table without (vs. with) a dot marking the point of reaching, (Bekkering et al., 2000; see also Carpenter et al., 2002, 2005; Williamson and Markman, 2006). On the other hand, infants tend to emulate the goal when the model shows an irrational means (e.g., pushing a toy through a tube using a stick toward the free end as opposed to toward the dead-end, Want and Harris, 2001); when the model uses a means for a clear reason but that is not applicable to themselves (e.g., switching on a light with the head, with the model's hands being occupied, Meltzoff, 1988; Gergely et al., 2002; Zmyj et al., 2009); when the means used successfully by the model seems accidental ("Whoops") rather than intentional ("There") (Carpenter et al., 1998); when the information available from the model is degraded (e.g., obtaining a reward from a box following a video rather than a live model, McGuigan et al., 2007). In addition, young children are more successful in their imitation when the demonstration comes after the intention of the model is shown (Carpenter et al., 2002; Southgate et al., 2009).

The above studies, many of them involving children older than 2 years, show the importance of taking into account different factors that can influence the child's reproduction of an action modeled by an adult. However, in contrast with our task, many of the actions to be repeated by the child were simple and probably familiar to the child (with a few exceptions: Carpenter et al., 1998; Want and Harris, 2001; McGuigan et al., 2007). In our original study, the task was difficult and infants did not spontaneously succeed at retrieving an out-of-reach toy with a rake placed within reach but not next to the toy. We thought that the goal of the action was clear to the infant since the demonstration always took place after the infant had tried unsuccessfully to retrieve the toy (we later questioned this assumption, as we will see further). The means used by the model was always direct (the model grasped the rake and raked the toy toward himself or herself). Finally, in our task there was no other way to succeed than the one shown by the adult. Before discussing the factors that could explain why infants failed to copy the demonstration in our task before 18 months of age, we will briefly review what is known about the development of means-end actions of which tool use is a special example.

FROM MEANS-END TO TOOL USE

A means-end task is a task in which the goal of the action cannot be manually reached directly by the actor, who has to perform intermediate actions or "means" (Piaget, 1936). One of the earliest cases when infants are confronted with the impossibility of directly grasping an interesting object is when the interesting part of the object is at the end of a handle, too far away to be grasped directly (e.g., a rattle). For instance we observed that when a bright ball is at the end of an uninteresting rigid handle, 6-month-old infants point toward the ball while ignoring the handle. In contrast, most 8-month- and 10-month-old infants immediately grasp the handle while looking at the ball (Fagard et al., 2015).

When the uninteresting part is not rigid, so that the composite object looks like two objects rather than a single one, for instance a toy at the end of a string or placed on a cloth, it takes a few more weeks for the child to understand that she or he can pull the string or the cloth to retrieve the object of interest (Piaget, 1936; Fagard, 1998; Willatts, 1999; Buttelmann et al., 2008).

Bates et al. (1980) compared 9–10-month-old infants retrieving an out-of-reach toy placed either on a cloth, at the end of a string, or at different positions near three kinds of utensils likely to help the children retrieve it (hoop, crook, or stick). The children succeeded in conditions where toy and means to retrieve it were physically linked ("unbreakable contact," cf. means-end situations just mentioned) but less often when the contact was breakable, and not at all in the condition with no contact. The authors concluded that at 10 months, solving the problem is easier when the spatial arrangement suggests a link between the means to retrieve it and the toy.

A generally accepted definition of tool use is the ability to use one object to extend the limit of our physical body in order to act upon another spatially independent object (Beck, 1980). Infants' first successful use of such a real tool is likely to be with a spoon, starting around the age of 1 year. This skill progresses considerably during the second year (Connolly and Dalgleish, 1989). Note that the case of the spoon is particular, in the sense that prior to using the spoon themselves, infants have many opportunities to see their family and other people use a spoon to eat.

Using unfamiliar tools to bring an out-of-reach object within reach is succeeded later. A few studies have focused on how infants learn to use such a new tool (see Greif and Needham, 2011 and Keen, 2011, for reviews). Most of them have focused on perceptual factors, all stressing that difficulty increases with the size of the spatial gap between the tool and the object to be acted upon (Bates et al., 1980; van Leeuwen et al., 1994), and more generally with the number of steps needed to achieve the required result (Smitsman and Cox, 2008). In these studies, emphasis was put either on the sensorimotor progress leading to skillful tool use (Connolly and Dalgleish, 1989), on the perceptual constraints which make using a tool a real cognitive problem for the infant (Bates et al., 1980; van Leeuwen et al., 1994; Smitsman and Cox, 2008), or on the role of familiarity or novelty in the capacity to use a tool or to transfer and generalize knowledge to new tools (Brown, 1990; Barrett et al., 2007). In other words, most of these early studies were concerned more with cataloging the factors inducing success than with understanding the actual mechanisms underlying tool-use learning, in particular trial and error and observational learning.

In the following section we recall data from a series of recently published studies on the emergence of tool use (Rat-Fischer et al., 2012; Fagard et al., 2014), in which we investigated to what extent trial and error and observational learning respectively allow infants to learn how to use a tool. Here we aim at summarizing the parts that concern observational learning. Thus, we will only briefly recall the methodology, referring the reader to the original articles for further details.

USING A TOOL TO BRING A FAR-AWAY TOY INTO REACH

Our paradigm consisted of presenting infants with a desirable out-of-reach toy, and with a T-shaped rake-like tool, long enough to retrieve the toy. The "rake" was within reach and constructed out of white cardboard with a 20-cm-long handle (Fagard et al., 2014). The toys were small, bright, and salient whereas the rake was white and intentionally unobtrusive so that infants would be attracted to the out-of-reach toy more than to the rake. We investigated several spatial arrangements of toy and rake (toy inside/against the rake, toy inside the rake but not against, toy to the side of the rake). We followed five infants from 12 to 20 months in a longitudinal study (Fagard et al., 2014) and 60 infants aged 14, 16, 18, 20, 22 months, in a cross-sectional study (Rat-Fischer et al., 2012). Here only the condition "toy to the side of the rake" will be considered (see **Figure 1**) since it was only in this condition that we investigated the effect of demonstration in further experiments. For more details, see Rat-Fischer et al. (2012) and Fagard et al. (2014).

In the longitudinal study, all infants younger than 16 months failed to retrieve the toy, except for one isolated success that the infant could not repeat. There was a sudden increase of spontaneous success between age 17 months and age 18 months. At around 18 months, all five infants succeeded at least at some

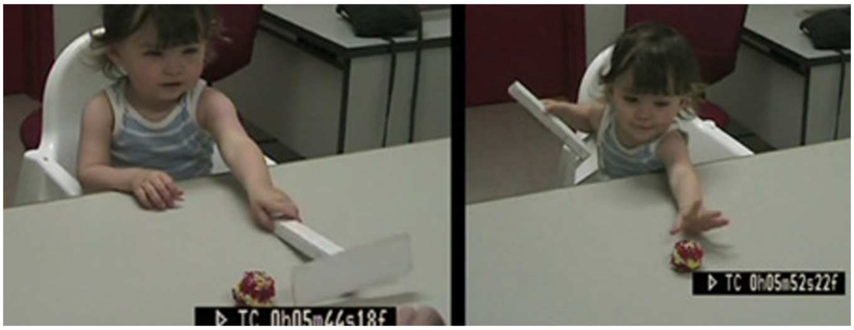

FIGURE 1 | Typical spontaneous behavior of a 16-month-old when an out-of-reach toy is presented to the side of a rake (spatial gap): the child grasps the rake, discards it, and begs for the toy.

trials. In the cross-sectional study, where each child had only one session, there was 0% spontaneous success at 14 and 16 months, and the percentage slowly increased to reach 10% at 18 months and about 30% at 22 months.

Thus, spontaneous success at tool use when the tool and the out-of-reach object are spatially separated developed slowly during the second year, though faster in the longitudinal study when the infants were given the test every month from their first birthday. These results were not surprising in light of earlier studies showing that a spatial gap between tool and object renders the task extremely difficult for children less than 2 years (Bates et al., 1980; Brown, 1990; van Leeuwen et al., 1994). What we expected less is that demonstration by an adult did not increase the rate of success before 18 months, as we will see in the next section. Since observational learning of means-end has been shown possible as of 12 months of age (Meltzoff, 1988; Elsner and Aschersleben, 2003; Elsner et al., 2007), and since infants are able to use a spoon at about the same age (Connolly and Dalgleish, 1989), we expected the demonstration in our situation to be useful before 18 months of age.

FIGURE 2 | Classic demonstration.

CLASSIC DEMONSTRATION OF A TOOL-USE ACTION

In both the longitudinal and the cross-sectional studies, each time infants failed to retrieve the toy, an adult (the experimenter or the parent) gave two consecutive demonstrations, from the infant's point of view (i.e., the experimenter or parent moved the rake and toy toward the child, see **Figure 2**). Then the infants were tested again.

In the longitudinal study, none of the infants succeeded in retrieving the toy with the rake immediately after demonstration before the age of 18 months.

To check whether the demonstration had some effect even though infants were not actually able to retrieve the toy, we defined a performance score between 0 and 4 as follows. 0: no interest neither in the toy nor in the rake; 1: mostly interested in the out-of-reach toy, pointing toward it and trying to retrieve it without using the rake; 2: mainly interested in manipulating the rake; 3: repeatedly bringing the rake to bear on the toy but seemingly not with the purpose of retrieving the toy; 4: successful or near successful retrieval of the toy with the rake. There was no difference in score before versus after demonstration during the first five sessions (up to age 17 months). Only at the sixth session (age 18 months) did the statistics show that infants scored significantly higher after the demonstration (see **Figure 3**). We found similar results in the cross-sectional study (Rat-Fischer et al., 2012). Thus infants started to benefit from demonstration quite late, not before 18 months.

The relatively late effect of demonstration is consistent with other work showing that proper understanding of the causal structure of means-end tasks in observational learning only matures in the second half of the second year (Meltzoff, 1995; Bellagamba and Tomasello, 1999; Huang et al., 2002). However, our observation of the absence of an effect of demonstration before 18 months contrasts with the studies mentioned above showing that infants can learn to solve a means-end task from observation of a demonstration by an adult from the beginning

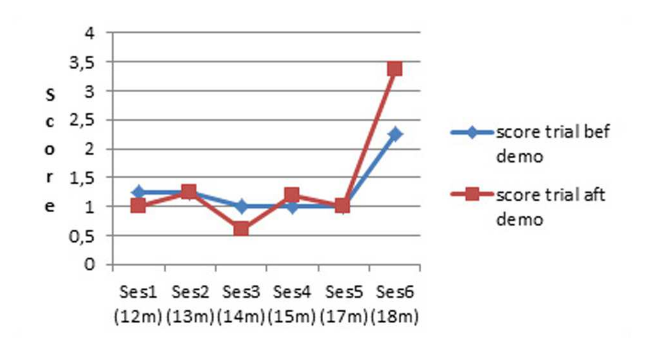

FIGURE 3 | Compared score before and after a classic demonstration (longitudinal study).

of their second year of life (Provasi et al., 2001; Elsner et al., 2007; Esseily et al., 2010). This led us to investigate the reasons why repeated demonstrations were not effective in our studies, in other words, what are the factors that could explain why infants failed to copy the demonstration in our task? The first possibility we investigated was that infants were not able to interpret the demonstration because they did not sufficiently understand the intention of the demonstrator. To test this possibility, we provided the infant with cues about the demonstrator's intention prior to demonstration.

SHOWING THE OBSERVER'S INTENTION PRIOR TO DEMONSTRATION

In this study (Esseily et al., 2013), we tested 70 16-month-old infants for tool use. The toy consisted of a small car which could be rolled along the table. We used the same rake as for the longitudinal and cross-sectional studies described above, and presented infants with a condition with a spatial gap between rake and toy. We chose age 16 months because we knew from the two previous studies that at this age infants could not spontaneously succeed at this task when the toy is not contiguous with the rake. We nevertheless used a control group with no demonstration (spontaneous group), which we could compare with two demonstration groups and two other control groups ($N = 14$ in each group). For the demonstration groups, the experimenter sat perpendicular to the infant and received the car from another person seated in front of the child. The experimenter played with the car for a few seconds, and then rolled it along the table in front of her so that it ended up out of reach, but within reach of the rake. Then, depending on the group it belonged to, each infant either received a classic demonstration (the experimenter simply grasped the rake and used it to retrieve the car), or the infant was shown the intention of the experimenter before demonstration. To do this, once the toy was out of reach, the experimenter stretched her arm and hand toward the car, obviously trying to grasp it and said, "I can't get it" (see **Figure 4**). She then used the tool to retrieve the car. In both conditions the same scenario was repeated twice (for more details about the protocol, see Esseily et al., 2013). After demonstration, infants received the same test as was given directly at the beginning of the session to the infants of the spontaneous group. To make sure that a difference between the classic and the prior intention demonstrations could not be due to the fact that the attention of the infant was enhanced on the car, rather than to understanding of the experimenter's intention, we added another control group (Stimulus enhancement condition). In this condition, once the car had been rolled out of reach by the experimenter, the person seated across from the infant made the car move by itself for a few seconds by manipulating a magnet under the table. The experimenter then performed the demonstration as in the Classic demonstration condition, followed by the test. And to make sure that a difference between the classic and the prior intention demonstration could not be due to more "motor resonance" (Paulus et al., 2011) when the experimenter showed her intention (since here the arm movement toward the car is repeated twice), we added a further condition where the experimenter stretched her arm toward the empty place where the car was located in the demonstration condition (Motor resonance condition). The experimenter then performed the demonstration as in the Classic demonstration condition, followed by the test.

FIGURE 4 | Showing the intention prior to demonstration.

We compared infants' scores for the first action at the test, the best action and the mean score for all actions. We found that there was a significant effect of condition, due to the difference between the prior intention group and all other groups. Infants used the rake in connection with the toy significantly more often after watching the experimenter showing her intention prior to demonstration than after a classic demonstration. And this effect is unlikely to be due to stimulus enhancement or to motor resonance (see **Figure 5**).

This result suggests that one of the reasons infants do not learn from observing a demonstration of unfamiliar tool use is that they do not understand the intention of the experimenter when he or she does the classic demonstration. This is consistent either with the teleological reasoning theory suggesting that infants need to understand the intended goal of the experimenter in order to understand her actions and selectively imitate them (Gergely and Csibra, 2003), or with a more mentalistic view (Buttelmann

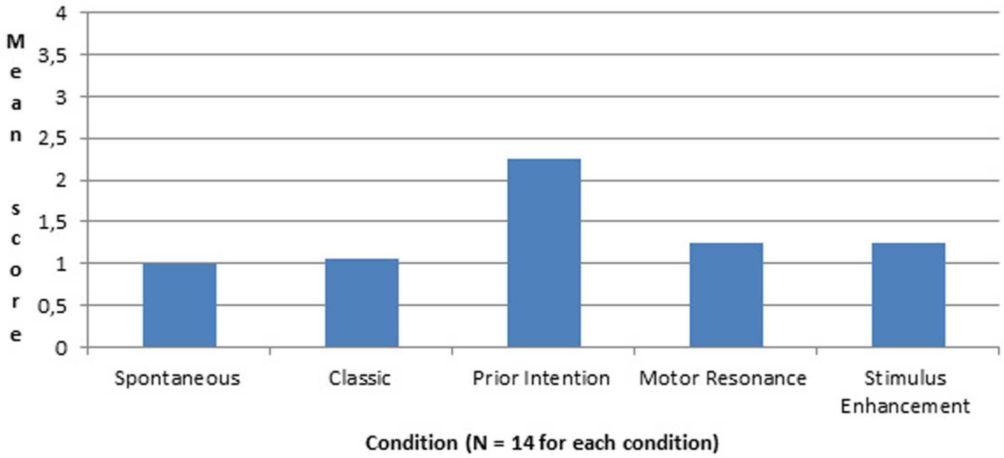

FIGURE 5 | Mean score at the test following demonstration (except for the Spontaneous group) as a function of condition.

et al., 2008). It is in accordance with the studies showing more successful imitation of the means when the demonstration comes after the intention of the model is shown (Carpenter et al., 2002; Southgate et al., 2009).

IMPLICIT REPEATED DEMONSTRATION OF TOOL USE

Another possibility to explain why in previous studies we failed to show observational learning may be that providing a few demonstrations in a single session is not an effective way to learn. In real life, infants have ample opportunity over many months to observe adults around them using tools. For example, as already mentioned, infants start understanding the affordance of a spoon after many opportunities to watch the functionality of the spoon when seeing people around them eat with a spoon. In addition, parents' or caregivers' demonstrations are implicit rather than explicit as in the demonstrations used in our studies. Parents rarely tell their children "look how I hold my spoon to eat"! We decided to investigate what would happen if infants had a similar opportunity, over an extended period of time, to watch an adult repeatedly use a rake to move objects. We opposed this condition with a condition where infants had the opportunity to manipulate a tool in the presence of toys, all within reach, without any demonstration from the adults. Thus we contrasted the effect of implicit repeated demonstration without practice with that of practice manipulation without demonstration.

In this study Somogyi et al. (2015), 18 infants were followed from the age of 14 months over 6 weeks. We used the same rake as for the previous studies, and toy and rake were presented with a spatial gap between them. We knew from the previous studies that in this age range, and with a spatial gap, infants would not spontaneously succeed. We compared the performance at 16 months depending on the kind of familiarization received with the tool. In one group (Visual familiarization, 10 infants), the infants observed an adult use a rake to bring a toy toward the infant, doing so without any verbal comment so as to avoid explicit teaching. The action was repeated eight times, each time with a different toy. The infants were never given the rake during this familiarization phase.

In the other group (Manual familiarization, 8 infants), the rake was placed on the table near the infant, next to a few toys, and the infants were allowed 5 min to freely interact with the rake and the toys. No instruction or demonstration was given. We decided to use this manual control group in response to colleagues' suggestions that perhaps infants do not learn by observation because they are not manually familiar with the tool and thus the action is motorically too demanding, making it difficult for the infant to pick up the relevant information during demonstration.

All infants came to the lab for the first session: they were first tested on the spontaneous use of the rake as in the condition of spatial gap described above, to confirm that they all spontaneously failed at the task. They were then assigned to one of the two groups. All infants of the Visual group received Visual familiarization from the experimenter and all infants of the Manual group received Manual familiarization as described above. For both kinds of familiarization the parent present in the lab was taught the procedure he or she would have to use once a week at home with the infant for the following 5 weeks. In addition, one of the experimenters went to visit all the families every other week so as to check that the familiarization had been well understood by the parent. All infants came to the lab for the seventh session: they were first tested on the spontaneous use, and if they failed they were given two classic demonstrations from the experimenter followed by a test.

We observed a significant effect of test time and a significant interaction between test time and familiarization condition, indicating a significant effect of familiarization in the case of Visual familiarization, but not in the case of Manual familiarization.

We also compared the highest score obtained at the seventh session before and after demonstration, as a function of the kind of familiarization. Again we found a significant interaction, with a significant effect of familiarization in the case of Visual familiarization, but not in the case of Manual familiarization. This shows that infants of the Visual familiarization group increased their performance significantly more after demonstration than infants of the Manual familiarization group (see **Figure 6**).

The interesting point raised by these results is that they show that infants can improve their performance at tool use without manual familiarization with the tool. Repeated purely visual demonstrations of the functionality of the tool, made in a natural way, without explicit reference to its use, is enough to significantly advance the age of successful tool use.

These results first show that it is not the lack of manual skill which leads to the absence of learning from classic demonstration. They also suggest that infants may need several demonstrations over an extended time period to learn by observation. Most importantly, our results suggest that implicit demonstration in an ecological setting may be more efficient than explicit teaching.

MAKING THE INFANT LAUGH DURING DEMONSTRATION

Evidence from an additional study we performed suggest another, less studied, factor influencing observational learning, namely emotional state. In a pilot study where we were pre-testing ways of giving the demonstration, we observed with surprise that, when occasionally infants were amused by our demonstration and laughed, these laughing babies would imitate us immediately after a demonstration. They did this with a level of skill that we had never observed after other demonstrations. We thus decided to experimentally test the effect of laughing on the ability to learn from a demonstration.

In this study (Esseily et al., 2015), we tested 51 18-month-old infants. We chose this age because it is the youngest age when classic demonstration of tool use starts to be effective. We eliminated 11 infants who succeeded spontaneously at the first tool-use test given before the demonstrations started. We used the same rake as for the previous studies and toy and rake were presented with a spatial gap between them. Among the 40 infants who failed spontaneously at the first test and thus were kept in the study, 10 infants received a classic demonstration, and the other 30 infants received a humorous demonstration. In the humorous demonstration, the experimenter took the rake with one hand, used it to bring the toy closer, then reached for the toy with the other hand and threw it onto the floor immediately. Since only one third of the infants laughed after such a demonstration, we ended up with three groups, Classic demonstration group (10 infants), Humorous demonstration/infants not laughing group (20 infants), Humorous demonstration/infants laughing group (10 infants). In all three groups the infants were tested before and after eight demonstrations, which varied according to the group the infant was assigned to.

Our results showed that the percentage of infants who successfully retrieved the toy using the tool is 30% in the Classic demonstration group, 20% in the Humorous demonstration/infants not laughing group, and 100% in the Humorous demonstration/infants laughing group, with these differences being statistically significant. The 30% success in the Classic demonstration group is close to the value found at 18 months in the spatial gap condition in Rat-Fischer et al.'s (2012) cross-sectional study. Interestingly, the laughing infants did not completely mimic the experimenter since only three of them threw the toy on the floor after retrieving it. All seven others kept the toy to play with. Thus, what was impressive is the way all laughing infants were able to make use of the demonstration to understand the usefulness of the tool in bringing the toy closer (see **Figure 7**).

Note that to be sure that success was due to the effect of laughing, and not due to differences in attention between the two groups, we checked and confirmed that the non-laughing infants looked at the experimenter during demonstrations as much as the laughing infants.

Two interpretations seem possible to explain these results. A first interpretation could be that the infants who were able to appreciate humor were more advanced in their social referencing or cognitive abilities. However, a suggestion that this is not correct comes from our observation that even the gazes of non-laughing infants were directed at the experimenter after she threw the toy on the floor, indicating that even non-laughing infants perceived the incongruity of the situation though it did not make them laugh. Nevertheless, a possible difference in social skills between laughing and non-laughing infants still needs to be explored. The second hypothesis is that of the role of positive emotions on learning, for example through endorphin release, known to facilitate cognitive flexibility (Ashby et al., 1999). This would fit with the observation we made in another study, showing that when infants are put in a positive emotional state, for instance when the experimenter mimics the infant's action before the tool-use task, infants achieve higher level of success than when the test follows a more neutral pre-session (Somogyi and Esseily, 2014).

DISCUSSION

The goal of this article was to explore observational learning as a mechanism for learning tool use in the second year of life. We reviewed four published studies from our laboratory in which the demonstration was varied. In these studies there were four different conditions of demonstration: classic; showing intention prior to demonstration; repeated implicit demonstrations; and humorous demonstration. In addition, in the implicit demonstration study we opposed the benefit of implicit observational learning to that of manual familiarization without demonstration. The infants were tested at 16–18-months of age. In this age range, most infants who had not been first familiarized with the tool failed at the task (Rat-Fischer et al., 2012; Fagard et al., 2014).

When the demonstration was **classic**, i.e., when an adult explicitly showed the infant how to use the tool to retrieve the toy, there was no benefit from the demonstration at 16 months. Demonstration led to some successes starting at

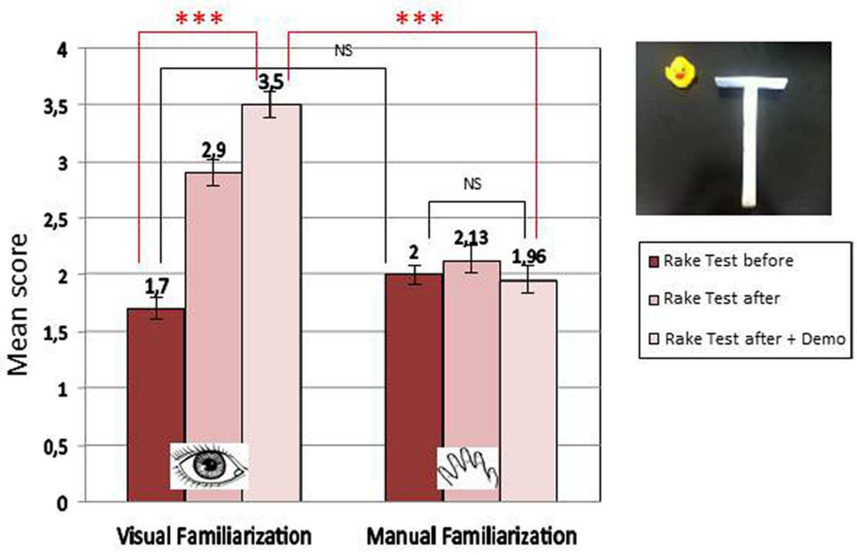

FIGURE 6 | Mean score before and after familiarization as a function of time and condition of familiarization (*** $p < 0.0001$).

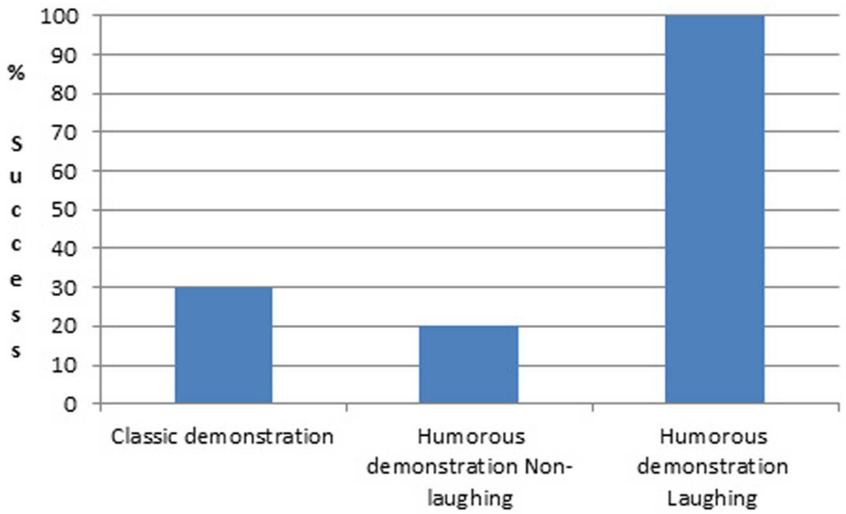

FIGURE 7 | Mean percentage of success as a function of group.

18 months of age. This is late, compared with the success of 12- to 15-month-olds at other means-end tasks following demonstration (Provasi et al., 2001; Buttelmann et al., 2008; Esseily et al., 2010).

When the demonstration was preceded by a gesture toward the toy (**Prior intention**), thus indicating to the infant that the experimenter wanted to get the toy but could not grasp it directly, the effectiveness of a demonstration significantly increased: infants tried harder to retrieve the toy with the tool, even if they often did not fully succeed. Understanding the intention of an agent emerges around the first year of life (Bellagamba and Tomasello, 1999), especially when social cues are given (Carpenter et al., 1998). Our results are in line with studies showing that infants succeed more after demonstration if they have been informed about the experimenter's intention (Carpenter et al., 2002; Southgate et al., 2009).

We then investigated whether the number of demonstrations could be an issue. We wanted to simulate a situation comparable to that of the spoon, where over an extended period of time, infants have many opportunities to watch people around them use a spoon, but without this observation being an explicit teaching situation. Thus in our experiment parents pushed the toys toward the infants using the tool, and did this without commenting, as if it was a natural thing to push a toy toward the infant using a rake (**Implicit repeated demonstrations**).

In the same study, we contrasted this implicit visual training (the infants never had the opportunity to touch the tool) with a condition of manual familiarization without demonstration. The results showed a significantly greater benefit from visual familiarization compared to manual familiarization. In the test session not only did the Visual familiarization infants succeed spontaneously more often than the Manual familiarization infants, but among those infants who failed spontaneously, only those in the Visual familiarization group succeeded after demonstration.

Results from this third experiment show that 16-month-old infants rely more on observation than on their own motor experience when learning a new task that is relatively complex for their age. This conclusion extends the results of earlier studies involving older age groups (Hopper et al., 2010; Whiten and Flynn, 2010; Beck et al., 2011). This does not mean that manipulation is unimportant. Instead it is likely that observational learning and manipulation play a different role depending on the stage of learning. In our tool-use task, there are two factors of difficulty: first children must understand the affordance of the rake; once they know that they can use the rake to retrieve the toy, they must learn how to manipulate it in order to succeed. It was clear in our observations of the first behaviors of the children that they did not understand the affordance of the rake: they discarded it, or played with it after begging for the toy and without pointing the rake toward the toy. Once they tried to use the rake to retrieve the toy, the first such trials were unsuccessful because they did not know very well how to manipulate the rake, but success came rather quickly and within the same session. Observational learning seems more efficient than manipulation for discovering a complex affordance such as for an unfamiliar tool to retrieve an out-of-reach object, which requires bridging the gap between tool and toy before pulling back the toy with the tool. In turn, practice is important for refining the manual skill allowing the task to be done.

In the last study we checked the effect of laughing on observational learning (**Humorous demonstration**). We compared the effect of a classic demonstration with that of a humorous demonstration where the experimenter threw the toy on the floor after retrieving it with the tool. Only one third of the infants laughed, but 100% of the laughing infants fully succeeded after the demonstration, whereas there was a significantly lower percentage of success among the non-laughing infants and the infants in the classic demonstration condition. One important finding was that laughing infants' success did not involve systematic mimicry of the adult's action: the laughing infants clearly learned the affordance of the tool rather than a specific action of throwing the toy on the floor.

To summarize, this series of studies suggests that there might be several reasons why infants younger than 18 months do not learn to use a tool from a classic demonstration. First, not understanding the goal of the demonstrator may keep them from making sense of what they observe. Second, two demonstrations may not be enough to learn a complex affordance such as that of a tool: repeated demonstrations over an extended time period (weeks) may be necessary. Third, explicit teaching may not be the best way to help infants learn how to use a new tool. Fourth, an unexpected outcome leading to a shared positive emotional state is extremely effective in favoring learning from a demonstration. Another important conclusion from these studies is that, at least in the case of the rake, whose affordances may not be known to a child under 2 years of age, observational learning may be more important than manual practice in discovering new functions.

These findings share common interpretations with the studies on the factors influencing infants' abilities to imitate mentioned in the introduction (opacity of the means, of the goal, of the model's intention, irrationality of the means, etc.). Two interpretations can be proposed to explain them. One is that there is a cognitive load in understanding the demonstration of the model: the infant may not know what to attend to, what part of the action is important for success, when to pay attention, what is the affordance of the rake, etc. When the infant is shown the model's intention before demonstration, when the goal is made clearer, when more demonstrations are provided, then the child better understands the affordance of the rake and how he or she should proceed to act like the model. Another, non-exclusive, interpretation is that learning is always based on social cues and interactions: not knowing how to reach a goal may be stressful for the young child, just as it is for adults, and the social cues given to the learner, and more generally the social context of the demonstration, may make a huge difference in the efficacy of the modeling of the action; this might explain why when there is no implicit pressure (such as "do like me"), or when the unexpected outcome puts the child in a positive emotional state, children are more likely to understand the means used by the model to retrieve the toy.

In conclusion, observational learning of complex new tasks in young children (as opposed to imitation of simpler tasks) is a somewhat neglected topic in developmental psychology. This review of studies we have done in our laboratory suggests that observational learning may be an important factor to consider in understanding the acquisition of tool use, in addition to more traditionally studied factors such as perceptual constraints, exploration and trial and error. Our review suggests that further work on observational learning should profitably include work on how a child interprets a demonstrator's intentions, and on how implicit observation of non-teaching situations over extended time influences learning. Such studies may have pedagogical implications as concerns teaching new skills to very young infants.

AUTHOR CONTRIBUTIONS

JF and JO have co-supervised most of the experiments presented in this article. They wrote the article. They also conducted the longitudinal study presented first. LR-F is the main investigator of the first cross-sectional experiment (Classic demonstration), and the co-investigator of the other experiments presented in this article. She wrote the article where she is first author and participated to the other articles. RE is the co-main investigator with LR-F of the experiments "Intention prior to demonstration" and "Humorous demonstration," and she wrote the articles where she is first author. ES is the main investigator of the experiment "Implicit repeated demonstration" and she has written the corresponding article.

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REVIEW
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Infants' Understanding of Object-Directed Action: An Interdisciplinary Synthesis

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Recognizing that the object-directed actions of others are governed by goals and intentions is a crucial component of human interaction. These actions often occur rapidly and without explanation, yet we learn from and predict the actions of others with remarkable speed and accuracy, even during the first year of life. This review paper will serve as a bridge between several disparate literatures that, we suggest, can each contribute to our understanding of how infants interpret action. Specifically, we provide a review not just of research on infant goal attribution *per se*, but also incorporate findings from studies on the mirror neuron system and infant object cognition. The integration of these various research approaches allows for a novel construal of the extents and limits of early goal attribution – one in which the importance of the entire action context is considered – and points to specific future research directions.

Keywords: infant goal attribution, mirror neurons, object cognition, social cognition, action prediction

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INTRODUCTION

For 20 years, we have known that infants are able to encode the object-directed actions of others in terms of their goals (e.g., Gergely et al., 1995; Meltzoff, 1995; Woodward, 1998). In the intervening years, a great deal of thought and experimental effort has gone into untangling exactly how it is that infants produce these goal attributions. Indeed, the ability to attribute goals to others – a component of social learning, prosocial behavior, and communication, with consequences throughout the lifespan – has been of interest to researchers in other fields as well who, in turn, bring their own theoretical backgrounds and techniques. The cross-disciplinary interest is in part due to the complexity of seemingly simple actions. For example, consider an infant who is witnessing an adult reach toward an apple. In addition to gathering evidence that the infant construes the action as being goal-directed, researchers might be interested in how that action is represented at a cellular level in the infant's brain, how the infant garners information from the shape of the experimenter's hand, or how the features of the apple are represented and maintained in the infant's memory. These are all interesting and valuable approaches to our understanding of object-directed actions, but there have been limited attempts to synthesize the contributions of different fields.

At best, a fragmented view of the research findings is limiting: to the observing infant, the topics of these separate lines of research all represent viable streams of complementary information. At worst, this fragmentation can lead to poorly controlled experiments as researchers may not be well versed in the theoretical and methodological insights from other related areas. Indeed, as these approaches all represent rich and active fields of study, maintaining a current understanding of these issues is a daunting task. However, infants obtain and implement their ability to represent the goals of others in a world that is complex and uncontrolled, and so piecing together how these streams of information interact together is crucial to forming a true understanding of infant goal attribution.

The aim of the following review is to synthesize the work from the last 20 years (approximately) that is explicitly related to infant goal attribution with research from the neuroscientific study of human and non-human animals and object cognition. To do so, we have organized the review into five broad (and subdivided) categories of influence that together constitute the *action context*: the experience and brain maturation of the infant observing the goal-directed action, the agent who is enacting the goal-directed action, the components of the action taken to achieve the goal, the nature of the goal-object itself, and the environment in which the goal-directed action occurs (**Figure 1**).

Before starting, however, it is important to present a few caveats. By 'goal attribution,' we specifically refer to a process by which an infant forms either an expectation or a prediction regarding the target and nature of another's ongoing or future action. Though 'goal attribution' in this sense could be applied to a number of types of events, in the following paper it refers almost exclusively to an object-directed[1] reaching action. Second, categorizing aspects of the action context is not meant to imply orthogonality between them. As will be clear throughout the review, there is substantial overlap between these categories. Finally, we are not proposing that that this organization reflects any sort of functional model of infant goal attribution, nor do we suggest that the categories of influence on infant goal attribution are necessarily processed simultaneously or even in every circumstance. Rather, we have synthesized a wide variety of studies on a wide range of influences on infants' attribution of goals and present them without attempting to make strong claims as to the relative importance of each type of influence. In part, this is due to a lack of the empirical evidence necessary to do so. However, the primary goal in using this organizational framework is to show the potential sources of information vying for infants' attention in a way that draws attention to the importance of the entire context in which goal-directed action occurs.

THE OBSERVER

In the action context discussed in this paper, the observer is an infant who is watching an agent perform a goal-directed action. In a seminal study, Woodward (1998) demonstrated that infants at 9-months of age are sensitive to the goals of others. In a procedure that has since become widely utilized, 6- and 9-month-old infants first watched as a hand moved out onto a table containing two objects. The hand would approach and grasp one object from the pair, and would remain in this position until the end of the trial. This action was repeated upon the same object until the infants habituated (i.e., their looking time to the event decreased to a predetermined criterion). At this point, the locations of the objects were switched, and the hand reached either toward the same object in a new location or

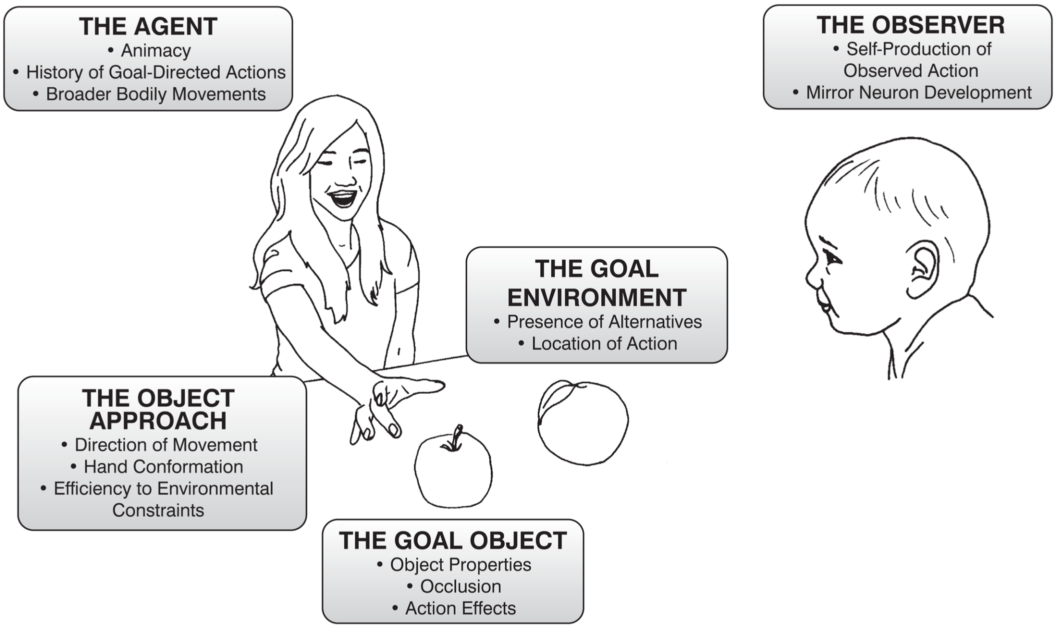

FIGURE 1 | Description of the elements of an object-directed reach that can influence infants encoding of the goal of that reach. The following paper will discuss each of the categories listed above and expand upon how the listed factors influence infant's judgements.

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[1] In most cases in this review, an object is a discrete and visually distinct artifact of a size easily graspable by an experimenter, such as a teddy bear or a ball, as this is typical of what is presented in the majority of the experiments discussed. However, it is useful to recognize that the category 'object' is exceptionally broad and could potentially encompass nearly any physical feature of the infant's environment, including the bodies of agents or that of the infant themselves.

the previously untouched object in the previously reached for location. Infants dishabituated (increased looking behavior) to the latter, indicating that they encoded the original reach as directed to a particular object. It has subsequently been shown that infants make predictions, as measured by eye gaze, regarding which object will be reached for within this paradigm (Cannon and Woodward, 2012).

Woodward's experimental procedure has been remarkably fruitful and has revealed much about how infants view the actions of others. For instance, some researchers, performing variations on Woodward's (1998) classic experiment have shown that even younger infants attribute goals to others (e.g., 5 months, Luo and Baillargeon, 2005). Tests with younger infants have found more mixed results (Sommerville et al., 2005; Luo, 2011). This change in behavior over time, which appears to center on about 5 months of age, suggests a likely role for both experience and brain maturation. In this way, age is one characteristic of the observer that influences the way they perceive the actions of others.

Self-Production of the Observed Action

Several studies from Sommerville et al. (2005) have emphasized the role of action experience in the development of goal attribution. Sommerville et al. (2005) placed Velcro mittens on the hands of 3-month-old infants and gave them time to interact with Velcro objects in their vicinity. Typically, infants begin to reach for objects in their vicinity sometime between 3- and 5-months of age, so the infants in this study were old enough to extend their hands and contact the objects, but not yet coordinated enough to have much first-hand experience with reaching and grasping prior to their session with the 'sticky mittens' (von Hofsten, 1991; Thelen et al., 1993; Berthier and Keen, 2006). When these infants took part in a version of Woodward's (1998) experiment featuring an experimenter wearing the same gloves, they expected the actor to act consistently following the switch in target object locations, while inexperienced infants showed no expectations. In particular, the role of first-person experience seems to be particularly important, as infants who have simply observed others using the Velcro mittens show no expectation for consistent goal-related action (Woodward, 2009).

Further, there is a relation between the ability to produce an action and to predict the goal of an action (Falck-Ytter et al., 2006). In this study, infants watched a video in which an experimenter reached toward objects on a stage and lifted them across the stage and into a container. Adults and 12-month-olds both showed predictive gaze toward the target. Six-month-olds, however, lacking the ability to perform such an action themselves, did not exhibit anticipatory gaze toward the target. Kanakogi and Itakura (2011) similarly demonstrated a relation between object-directed action prediction and the ability to produce object-directed reaches by examining infant eye movements. Four-month-old infants, who lacked the ability to perform grasping actions, did not make anticipatory gazes, but 6-, 8-, and 10- month-old infants, did gaze toward the target of the reach before the arrival of the experimenter's hand.

More recently, infants' ability to predict the goal of specific types of object-directed reaching actions were measured alongside their ability to perform the grasping actions themselves (Ambrosini et al., 2013). Six-, 8-, and 10-month-old infants watched a video in which a small ball and a large ball were present on a table. The infants watched as an experimenter made reaches toward the objects with either a closed fist, a hand shaped for a whole-hand grasp, or a hand shaped for a precision pincer grip. Infants are able to make whole-hand grasps at all three of these ages, but the pincer grasp typically develops around 8-months of age or later. While the experimenter made reaches to both the large and small balls with the closed fist action, the other reaches went to the appropriate target for their reach type (whole hand to large ball, pincer to small ball). All infants showed an advantage in goal anticipation toward the whole hand grasp compared to the fist-to-large ball reach. However, predictive advantage for precision grasping was only present and 8- and 10-month old infants, and was greater in the 10-month olds, consistent their increased experience with this action over the younger infants. Relatedly, 10-month-old infants who received direct experience with using a cane to reach a toy were later sensitive to the goal of a cane-using actor, yet infants who had observed another person training, or who had received no training, were not (Sommerville et al., 2008).

In addition to experience, the infant's own engagement also seems to play a role in their growing understanding of others actions. Infants are not passive observers of other's actions, though often positioned that way in experimental settings, and some researchers have made a case that infant participatory role in others actions is more crucial than it is typically given credit for (Reddy and Uithol, 2015). Moll et al. (2007) demonstrated that 14-month-old infants had stronger recognition of the goal of an agent if they had engaged directly with an experimenter as opposed to watching that experimenter have an interaction with another person. Others have shown that mother-infant interaction style can have an influence on the age at which infants are able to demonstrate goal attribution (Hohenberger et al., 2012; Licata et al., 2014). The infant's own part in influencing the goal directed actions of others is clearest when considering that in the early months of life (and to a lesser extent into the toddler years) the goal-directed actions most frequently observed by an infant will feature the infant themselves as the target of that action (picking up, feeding, diaper change, dressing, etc.). Indeed, infants make postural adjustments in anticipation of infant-as-object action from their mother as early as 2-months of age (Reddy et al., 2013). A stronger understanding of how infants level of engagement with others interacts with their own ability to produce actions will likely prove crucial to a complete picture of how goal attribution influences infants' behavior in their day-to-day lives.

Though infants' own production of action does seem to be important to their interpretation of others' behavior, its precise role remains unclear. Infants also attribute goals to non-human agents (Shimizu and Johnson, 2004; Luo and Baillargeon, 2005; Johnson et al., 2007), to novel tool-use actions (Hernik and Csibra, 2015), and to actions that are biomechanically impossible (Southgate et al., 2008), situations with which infants could not possibly have first person action experience. In turn, as will be seen in section "Mirror Neuron Development," the attribution of goals to animated, non-human agents has also called into question the dominant mirror neuron theory of action comprehension (e.g., Hamilton and Ramsey, 2013).

Mirror Neuron Development

Another aspect of the observer that influences their perception of others' actions is their brain development. Imaging studies of the infant brain are notoriously difficult, though it has become more and more common in recent years. A good deal of the work relating brain measures to infants perception of action has been focused on the topic of mirror neurons and action mirroring, so we will provide here an overview of this topic before moving on to examples more specific to the topic of this review.

Mirror neurons are visuomotor neurons that discharge both when an individual performs a particular action and when that individual observes another performing a similar action (Rizzolatti and Craighero, 2004). Since their discovery, mirror neurons have been posited as a mechanism by which we might understand the motor activities of others (e.g., Gallese et al., 1996; Rizzolatti et al., 1996). These neurons were first discovered in the ventral premotor cortex, area F5, of macaque monkeys (*Macaca nemestrina*) and were demonstrated to be active both during the production of an action and while witnessing another performing that action (di Pellegrino et al., 1992). The first evidence that this class of neuron exists in humans emerged almost 20 years ago, but their existence remained controversial until recently, when the mirror activity was directly observed in neurons in the brains of surgical patients (Fadiga et al., 1995; Mukamel et al., 2010). More commonly, mirror activity is observed via electroencephalography (EEG) in the desynchronization of the mu rhythm, which occurs during the production and observation of action and which has been observed in both infants and adults (Cochin et al., 1998, 1999; Rizzolatti and Craighero, 2004; Nyström, 2008). A recent meta-analysis of fMRI studies with human participants found persistent evidence for 'classical' mirror neuron activity in inferior frontal gyrus, ventral premotor cortex, and IPL, as well as in less expected areas such as primary visual cortex and cerebellum (Molenberghs et al., 2012). Mukamel et al. (2010) observed mirroring in SMA, as well as in more unusual areas, such as hippocampus, entorhinal cortex, and parahippocampal gyrus, which has led to the suggestion that mirror neurons may represent a widely distributed minority of neurons (Keysers and Gazzola, 2010).

Since the activity of mirror neurons was first observed, they have been posited as a potential mechanism for the understanding of action. The *direct matching hypothesis* posits that observed actions activate a resonance mechanism that directly maps the observed action onto one's own internal motor representation of that motor action, and thus mirror neurons allow us to understand others' actions through a simulation of their acts (Rizzolatti et al., 1996; Iacoboni et al., 1999). In one study with adults, it was shown that Transcranial Magnetic Stimulation of the hand motor area, but not of the leg area, produced deficits in predictive saccades while watching a reaching hand (Elsner et al., 2013). It has been proposed by proponents of this theory that mirror neurons represent an evolutionarily selected innate endowment (Rizzolatti et al., 1996; Gallese et al., 2007); indeed, some studies have provided support for this through the use of EEG with rhesus macaque neonates during observation and production of facial movements (Ferrari et al., 2012).

This direct matching hypothesis has been criticized recently, for a variety of reasons. For example, mimed actions (a grasp without a target) do not activate mirror neurons, yet if mirror neurons were simulating acts to determine their goal, then the mirror neurons would have to activate in order to determine that there was no goal to a mimed act (Csibra, 2005). Similarly, a number of studies have shown mirror neuron activation in response to the actions of members of a different species (Buccino et al., 2004), computer animated agents (Hamilton and Ramsey, 2013), or by a robotic claw (Gazzola et al., 2007). Additionally, studies of people with apraxia have shown a dissociation between the ability to produce and recognize actions (Negri et al., 2007; Hickok, 2009).

More recent theories regarding the role of mirror neurons in goal understanding have made attempts to incorporate the response to actions that could not be represented in the motor system. One suggestion is that there is a secondary mechanism to motor mirroring, a 'mentalizing network,' that attempts to represent the actions of others in terms of their underlying intentions (Rizzolatti and Sinigaglia, 2010). Under this formulation, the mirror system recognizes a reach to a cup as serving the goal of drinking water, while the mentalizing system could represent the reasoning underlying that action (e.g., to alleviate thirst or to rinse a bad taste from one's mouth). Others have suggested that there are neurons within the motor system that are activated in response to the *goals* of produced and perceived motor acts (Gazzola et al., 2007). By this account, observers are directly matching the goals of others to their own goal representations, rather than matching the kinematics of an action to one's own representation of that action. Support for this interpretation includes the finding that monkey mirror neurons in F5 will discharge to the closing of a set of pliers on a goal, even pliers requiring different hand movements to operate (Umiltà et al., 2008). Additionally, there may be experiential effects on mirror neurons, as these effects can only be observed after the monkeys have had extensive experience with the tools (Ferrari et al., 2005; Umiltà et al., 2008; Rochat et al., 2010; Cook, 2012). Indeed, there is evidence from human infants that suggests that first-person experience with observed actions influences motor cortex activation in response to observed actions in a way not observed following strictly observational experience with an action (van Elk et al., 2008; Gerson et al., 2015; Cannon et al., 2016).

These theories describe mirror neurons as an innate evolutionary endowment, the development or dysfunction of which during infancy has been suggested to be related to a number of phenomena beyond action understanding, including neonatal imitation (Rizzolatti et al., 2001), autism spectrum disorder (Williams et al., 2001), and language development (Rizzolatti and Arbib, 1998). However, it has also been suggested by Heyes (2010) that mirror neurons are not innate, but are instead tuned through the correlated sensorimotor experiences of observing and executing the same actions. This *associative hypothesis* reduces the role of mirror neurons in action understanding compared to the direct matching hypothesis, supposing rather that mirror neurons make up one component of many that are used to a variety of social-cognitive functions. It is suggested that mirror neurons do not 'do' any specific thing, but that their function is determined on an individual level based on the sensorimotor experience of that individual (Heyes, 2013). Cook (2012) proposes that associative processes are more compatible with the activation of mirror neurons in response to learned acts, such as tool use, dance, and in association with sensory stimuli. However, while the associative hypothesis does provide room for developmental and learning processes, it also does not provide a specific account of what it is that this population of neurons contributes to the production or understanding of actions.

From the research with infants that does exist to date, a model is proposed in which goals are initially identified outside the motor system through the presence in the action of various cues to goal-direction, but once they have been identified, the motor system is recruited for predictive motor simulation (Southgate, 2013). This simulation does not need to precisely match the observed action, but rather is an emulative simulation of how the goal might be achieved. Southgate supports this view with evidence that infants show motor activation to actions for which the infants could not have a corresponding motor representation (Southgate and Begus, 2013). In this sense, experience matters in that it provides a template for the prediction, but the experience does not necessarily have to match the observed action.

Summary and Outstanding Questions

There is evidence that infants' own experience with the production of object-directed actions has an influence on their ability to understand and predict the ongoing actions of another. However, the attribution of goals in situations in which infants could not possibly have had experience suggests that action production is not entirely required for goal attribution, or that some experiences can be extrapolated into an understanding of otherwise seemingly impossible situations. There must also be a mechanism for the programming or reprogramming of mirror neurons through motor experience, and there is some evidence to suggest that this may relate to first-hand experience rather than observation (Gerson et al., 2015; Cannon et al., 2016). The evidence for the importance of experience is compatible both with the converging data suggesting that action mirroring in the motor cortex is in some way involved in goal attribution and the more recent suggestion that mirror neurons may be sensitive to goals rather than to particular actions.

Given the lack of concrete evidence for the existence of this population of neurons in the brains of human infants, it is unclear whether researchers are observing true mirroring (neurons firing in response to the same action, both when produced and observed) simply motor activation in response to object-directed actions (some neurons firing in relation to produced actions, adjacent neurons responding to observed actions). However, providing a definitive answer to this question will require great technological advancements to achieve the required spatial resolution in a non-invasive fashion. Here, our aim is not to argue against the existence of mirror neurons in human infants, but merely to call for caution in the interpretation of less direct measures of neural activity, especially in studies where neural activity during action production is not measured.

THE AGENT

Infants understand object-directed events to be attributes of the actor (the 'agent'); goals are not generalized from one individual to another (Buresh and Woodward, 2007; Henderson and Woodward, 2012). In this section, we present findings that suggest that the agent who performs the object-directed action provides a number of signals to the observing infant, including their animacy, their history of actions, and their broader bodily movements. In section "The Object Approach," we will discuss the signals presented by the more fine-detailed mechanics of the agent's goal-directed action.

Animacy

Infants appear to limit goal attributions to animate and animated entities, suggesting that distinguishing the animate from inanimate is an important component of this ability. The exact properties of entities that result in the percept of animacy for adults and infants are the topic of a rich body of research (for a review, see Rutherford and Kuhlmeier, 2013) with foundations in the work of Heider and Simmel (1944) and Bassili (1976). Here, we emphasize research that specifically pertains to infants' recognition of action that is directed to goal objects during the first 2 years of life.

Early, seminal research alluded to the special status of animate (in this case, human) motion to infant goal attribution; in Woodward (1998), infants increased visual attention to a rigid stick moving in a new path of motion rather than to a new goal object, and 18-month-olds in Meltzoff (1995) re-enacted the goal-directed behavior of a human actor but not a machine. Subsequent work has demonstrated that infants encode the actions of agents as directed to particular goal objects if there is evidence that the agent is self-propelled or, relatedly, can change direction (Luo and Baillargeon, 2005; Luo and Johnson, 2009), that the agent can interact contingently with other agents (Shimizu and Johnson, 2004; Johnson et al., 2007), and that the agent is capable of biological motion (Yoon and Johnson, 2009). In these studies, the goal-directed actions are limited to approaching or gazing at objects, owing to the limited physical affordances of the animated agents. As will be seen in section "Hand Conformation," however, infants appear to consider more fine-grained physical affordances when agents with more articulated appendages (e.g., hands) are depicted.

History of Goal-Directed Actions

Many studies of infant goal attribution use a procedure in which the infant observes an agent repeatedly performing a goal directed action before an alteration is made to the scene, at which point the infant's recovery of interest in the scene is measured by looking time. The amount of exposure differs between studies: some use infant-determined habituation paradigms (e.g., those that closely follow Woodward, 1998) while others use familiarization paradigms in which exposure is predetermined by the experimenter (e.g., Luo and Baillargeon, 2005; Hernik and Southgate, 2012). Yet, the fact remains that in these studies, one of the primary pieces of information available to infants regarding what the agent will do in test trials is what the agent has done in the past. Indeed, in more recent studies measuring eye-gaze during the observation of action, infants predict the target of an action, but must see the completed action at least once before doing so (Henrichs et al., 2012; Brandone et al., 2014).

Infants also appear to consider an actor's new goal directed action in relation to previous action in a different setting. By at least 9 months, infants discriminate between approach behavior to two different characters based on the agent's previous interactions with the characters in another environment (i.e., helping or hindering, Kuhlmeier et al., 2003; Hamlin et al., 2007; Kuhlmeier, 2013). Relatedly, at the same age, infants who have observed an agent repeatedly manipulate an object in a certain manner (e.g., slide it) look longer if she selects an object that, due to a change in the physical setting, cannot be manipulated in the same way (Song and Baillargeon, 2007). These results suggest that infants are considering not only what an agent is doing in the present, but also what an agent has done in the past. Future studies might consider how others' past inconsistencies influence infants' later expectations and predictions.

Broader Bodily Movements

The agent's bodily motion, beyond the movement of a reaching arm and hand (see The Object Approach), also appears to be an informative signal relevant to infant goal attribution. Head direction and eye gaze, like a reach, appears to be construed as object directed. Four-month old infants who saw an actor gaze at one of two objects reliably looked less at the object that had been the target of the actor's gaze, even in the absence of the actor, suggesting that the infants found the object that had not been cued by the actor's gaze to be more novel (Reid and Striano, 2005). More relevant to the topic of this paper, by at least 12 months of age, infants who were habituated to an event in which an agent gazes toward and smiled at one of two objects later looked longer at events in which the agent held the object that they had *not* previously gazed toward (Phillips et al., 2002). Thus, eye-gaze appears to be interpreted as object directed and may provide information to infants as to an agent's subsequent object-directed reaches.

Further examples of infants' use of movement in their interpretation of goal directed action come from infant-directed action, the 'motionese' described by Brand et al. (2002). In this study, mothers were asked to demonstrate the properties of five novel objects to either an adult partner or to their own infants. Compared to their interactions with the adults, the mothers' demonstrations to their infants occurred in closer proximity to the infants, with greater enthusiasm and repetition, and exaggerated but simpler movements. This finding has been expanded upon by others who have demonstrated that parents' engagement in 'motionese' in object-directed actions witnessed by their infants both increases the attention paid by infants to the action and influences the infant's own later exploration of that object (Brand and Shallcross, 2008; Koterba and Iverson, 2009). Thus, it is possible that outside of laboratory examples of simple object directed reaches, in which 'motionese' is typically limited, infants may regularly use these movements in their interpretation of others' object directed actions.

Summary and Outstanding Questions

The agent performing an action represents a particularly rich source of information to infants. Infants are capable of interpreting information from the agent's gaze, from their history with that agent, and from cues that the agent may be providing specifically in an attempt to enhance communication. However, a number of questions remain about what infants take away from this type of information. For instance, while we know that infants use historical information about agents to shape their expectations for those agents, it is unclear exactly how long lasting this influence is, or how durable to changes in the broader environment. Sommerville and Crane (2009), for example, found that 10-month-old infants' goal attributions may not extend across a change in the room in which the action is occurring. In most goal attribution studies, repeated action is followed closely in time by a test, but it is unclear how readily this translates to infant's viewing of everyday action.

THE OBJECT APPROACH

The way that a goal object is approached is also a source of information for infants attending to the action. Indeed, these actions are typically as direct as possible while also being 'honest' in that in order to act upon an object, one must necessarily bring themselves into contact with that object in a manner that affords the particular action.

Direction of Movement

A feature of goal attribution studies that is not often discussed is that the *completion* of the object directed goal is typically witnessed by the infant viewing the reaching. It is thus interesting to consider how infants respond when a portion of their viewing of an action is disrupted. Daum et al. (2008) presented 6- and 9-month-old infants with a video of an experimenter beginning a reach toward one of two objects on a stage, from both the point of view of the experimenter and that of an onlooker. When the experimenter's hand passed between the midpoint between their starting position and the target object, the video stopped and the infants were simultaneously presented with still frames of completed reaches: a plausible outcome depicting the experimenter holding the object that was on reach trajectory, and an implausible outcome in which the other object was grasped. Infants looked longer toward the displays presenting the implausible outcomes, suggesting that they had formed an expectation as to the target of the reach from the direction of the arm during the initiation of the reach.

Repeated actions that approach the same object but from different starting locations also appear to indicate to infants that, in general, the actions are goal-directed. Evidence for the influence of this 'equifinal variation' comes from studies in which infants observe an agent who does not grasp an object, but approaches it through variable routes. In a variation on the Woodward (1998) design, for example, Biro and Leslie (2007) found that 6-, 9-, and 12-month-old infants looked longer when a new object was approached after previously observing a hand or paper tube repeatedly poke a different object from multiple directions. In later studies, both 3-month-old (Luo, 2011) and 6.5-month-old infants (Csibra, 2008) appeared to view the actions of an unfamiliar, non-human agent as directed to a goal object if the agent approached the target object efficiently and with variation in target approach.

Hand Conformation

At some point during the first year of life, infants begin to consider the appropriateness of the conformation of an agent's hand to the action they are taking. For example, 9-month-olds who observed repeated, non-functional but object-directed action (an approach with the back of a hand) did not respond to changes in the target object as they do with grasping actions (Woodward, 1999). Similar results have been found in other studies, in which infants made anticipatory gazes toward the target of a grasping reach, but not toward the target of a back-of-hand reach (Kanakogi and Itakura, 2011; Krogh-Jespersen and Woodward, 2014). Additionally, infants are less likely to choose the same target as an experimenter when that experimenter has used a back of hand action (Hamlin et al., 2008). Neuroscience techniques have found converging results. Using EEG, Southgate et al. (2010) found that 9-month-old infants did *not* show motor activation in response to the viewing of a back of the hand action.

Infants also use hand conformation to form expectations about the action that will be performed. Six-month-old infants who were able to produce a pincer grip looked longer when a pincer grasp or a palmar grasp were used on apertures inappropriately sized for those grasps, while infants lacking a pincer grip showed no expectations (Daum et al., 2011). Relatedly, Gredebäck et al. (2009) performed a study in which infants viewed an experimenter either reach for objects and move them across a stage or move a closed fist to each object and then the opposite side of the stage, mimicking the arm movement in the other condition. At 14-months, but not 10-months, infants made predictive gazes to the targets of reaches, but their gaze followed the closed fist reactively. Similarly, as noted in section "Self-Production of the Observed Action," the pre-shaping of the hand to the size of the target plays a significant role in infants' ability to predict the target of a reach, depending on their ability to produce that grip themselves (Ambrosini et al., 2013).

Efficiency to Environmental Constraints

An additional cue comes in the form of the path taken by the agent toward their goal object. This information has a prominent role in one of the most cited models of infant goal attribution ('the teleological stance,' Gergely et al., 1995; Csibra and Gergely, 2007). The model posits that the end state of an action may (or may not be) seen as the goal of the action depending on whether the action culminating in that end state is deemed to be efficient in relation to the current environmental constraints. To use a concrete example, by at least 9-months of age, infants consider the goal of an animated ball to be 'to approach the other ball' when its means (jumping over a barrier) of getting to this end state is rational given the situational constraints (a barrier is between the balls; Gergely et al., 1995). Similarly, Southgate et al. (2008) found that 6- to 8-month-old infants looked longer at a less efficient motion path (e.g., unnecessarily moving other objects before reaching for a goal object) than a biomechanically impossible motion path (e.g., 'snaking' around an obstructing object before reaching for a goal object), suggesting that these infants had a stronger expectation for efficiency of action than for possibility of action. Subsequent research using procedures based on Woodward (1998) and eye-tracking of predictive gaze have further suggested that inefficient action may actually prevent 7- to 12-month-old infants from encoding an action as goal-directed (e.g., Biro et al., 2011; Hernik and Southgate, 2012; Verschoor and Biro, 2012; Biro, 2013).

The empirical focus on the role of action efficiency in infant goal attribution has also led to a critical reappraisal of how we measure whether an infant construes an action as being goal directed. Take, for example, infants' observation of a reach for an object sitting alone on a table (or in the case of computer-animated agents, an approach toward an object). After habituation or familiarization to this event, infants do not discriminate between reaches for this same object and reaches for a new object that has been added to the table. This null result has been found across many studies and laboratories (Luo and Baillargeon, 2005; Biro et al., 2011; Luo, 2011; Hernik and Southgate, 2012). Some have interpreted these results to suggest that infants do not see reaches toward singly presented objects as being goal-directed because there is no evidence for efficiency of action. Indeed, in conditions in which an agent efficiently circumvents a barrier to get to the object, infants then appear to discriminate between the agent's actions on the old object versus a newly presented object (e.g., Hernik and Southgate, 2012). Yet, as noted by Kuhlmeier and Robson (2012), it is hard to consider a simple reach toward a single object in the absence of obstacles as anything other than goal-directed and efficient. While it has not been definitively demonstrated that the mirror neuron system is a mechanism for goal attribution in humans, it should be noted that mirror neurons were initially discovered in rhesus macaques because of activation in response to a simple, unimpeded reach toward a single object (di Pellegrino et al., 1992). Indeed, current work on human infants also suggests motor activation in response to the viewing of simple reaches (Nyström, 2008; Southgate et al., 2009).

Instead, it is possible that efficiency of action is particularly important on tasks in which infants must encode the features of a goal object, as is required on tasks in which test trials examine a looking time difference between reaches that continue to be directed to a previous goal object and reaches to a new object (e.g., similar to Woodward, 1998). In these tasks, infants only 'pass' if they have initially encoded the agent's reach as being directed toward 'that object' as opposed to being directed toward 'an object' (Kuhlmeier and Robson, 2012). Thus, it may be too early to claim that infants do not attribute goal-directedness to agents who reach for singly presented objects, though exactly how the goal object itself is encoded may be limited (see also Object Properties and Presence of Alternatives).

Summary and Outstanding Questions

From the work reviewed in this section, it is clear that the movement features of the reaching action are a rich source of information to infants. How the action occurs with respect to environmental constraints is a key component to infants' attribution of goals to others. Biomechanical information, in terms of hand shape and direction of movement, also plays a strong role, particularly in the anticipation of action outcomes. However, a number of questions remain about the processing of this information. In particular, it is worth considering the difference between the functionality of an action and the intentionality of an action. The extension of an arm to place the back of one's hand on an object is clearly an intentional act, but this action is also treated differently than other actions with a more obvious functionality vis-à-vis an object, on both a neural and behavioral level. Yet, it remains unclear whether infants are failing to attribute a goal or whether the goal of the action seen as something other than the object upon which the action is terminated.

THE GOAL OBJECT

One distinct way in which the object acted upon influences the way infants process that action as goal directed is through its very presence or absence. This factor has been especially studied in the mirror neuron literature. Rizzolatti and Craighero (2004), in a discussion of the basic properties of mirror neurons, write (emphasis added):

> "There are two classes of visuomotor neurons in monkey area F5: canonical neurons, which respond to the presentation of an object, and mirror neurons, which respond when the monkey sees object-directed action (Rizzolatti and Luppino, 2001). *In order to be triggered by visual stimuli, mirror neurons require an interaction between a biological effector (hand or mouth) and an object*. The sight of an object alone, of an agent mimicking an action, or of an individual making intransitive (non-object-directed) gestures are all ineffective."

In both adult humans and macaque monkeys, mirror activation has been shown in response to an object-directed action, but not to viewing the same motion performed in the absence of an object (di Pellegrino et al., 1992; Gallese et al., 1996; Umiltà et al., 2001; Muthukumaraswamy et al., 2004). Mirror response in the absence of an object-directed action has been observed, but only in a small minority of studies (Calvo-Merino et al., 2006).

Infants show motor activation in response to an apparently object-directed action but not in response to mimed grasping actions (Southgate et al., 2010). In this experiment, 9-month-old infants were measured with EEG as they watched a demonstrator either make a reaching grasp or a non-functional back-of-hand movement, either in the absence of an object or behind an occluder. Infants exhibited greater motor activation only while observing reaches behind an occluder. Even though the infants could not see the object upon which the reaching object terminated (in this case, one was not actually present), this was the only condition in which the infants could infer an outcome with which they have any experience. Indeed, this is not the only sense in which the availability of the objects matters to infants. For instance, Scott and Baillargeon (2013) demonstrated that infants also consider the mental and physical ease with which objects can be obtained.

Object Properties

Though the presence of an object appears to be an important factor in infants' construal of reaching events, by 12-months of age, infants may not differentiate between reaches to objects that are visually different but of the same kind. Following a procedure based on Woodward (1998), Spaepen and Spelke (2007) found that infants who were habituated to reaches toward one of two objects (e.g., a doll) dishabituated to reaches to a new object if the new object was of a different type (e.g., a truck) but not to reaches to a featurally distinct object of the same kind (e.g., another doll). Follow-up experiments revealed that infants could discriminate between the novel objects and the old, but that when the two objects available during habituation were of the same category, the infants did not look longer toward inconsistent choices within that pair at test.

From the first few months of life, object properties have been shown to have an influence on infant looking behavior, in the absence of any goal directed action, and in different ways than seen in adults (Adams, 1987; Henrichs et al., 2012; Taylor et al., 2013). Infants' own experience with certain object properties, such as weight, also influences the way infants view objects and the actions of others upon those objects. For instance, 11-month-old infants show preferential reaching toward objects they expect to be lighter (Paulus and Hauf, 2011). Infants also show differential *mu* desynchronization when watching an experimenter lift an object based on their experience with that object weight (Marshall et al., 2013a,b).

The affordances of an object, and the infant's experience with the use of a particular object, also influence infants' expectations for action on that object For instance, one study found that 12-month-old infants, after watching an experimenter reach for and grasp one of two objects, demonstrated stronger motor cortex activation in response to 'extraordinary' events (e.g., phone to mouth, cup to ear) than to 'ordinary events' (phone to ear, cup to mouth; Stapel et al., 2010). This result was interpreted as demonstrating increased goal-related planning from the infants as they re-evaluated the unusual action during its execution. In a similar paradigm, Hunnius and Bekkering (2010) examined the anticipatory gaze of infants at a number of ages (6-, 8-, 12-, 14-, and 16-months) and found that infants were more likely to make anticipatory gazes toward the functional target than the non-functional. In another study, it was determined that infants 20-month-old infants, but not 14-month-olds, can predict the intended use of a multi-purpose tool based on the way it is grasped initially (Paulus et al., 2011).

Taken together, these studies suggest certain object properties are more likely to attract infant gaze, influence infants own predilections toward acting upon those objects, and influence the expectations infants have for others' actions upon those objects. Moreover, infants bring their own experiences with objects to the experiment with them, which can impact the expectations infants have for the actions taken upon those objects. The way that experience with objects influences infants' expectations for others actions upon those objects is ripe for study (e.g., whether the onset of eating solid food narrows expectations for the types of things that an experimenter might bring to their mouth).

Occlusion

Though infants are able to process the features of goal objects while they are within view, they have difficulty binding these features to their representation of the object while it is out of view. Yet, a key component of the goal attribution studies discussed thus far is that the objects are typically out of the infant's sight for some amount of time during a testing session (e.g., when a curtain is lowered or when the locations of the objects are switched[2]). Thus, in order for an infant to show looking time differences for object-directed reaches in a Woodward (1998) style design, the infants must not only have attributed a goal to the actor, but also remember the identity of at least one of the objects that were available to her, even through occlusion. The following section will outline studies demonstrating infants' difficulty maintaining feature-rich object representations in a way that is robust to occlusion, followed by a discussion as to how this research pertains to infant goal attribution studies.

Experiments on infant object understanding often relate to two concepts, object individuation and object identification. Object individuation refers to the formation of distinct representations for the object/s in question ("there are two things"), while object identification refers to individuating objects and binding at least some of the features of that object to ones representation of that object ("there is a yellow ball and a pink bear"). Research suggests that infants first gain the ability to individuate objects. These spatiotemporally defined representations allow the infant to perform operations such as addition (e.g., 1 object + 1 object = 2 objects: Wynn, 1992), though the identity of the objects is not represented (e.g., 1 Elmo + 1 Elmo = 2 Ernies: Simon et al., 1995).

The earliest ages at which infants have been shown to notice a change in the identity during the presentation of multiple occluded objects is 6-months, at which point infants can identify a single object from a pair, and only if the spatiotemporal distinction is maintained between the objects during occlusion through the use of separate occluders for each object (Kaldy and Leslie, 2005; Kibbe and Leslie, 2011). However, even by 12-months of age, infants still have some difficulty maintaining robust, feature-rich representations of objects that have gone out of sight. For example, after observing a rubber duck and a toy truck emerge one at a time from opposite sides of an occluder, 12-month-olds (but not 10-month-olds) looked longer when the occluder dropped to reveal only one object (e.g., the duck). That is, prior to 12 months of age, infants do not appear to represent the occluded duck that they just saw as a 'duck' but as a featureless object that can emerge again as a truck (Xu and Carey, 1996). In a later experiment, the objects used varied either on size, color, and pattern, with the aim of determining which perceptual information would be sufficient to prompt infants to individuate multiple objects in the absence of clear spatiotemporal cues. Here, though, 12-month-old infants did not individuate, succeeding only when the objects differed in kind (Xu et al., 2004).

Findings such as these are difficult to reconcile with the results of goal attribution studies, in which 5- and 6-month old infants (and in some cases, 3-month olds), appear to notice when two objects have switched location while occluded by a single occluder. This situation lacks any spatiotemporal evidence of a change to the objects, and so infants must have bound some features to their representations of at least one of these objects in order to show differential looking time toward an actor reaching their prior goal object versus a different one. It is possible that other factors, of the sorts so far discussed in this review, may be prompting infants in goal attribution studies to form more robust, feature-bound object representations than infants in tasks specifically measuring object identification. This proposal will be addressed again in section "Presence of Alternatives."

Action Effects

The binding together of an action and the perceived effect of that action on the world appears to occur from as early as 2-months of age (Rochat and Striano, 1999; Verschoor et al., 2010). In a series of experiments, Verschoor et al. (2010, 2013) demonstrated that infants (ages 7-, 9-, 12-, and 18-months) can bind an action and its effect in a bi-directional way, and that infants after 12-months of age are influenced in their action selection by action effects. Detecting relationships between actions and their effects also impacts infants' understanding of others' object directed reaches. In previous sections, we noted that when an infant views non-functional back-of-hand action toward an object, they show different neural response than to grasping actions and also do not show changes in looking time when the target of the action is changed (Woodward, 1999; Southgate et al., 2010). However, when this back-of-hand action is presented along with a salient action effect, such as moving the object contacted, infants become sensitive to later changes in the target of the action (Király et al., 2003; Biro et al., 2014).

Further evidence for binding between object directed actions and their effects comes from measures of *mu*-desynchronization. Paulus et al. (2012) demonstrated that 8-month-old infants show greater *mu*-desynchronization when presented with the sound of a special rattle they had been trained to use, compared to other familiar and unfamiliar sounds. Nine-month-olds, when

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[2] A notable exception to this occlusion during the changing of the location of test objects (the only example of which the authors are aware) is found in Spaepen and Spelke (2007). In this work, two experiments occurred in which infants were habituated to a pair of objects of the same category (two distinct trucks or two distinct dolls), and their locations were switched before test within the view of the infants. This was done to examine whether the loss of spatiotemporal information was to blame for infants failure to show looking time differences toward inconsistent action upon objects of the same category when the location switch was occluded. As all three of these experiments presented null results; however, the conclusions that can be drawn from these results pertaining to the current discussion are limited.

presented with the sounds from a rattle that they have only ever seen shaken, show increased motor activation, despite having never produced the action to cause that sound before themselves. In sum, infants appear to bind novel action effects to their motor representations of actions already within their motor repertoire (Paulus et al., 2013).

Summary and Outstanding Questions

In this section, we have presented aspects of the goal object that appear to be relevant to infants' understanding of object-directed action. The mere presence or absence of an object and whether or not the action upon the object has any perceptible effect have a strong influence both on the neural processing of the object-directed action and, relatedly, upon the infants behavior in response to the action. The features of the targeted object and its affordances also influence infants' expectations for others actions upon them.

Of particular interest is how infants' ability to represent objects during occlusion is influenced by goal-directed action upon those actions. As brief occlusion of objects has been a commonplace feature of goal attribution studies since Woodward's (1998) original study, the discrepancy between the ages at which infants successfully encode the features objects in goal attribution studies (5–6-months, 3-months under certain circumstances) and object cognition studies (12-months, 6-months under specific circumstances) is worthy of examination.

THE GOAL ENVIRONMENT

Presence of Alternatives

As noted in section "Efficiency to Environmental Constraints," after observing an actor reach for an object sitting *alone* on a table, infants up to at least 9 months of age do not subsequently discriminate between reaches to this same object and reaches for a new object that has been added to the table (e.g., Biro et al., 2011). By some accounts, infants' difficulty in this task is due to the fact that though infants can attribute to agents both goals and preferences for objects, in the case of a reach or approach behavior directed to a lone object, there is no evidence regarding the agent's preference between the original object and the newly added object. Thus, in contrast with infants tested with the Woodward (1998) paradigm, infants have no basis for distinguishing between subsequent reaches to the old object or to the new one (e.g., Luo and Baillargeon, 2005). By another account, infants do not distinguish between reaches to the old and new object because they never encoded the original reach toward the single object as being goal-directed in the first place (Hernik and Southgate, 2012).

A third possibility, though, is that that infants fail to demonstrate expectations for action in a single-object condition because they did not encode the *specific* object the agent interacted with, not because they failed to perceive the action toward the single object as goal-directed or had no information regarding the actor's preferences. As noted earlier, tasks that are based on Woodward (1998) require infants to encode the features of objects that are reached for, and it is possible that the presence of an alternative object might influence infants' processing of the object that is being acted upon. In support of this claim, 9-month-old infants do not rely on the *identity* of a secondary, unchosen object as a prompt to encode the feature of an actor's target object, but do seem to rely on its mere presence (Robson and Kuhlmeier, 2013).

Yet, in other situations, the identity of potential alternative goal objects may be informative for infants in interpreting the object-directed reaches of others. For example, in one study, 9-month-old infants were tested in a paradigm involving multiple object pairings (Robson et al., 2014). Two objects (A and B) were present on a stage in front of an actor, who would reach out and choose one of these (A). In the next trial, there were also two objects on stage; this time the pair contained one object that had been seen before and one new object (B and C). Now, the actor reached for the previously ignored object (B). These trials alternated until infants reached habituation, at which point infants were shown just one of the pairings (A and B or B and C) and shown reaches that were either consistent or inconsistent (e.g., B when A and B were present) with the actor's previous goals. Infants looked longer toward inconsistent actions, suggesting that they must have been encoding not only the features of the target objects, but also of the alternatives. That is, a reach for B was inconsistent in the presence of A, but not in the presence of C. Using a similar method, 16-month-old infants were shown to demonstrate transitive inference, which again would rely on encoding the identity of the alternative objects (Mou et al., 2014). Thus, it is possible that infants may encode the features of alternatives when doing so is necessary to form expectations about which actions another might take.

Location of Action

Sommerville and Crane (2009) investigated 10-month-old infants' ability to represent goals across locations. They provided infants with unambiguous information about an actor's choice of objects by having the actor select one of two objects from a spot on the floor prior to testing. The infants then habituated to the selection of one object from a pair through means infants typically find ambiguous, either in the same room in which the pre-test reaching occurred, or in a different room. It was found that infants interpreted the ambiguous action as being about the target object only when the test was performed in the same room as the pre-test reaches toward that object. This suggests that, at 10-months of age, infants' representations of others goals may not be durable to changes in the broader setting.

However, in other studies, changes of scenery have not disrupted infants' representations of others' goals. As noted in section "History of Goal-Directed Actions," by 9 months, infants discriminate between an agent's approaches to two different characters based on that agent's previous interactions with the characters in another environment (i.e., Kuhlmeier et al., 2003; Hamlin et al., 2007). At the same age, infants who have observed an agent repeatedly move an object in a certain manner look longer if she selects an object that, due to a change in the physical setting, cannot be moved in the same way (Song and Baillargeon, 2007). A potential explanation for this discrepancy could be that in experiments where infants attribute goals across settings, it is the agent's location that has changed, while the infant has remained in the same place. However, further study of the durability of infants' attribution of goals to changes in setting is necessary for making stronger claims about why this occurs in some cases and not others.

CONCLUSION

In this review we have discussed how context can influence the way an infant processes the object-directed actions of others. We have drawn from research on the mirror neuron system, object understanding, and infant goal understanding, compared findings and methodologies across these disciplines, and discussed how findings from each of these domains may have implications for the others. The primary goals of this review were to provide a relatively broad, though likely not exhaustive, review of several research areas and discuss their relevance to the problem of understanding infant goal attribution. The secondary aim was to highlight the variety of sources from which infants can draw information to inform their expectations of others' object-directed actions. In doing so, we have presented a number of observations and open questions pertaining to each of these information sources, but in concluding will attempt to do so on a broader scale.

One of the most readily apparent directions forward is to study how these various sources of information available to infants work together, or how infants prioritize these sources when they conflict. As a result of our striving to perform controlled experiments, we often create artificial environments in which only one of these many factors is variable, when in fact any of them could potentially matter and almost all of them will be variable in the real life situations in which infants actually employ goal attribution as a mechanism for learning. Broadly speaking, motor system activation, personal experience and physical ability, and teleological considerations all appear to contribute greatly toward infants' understanding of the goals of others, with none of these appearing to be able to explain this ability completely in isolation. Comparing ages and achievements across object cognition and goal attribution literature seems to point to concurrent changes in these cognitive abilities at around 5–6 months of age that make goal attribution possible. Further evidence would be required to make strong claims regarding simultaneous changes in the mirror neuron system at 5–6 months. However, as infants are developing their own reaching capabilities at this age, and given the change in infant behavior toward others reaches as their own grasping competence grows (Gredebäck et al., 2009; Daum et al., 2011; Ambrosini et al., 2013) and the evidence for change in mirror neuron function in response to experience (Ferrari et al., 2005; Umiltà et al., 2008; Rochat et al., 2010), such changes seem plausible.

Attributing a goal to someone else is complicated, and there is a great deal of information available to an infant watching an object-directed action that can influence their interpretation of that goal. It is important consider all of these factors, not only to form a fuller understanding of this phenomenon, but to inform our thinking about how the methods we use can constrain how we conceptualize an ability.

AUTHOR CONTRIBUTIONS

Both authors made substantial contributions to the conception, writing and editing of this work. Both authors have approved this work for publication and agree to be accountable for all aspects of the work.

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Action Experience Changes Attention to Kinematic Cues

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The current study used remote corneal reflection eye-tracking to examine the relationship between motor experience and action anticipation in 13-months-old infants. To measure online anticipation of actions infants watched videos where the actor's hand provided kinematic information (in its orientation) about the type of object that the actor was going to reach for. The actor's hand orientation either matched the orientation of a rod (congruent cue) or did not match the orientation of the rod (incongruent cue). To examine relations between motor experience and action anticipation, we used a 2 (reach first vs. observe first) × 2 (congruent kinematic cue vs. incongruent kinematic cue) between-subjects design. We show that 13-months-old infants in the observe first condition spontaneously generate rapid online visual predictions to congruent hand orientation cues and do not visually anticipate when presented incongruent cues. We further demonstrate that the speed that these infants generate predictions to congruent motor cues is correlated with their own ability to pre-shape their hands. Finally, we demonstrate that following reaching experience, infants generate rapid predictions to both congruent and incongruent hand shape cues—suggesting that short-term experience changes attention to kinematics.

Keywords: action anticipation, infancy, motor resonance, motor experience, social cognition

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INTRODUCTION

The ability to anticipate others' actions allows us to interact with our social partners effectively. By proactively shifting gaze toward the end point of an action before that action is complete, we can efficiently coordinate our actions with others. Research suggests that the ability to anticipate the actions of social partners begins to emerge in infancy and may be coupled with one's ability to produce these actions oneself (Gredebäck and Kochukhova, 2010; Kochukhova and Gredebäck, 2010; Kanakogi and Itakura, 2011; Cannon et al., 2012; Falck-Ytter, 2012; Ambrosini et al., 2013). Despite considerable interest in the link between action experience and action anticipation, it remains unclear how the motor system translates different experiences into predictions about others' actions—particularly early in life when the motor system is changing rapidly. The current study examines the effects of reaching experience on action anticipation.

Action experience happens on multiple time scales: across minutes, hours, months, and even years. To date, studies have investigated the relation between action experience and action anticipation by examining experience across two timescales: long term, developmental timescale (across months) and immediate experience (across minutes) timescale. The developmental timescale compares infants who have acquired one skill level to those who have acquired another (e.g., comparing walkers to crawlers). In comparison, research investigating the role of immediate experience examines whether providing action experience immediately before test (typically referred to as motor priming) changes action anticipation.

Research has shown that adults and infants are influenced by experience across both timescales.

Across the developmental time scale, research has shown that long-term experience (or expertise) performing an action changes how rapidly both infants and adults predict action events: those with more experience tend to anticipate the timing of others' actions more accurately (e.g., Aglioti et al., 2008; Stapel et al., 2016) and generate faster visual anticipations to the action endpoint (Gredebäck and Kochukhova, 2010; Kochukhova and Gredebäck, 2010; Daum and Gredebäck, 2011; Kanakogi and Itakura, 2011; Cannon et al., 2012; Ambrosini et al., 2013). For instance, infants with more experience grasping objects generate faster visual anticipations to grasping actions but not back of hand actions or mechanical claw actions—suggesting a correspondence between action prediction and motor development (Kanakogi and Itakura, 2011). The experience of reaching for objects continues to develop throughout infancy as infants acquire fine motor skills and reach more efficiently for objects. Ambrosini et al. (2013) investigated whether these additional developments in fine motor control (specifically in the ability to use a precision grip to grasp small objects) are correlated with action anticipation. Infants observed a person reach for one of two balls using either a whole-hand grip or a precision grip. Following action observation, they tested infants' own fine motor skills. They found that infants who used fewer fingers to grab small objects generated faster visual predictions to others' precision grip actions—suggesting that infants' fine motor ability is linked action anticipation. Thus, across a developmental timescale more experience performing an action is correlated with faster action anticipation.

While these findings show that long-term experience is related to infants' visual anticipation of actions, as yet, it is not known whether (or how) immediate experience affects action anticipation. Studies that have looked at global levels of attention indicate that there are effects of immediate experience on action perception. To illustrate, Sommerville et al. (2005) gave 3-months-old infants experience coordinating their gaze and manual contact for the first time either before or after testing infants' sensitivity to others' goals. They found that only those infants who received this action experience first, show global attention differences in response to the goal structure of others' actions. This finding and others like it (Hauf et al., 2007; Sommerville et al., 2008; Gerson and Woodward, 2012, 2013) suggest action priming can change some aspects of infants' attention to others' actions. While global measures of visual attention provide information at a gross-level of description, they do not provide information about changes in attention as events unfold.

To date, it remains unclear whether (in addition to global attention differences) action priming also affects fine-grained aspects of online visual attention. Two studies have examined the effects of action priming on one measure of fine-grained visual attention (i.e., infants' online action anticipation) and the findings are mixed. Gredebäck and Kochukhova (2010) tested action anticipation to puzzle actions before or after infants put together puzzles themselves. They found no differences across testing orders—suggesting that some types of experience may not influence infants' anticipation of others' actions. In contrast, Cannon et al. (2012) found some evidence that prior experience influenced infants' action anticipation. Specifically, (although they didn't find group level improvement following action priming) they found that the amount of action infants engaged in prior to the action observation task influenced how rapidly they anticipated others' actions (but only among those infants who acted first)—that is, infants who put more toys into the bucket generated faster predictions to the bucket during the subsequent action observation phase.

The current study was designed to address why we find these different effects of experience on action anticipation. We examined the effect of experience across these two timescales by systematically varying the infants' own experience prior to action observation. Infants were either assigned to engage in a reaching task before (i.e., reach first condition) or after (i.e., observe first condition) the action observation phase. We reasoned that the reach first condition would provide information about the immediate effects of action on visual anticipation. In contrast, the observe first condition would provide information about differences in spontaneous action anticipation as a function of developmental variability in motor skill.

As a test case, we also assessed one aspect of infants' motor skill: infants' own hand pre-shaping ability. By 13-months infants' own reaching behavior is anticipatory (von Hofsten and Ronnqvist, 1988; Claxton et al., 2003). For example, infants pre-shape their hands in anticipation of the size, shape, and orientation of objects before making contact with those objects (Lockman et al., 1984; von Hofsten and Fazel-Zandy, 1984; von Hofsten and Ronnqvist, 1988; Morrongiello and Rocca, 1989). Hand pre-shaping is both a motor behavior that infants engage in and a behavior that (during action observation) could provide information about the type of object a person is reaching for. As such, we expected that 13-months-old would be adept at using this kinematic cue to generate visual predictions about reaching events.

To determine whether 13-months-old infants recruit kinematic details of others' action to generate action predictions we designed an action observation task where infants observe one of two types of reaching events: either the orientation of an actor's hand matches the orientation of the object that the hand makes contact with (i.e., congruent reach) or the orientation of the hand fails to match the target object (i.e., incongruent reach). Previous research has compared action anticipation when kinematic cues are present (e.g., hand pre-shapes into a precision grip) vs. absent (e.g., fist reaches toward object; see Ambrosini et al., 2013). We reasoned that our task could be more challenging because in the incongruent reaching event, the hand pre-shaping information matches one object on the screen yet the actor always reaches for the object that is incongruent with hand pre-shaping. We hypothesized that 13-months-old infants would spontaneously generate faster visual predictions when the target could be predicted by (congruent cue) the hand pre-shaping than when the target could not be predicted by (incongruent cue) hand pre-shaping.

The first aim of the current study is to evaluate whether infants' own hand pre-shaping is correlated with their recruitment of kinematic cues independent of their immediate experience. To do so, we also assess infants' own hand pre-shaping ability by giving these infants the opportunity to reach for a toy after the action anticipation task (Observe first condition). We reasoned that by recruiting variability across a developmental timescale we could examine whether there is a relationship between spontaneous attention to others' actions and infants' own motor skill. In line with previous research, we hypothesized that infants who spontaneously pre-shaped their hand more (in the observe first condition) would generate faster visual predictions when the kinematic cue was congruent but that this relationship would not be found in the incongruent kinematic cue condition. This would provide converging evidence that infants draw on their experience pre-shaping their hands when they recruit kinematic cues to anticipate others' actions—particularly when kinematic cues are present and reliable.

Our second aim was to assess whether immediate action experience changes attention to kinematic cues. To do so, we gave infants the opportunity to reach for a toy before (Reach first condition) we assessed their action anticipation. We hypothesized that if immediate action experience facilitates attention to kinematics, then infants in the reach first condition would generate faster congruent predictions than the infants in the observe first condition because their motor system is already primed to attend to kinematics. Alternatively, if immediate action experience facilitates attention to goal, infants in the reach first condition may generate equally fast predictions on congruent and incongruent trials.

MATERIALS AND METHODS

Ethics Statement

The Institutional Review Board at the University of Chicago approved the protocol for this study and written consent was provided by infants' parents/legal guardians prior to participation.

Participants

Participants were 70 full-term 13-months-old infants (36 females, $M = 13$ months, 2 days, $SD = 9$ days, range = 12; 12–13; 21) recruited from a large metropolitan city. Half of the infants ($n = 36$) were randomly assigned to do the eye-tracking task before the reaching task (Observe first condition) and half of the infants ($n = 34$) were randomly assigned to perform the reaching task before watching the eye-tracking videos (Reach first condition). 44% of infants were European American, 25% were African American, 3% were Asian, 10% were Hispanic, and 17% were mixed ethnicity. An additional 46 infants were tested but excluded from analyses due to fussiness during eye-tracking ($n = 9$), equipment failure ($n = 7$), failure to calibrate or percent data collected less than 50% ($n = 11$), fewer than three trials of predictive looks ($n = 18$[1]) and refusal to participate in the behavioral task ($n = 1$).

Apparatus and Stimuli

Data were collected via corneal reflection using a Tobii T60 XL eye-tracker (accuracy 0.5°, sampling rate 60 Hz) with a 24″ monitor, from a viewing distance of ∼60 cm. Infants sat on their parents lap and parents were asked not to direct infant's attention during testing.

Infants watched a short video of a hand reaching for one of two rods. See **Figure 1** for screenshots of each phase of the video as outlined below. These rods always remained in the same location (i.e., the blue rod was always on the left and the red rod was always on the right). The videos were timed such that infants were given 1000 ms to notice the rods before the hand entered the scene. After this time, the hand entered the scene flat on the table (event duration: 1000 ms). The hand then formed a shape and paused in that shape for 2000 ms. While retaining this shape, the hand then moved forward equidistant between both rods (event duration: 1000 ms). The hand continued in a smooth motion deflecting toward one of the two rods until it contacted that target rod (event duration: 1500 ms). Once the hand grasped the target rod it paused in this position for 500 ms.

Procedure

Action Observation Task

Eye-tracking began with a nine-point calibration period, followed by two blocks of videos. Each block consisted of six identical trials in which a hand reached (once per trial) for an object using a hand shape that was congruent with the target object (i.e., the object that the hand ultimately grasps) or incongruent with the target object. Each infant received one block of congruent trials and one block of incongruent trials, with the order of trial blocks counterbalanced across infants. Pilot data indicated order effects; as such we do not report data from the second block here.

In the first block of trials, infants either watched one of four possible congruent reaches (congruent cue) or one of four possible incongruent reaches (incongruent cue). Congruent reaches always correctly anticipated the orientation of the rod before the midpoint of the reach (see **Figure 1**). In contrast, incongruent reaches failed to match the orientation of the rod up until the hand was about to make contact with it, and the initial posture of the hand was appropriate for the non-target object (see **Figure 1**). Across infants, the order of the blocks, the side reached to, the hand shape, and the orientation of the objects were counterbalanced.

Reaching Task

Either before (Reach first condition) or after (Observe first condition) the eye-tracking task, infants were encouraged to reach for a rod presented by an experimenter. The rod was presented ∼19 cm from the infant. The experimenter presented the rod in one of two orientations (horizontal or vertical). The order of presentation was constant for

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[1] In our analyses we excluded infants that did not generate three predictive looks because our primary analyses concerned average latency scores. Here, we report the number of participants in each condition that were excluded for this reason: Reach first-Congruent cue: $n = 3$; Reach first-Incongruent cue: $n = 8$; Observe first-Congruent cue: $n = 3$; Observe first-Incongruent cue: $n = 4$. This suggests that infants in the Reach first-Incongruent cue condition were twice as likely to be excluded for not looking to the target.

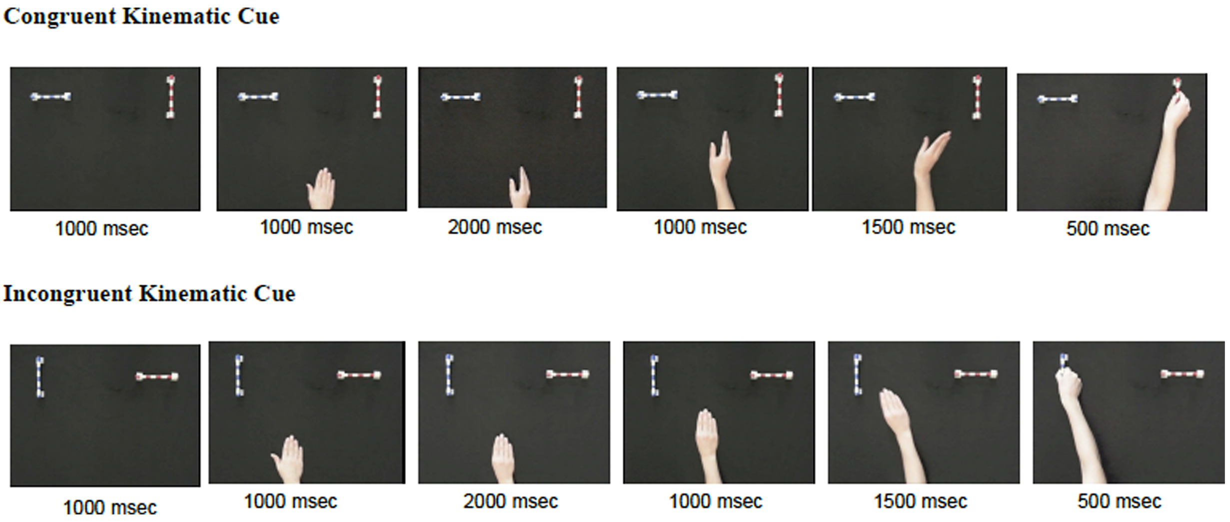

FIGURE 1 | Depiction of congruent (top) and incongruent (bottom) video events. These are two examples taken from a set of four possible congruent reaches and four possible incongruent reaches. Listed below each screenshot is the event duration. From left to right: Only objects present, hand enters scene flat on the table, hand forms shape and pauses, hand moves forward equidistant between the objects, hand deflects toward one of the objects, hand grasps object and pauses.

all infants. The experimenter first presented the rod in a horizontal orientation for five trials, then oriented the rod vertically for five trials, then alternated between horizontal and vertical orientation every trial thereafter. The experimenter presented the rod to the infant until they became fussy or lost interest. On average infants reached 19.48 times ($SD = 7.932$, range = 3–49)[2].

Eye-Tracking Data Reduction

Data were exported using the Tobii Fixation filter with the strict average eye selection criteria. Fixations were classified using 35 pixels/window velocity and distance threshold.

Areas of Interest (AOIs)

The current study only examines the timing of fixations that were directed toward the hand and objects areas of interest (AOIs; these AOIs are made visible in Supplementary Figure S1). The target object AOI was defined as the object that the hand ultimately reaches for, whereas the distractor object is the untouched object. These AOIs are ∼5° of visual angle off center. These AOIs were found in pilot testing to capture most visual fixations toward the object. Participants were unaware of these regions of interest as they were only present during the data reduction process.

Coding Criteria

In order to determine whether a look to the target AOI (or distractor AOI) was indeed generated based on attention to hand shape, we established the following criteria for all visual fixations to be included in this dataset: (1) infants had to first fixate within the hand AOI, (2) this fixation to the hand had to occur after the hand began to form its shape, (3) infants next fixation had to be toward one of the two objects. We recorded the time of first looks to both the target and distractor objects.

Latency to Predict the Target Object

Latency scores were determined by subtracting the time that the hand was outside of the target object AOI (see Supplementary Figure S2) from the time of the first visual fixation to the target object. Average latency scores were used to assess how rapidly infants visually anticipated the actions of others. Average latency scores that exceeded 2.5 SD from the group mean ($n = 1$) were removed from subsequent analyses.

Looks to the target object that occur after the hand enters the target AOI are considered reactive. Compared to other work on infant action anticipation, this is a rather conservative measure of which looks are anticipatory. Given this scoring system, negative values represent prospective looks to the target object, 0 is the time that the hand enters the object AOI, and positive values represent reactive looks to the target object.

Global Measures of Attention

Attention was also measured by assessing the duration of time that infants looked to the target object AOI, the distractor object AOI, and the hand AOI. We evaluated total attention to the event with a whole screen AOI and we also analyzed attention to each AOI separately. All summary statistics are computed as an average across all trials.

Distractor Predictions

Since action observation events provided hand shape cues that always matched one of the two objects, it is possible that infants that observe an incongruent cue would be more likely to generate predictions to the distractor object. To test whether there were differences in infants' propensity to generate first predictions to

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[2] Only 2 infants reached fewer than seven times. All other infants reached at least nine times.

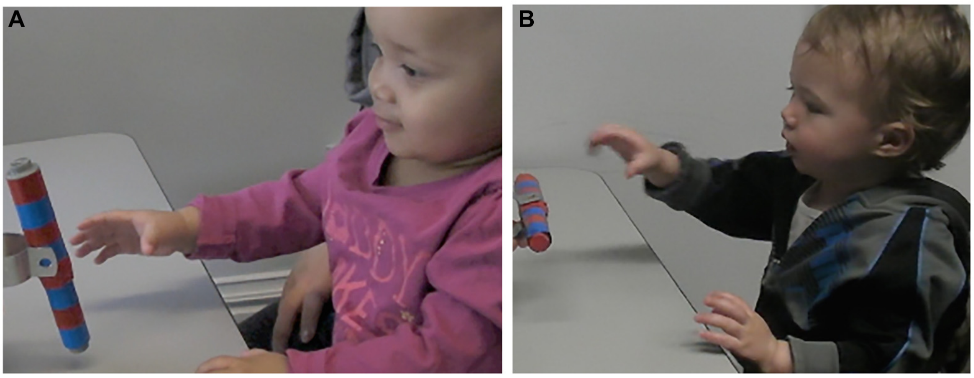

FIGURE 2 | Still image of infant hand pre-shaping behavior on horizontal rod orientation trials (A) and vertical rod orientation trials (B) of the motor behavior task.

the distractor, we analyzed the proportion of trials that each infant generated a predictive look to the distractor first. We averaged distractor predictions across all trials to create an average proportion of distractor predictions score.

Behavioral Data Reduction

We also coded infant reaching behavior during the motor behavior task to determine whether hand pre-shaping is related to action anticipation.

Hand Pre-shaping during Reaching

To examine the kinematics of infants' own movement, on each reaching trial we coded whether infants pre-shaped their hand to match the orientation of the target object prior to contact with the object (see **Figure 2**). Coding was performed offline using Interact, a digital coding program (Mangold, 2010). The initiation of the reach was identified as the first frame when the infant moved toward the rod. The end of the reach was identified as the time when the hand first touched the rod. Since infants could interact with the object any way they wished on each trial, we eliminated data from any trial where the infants' goal was not to grasp the object and trials where the hand shape was identified as ambiguous such that the coder could not identify whether it was a match or not. We found that on average infants pointed to the object instead of reaching on 0.314 ($SD = 0.692$, range = 0–3) trials and infants acted in a way that we couldn't identify as goal-directed on average 1.59 ($SD = 1.63$, range = 0–7) trials. After eliminating trials where the infant did not grasp the toy, we computed an average score indicative of the proportion of trials that the infants pre-shaped their hand to match the orientation of the rod as they reached. A second independent coder coded 25% of infants and the two coders were in agreement on 93% of trials.

RESULTS

In the design of the experiment, the testing orders provide information about two different timescales: developmental time scale and immediate experience time scale. The observe first condition, provides information about the relationship between spontaneous action anticipation and the kinematics of infants' own actions. In contrast, the reach first condition can tell us how immediate experience changes action anticipation. Below we present analyses to examine infants' attention to action kinematics and the relationship between infants' own actions and their anticipation of actions they observe. We begin with the observe first condition. Then, we present data from the reach first condition. Finally, we investigate similarities and differences between the two conditions to assess the effect of immediate experience on visual attention and infants' own reaching behavior.

Preliminary analyses indicated no reliable effects of gender, age (as a covariate), number of trials infants reached during action task (as a covariate), whether the hand reached to the right or left, handshape (horizontal vs. vertical grip) or rod orientation (horizontal vs. vertical) or the number of visual predictions generated (all $ps > 0.111$) on gaze latency. However, there was a main effect of the orientation of the target object [$F(1,62) = 3.984$, $p < 0.050$] on gaze latency—indicating that infants generated faster visual predictions to the vertically orientated target. This is unsurprising given that the vertical object AOI extends down closer to the hand than the horizontal object. Importantly, there were no interactions between target object orientation and condition (reach first vs. observe first) or cue (congruent vs. incongruent). Therefore, these factors were not included in subsequent analyses.

Observe First Condition

Figure 3A summarizes gaze latency scores across cue type (congruent vs. incongruent) for the Observe First condition. To begin, we asked whether infants reliably anticipated the hand's arrival to the target before the hand entered the target AOI. To determine whether infants reliably anticipated the hand's arrival, we compared average latency scores to 0—the time when the hand enters the target AOI. One sample t-test indicated that infants who observed congruent kinematic cues generated rapid saccades to the target and these looks to the target arrived before the hand entered the target object AOI [$t(17) = -4.728$, $p < 0.001$]. In comparison, infants that viewed incongruent

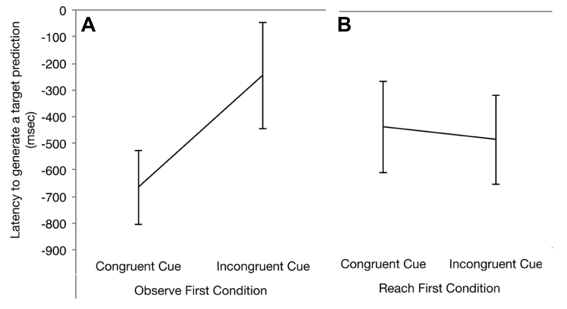

FIGURE 3 | Average mean latency scores for infants in the observe first condition (A) and reach first condition (B).

reaches did not look to the target before the hand entered the target AOI [$t(17) = -1.244$, $p < 0.230$]. An independent samples t-test was conducted on latency scores with trial type (congruent vs. incongruent) as the between subjects factor. Based on prior research, we also expected that infants would make faster predictions when hand pre-shaping matched the target object. Consistent with previous research, we found that gaze latency scores for congruent cues were faster compared to incongruent cues [$F(1,34) = 3.214$, $p < 0.041$, one-tailed]. Together, these findings suggest that infants spontaneously recruit kinematic cues to generate visual predictions.

In the action observation events the hand shape always anticipates one of the two objects. As such, it's possible that infants that watched incongruent reaches were more likely to generate predictions to the distractor object than infants that watched congruent reaches. If so, this could suggest that infants have difficulty ignoring kinematic cues. To test whether this was the case, Z-test of two population proportions was conducted on the proportion of distractor predictions with cue type as the between subjects factor. We found that infants did not differ in the proportion of distractor predictions generated ($Z = -0.209$, $p > 0.834$, congruent cue $M = 0.152$, $SD = 0.243$; incongruent cue $M = 0.150$, $SD = 0.189$). In combination with the gaze latency findings, this suggests that incongruent kinematic cues did not lead infants to produce wrong guesses about the target object. Nevertheless, saccades to the target were slower on incongruent compared to congruent trials. We suspect that this may be due to the availability of other cues (e.g., direction of motion) and because the trial always ended with the hand grasping one of the objects.

We next evaluated whether hand pre-shaping behavior correlated with how rapidly infants generated visual predictions. In line with previous research (Ambrosini et al., 2013), we found that the proportion of trials where infants' hand shape matched the orientation of the rod during the reaching task was correlated with how rapidly infants generated visual predictions ($r = -0.541$, $p < 0.021$) on congruent trials—that is, more hand pre-shaping behavior predicted faster visual predictions on congruent trials (see **Figure 4**). To examine whether this effect was driven by some infants being more motivated to reach for toys, we tested whether this relationship held when controlling for the number of times infants reached in the motor behavior task. We found that even after controlling for the number of trials infants reached, this effect remained significant ($r = -0.622$, $p < 0.008$). Critically, we found that this relationship was selective. Infants that viewed incongruent cues did not show this correlation ($r = 0.344$, $p < 0.177$). These findings suggest that motor experience is selectively linked to generating predictions when kinematic cues are present and reliable—not to actions where the target is incongruent with kinematic cues.

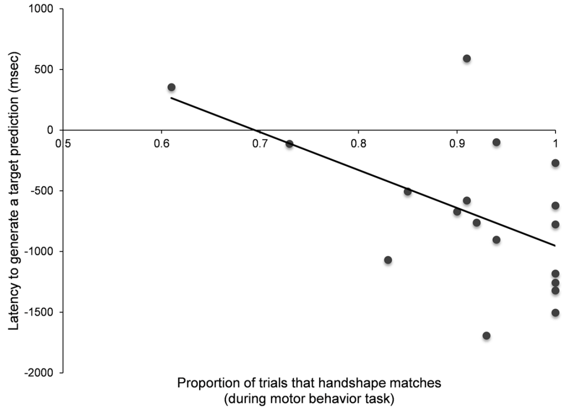

FIGURE 4 | Observe first- congruent cue condition. Mean gaze latency as a function of hand pre-shaping behavior.

These findings are concordant with a body of research (Ambrosini et al., 2011, 2013; Kanakogi and Itakura, 2011) demonstrating that motor skill is linked to action anticipation. In the next section, we test whether we see similar patterns of behavior following immediate action experience.

Reach First Condition

Next we examined whether immediate reaching experience changes recruitment of kinematic cues to generate visual predictions. **Figure 3B** summarizes gaze latency scores across cue type (congruent vs. incongruent) for the Reach First condition. To begin, we assessed whether infants reliably predicted the target. One sample t-test indicated that infants who observed congruent cues [$t(18) = -2.527$, $p < 0.021$] and incongruent cues [$t(17) = -2.877$, $p < 0.010$] generated predictive saccades that entered the target AOI before the hand. To determine whether gaze latency differed across cue type, we conducted an independent samples t-test on gaze latency with cue type (congruent vs. incongruent) as a between subjects factor. We found no significant effect of cue type [$t(32) = 0.377$, $p < 0.708$]. These findings suggest that infants who received reaching experience immediately before action observation generated rapid visual anticipations regardless of cue type.

Follow-up analyses indicated that (just like infants in the observe first condition) infants in the reach first condition did not show a difference in the proportion of distractor predictions across congruent ($M = 0.202$, $SD = 0.281$) and incongruent cue ($M = 0.247$, $SD = 0.292$) type ($Z = -0.788$, $p > 0.430$). Again suggesting that infants were able to generate predictions to the target object regardless of cue. We next asked whether the manner in which infants reached and grasped the toy was related to gaze latency. To do so, we examined the relationship between hand pre-shaping and gaze latency. We found no correlation between gaze latency and hand pre-shaping (ps > 0.198)—suggesting that planning one's own actions was not related to predicting others' actions.

Comparing Observe First and Reach First Conditions

To determine whether there were any group differences in motor behavior or visual attention that could account for differences in performance between our reach first and observe first conditions, we ran follow up analyses to compare the groups.

Motor Behavior Task Performance

We might find differences in infants' performance on the action observation task because infants in the observe first condition may have more advanced motor skills than those infants in the reach first condition or because reaching early or late in the testing session may result in differences in behavioral performance. To assess whether this was the case, we used an independent samples t-test to compare the proportion of trials where infants pre-shaped their hands in the motor behavior task across conditions (observe first vs. reach first). Results indicated no significant difference in the proportion of trials with hand pre-shaping across the reach first ($M = 0.89$) and observe first conditions [$M = 0.91$; $t(67) = -0.706$, $p < 0.483$].

Comparing Visual Attention to the Action Observation Events

We could have found differential recruitment of kinematic cues across conditions if infants in the reach first condition were not attending to the action observation videos as much as infants in the observe first condition or if reaching prior to action observation resulted in fatigue during the action observation session. To examine these possibilities, we next conducted a one-way ANOVA on total attention with condition (reach first vs. observe first) and cue type (congruent vs. incongruent) as factors. We found no difference in how long infants attended to the action events across condition (observe first vs. reach first), cue type (congruent vs. incongruent) and no significant interaction (ps > 0.372). To further assess whether allocation of attention differed across conditions, we examined whether infants attended to all parts of the action events equally. The two groups did not vary in allocation of attention to the hand (ps > 0.255), target object (ps > 0.234), or distractor object (ps > 0.297). Thus, infants attended equally to all aspects of the action events.

Gaze Latency

Analyses within condition (reach first vs. observe first) suggest that there are differences in gaze latency. As a way to evaluate how the latencies across conditions are related to one another we compared latency scores across both conditions. To assess whether there were significant differences in gaze latency across the two conditions we conducted an univariate ANOVA on gaze latency with condition (reach first vs. observe first) and cue type (congruent vs. incongruent) as between subjects factors. We found no significant differences in gaze latency across condition ($p > 0.973$) or cue type ($p > 0.346$) and no interaction ($p > 0.138$). This suggests that while we found differences in the relative speed at which infants generated predictions in the observe first condition, we do not find that these differences are significantly different from those infants in the reach first condition.

Overall, these findings suggest that infants can recruit kinematic cues to generate action predictions. Furthermore, infants spontaneously recruit their own motor skill to generate action predictions. We also found that the experience of reaching for objects changes action prediction: when provided experience reaching for objects prior to action observation, we find that infants generate equally fast predictions to congruent reaches and incongruent reaches. This effect is not driven by low-level attention to the observed stimulus and cannot be accounted for by the number of trials that infants reached for the toy.

DISCUSSION

The current study examined the relationship between action experience and action anticipation. Infants were randomly assigned to either observe actions before (Observe first condition) or after (Reach first condition) a motor task. To assess action anticipation we used a novel paradigm that varied the action observation event in terms of whether the hand pre-shaping did (congruent cue) or did not (incongruent cue) predict the orientation of the target object. Consistent with prior research, we found that infants who observed the action events first (Observe first condition) recruited kinematic cues to generate predictions. Additionally, we found that infants' own hand pre-shaping behavior predicted how rapidly they generated predictions when the kinematic cue was congruent with the target (see Ambrosini et al., 2013 for similar findings). In comparison, infants who engaged in a motor behavior task before observing action events (Reach first condition) generated rapid visual predictions to both congruent and incongruent kinematic cues. Together, these findings suggest that action experience across different time scales may influence action anticipation differently.

Action Anticipation: The Developmental Timescale Perspective

The observe first condition findings provide converging evidence for the claim that infants recruit kinematic cues when they are available (Ambrosini et al., 2013) and that there may be a correspondence between infants' motor abilities and anticipation of others' actions (Kochukhova and Gredebäck, 2010; Kanakogi and Itakura, 2011; Cannon et al., 2012; Ambrosini et al., 2013). Our design also expands upon this body of work by testing action anticipation when the motor cue is incongruent with the target object. Previous research has shown that infants generate faster covert shifts in the direction of a hand's opening compared to when an object appears to be incongruent with a hand's opening (Daum and Gredebäck, 2011). In contrast, the current study shows that infants use hand orientation information to generate online visual anticipations when an actor is choosing between two objects. Our findings harmonize with previous research—both studies show that infants are faster to generate predictions on congruent trials compared to incongruent trials. Further, we show that on incongruent cue trials, infants generated looks to the target that (on average) arrived at approximately the same time that the hand made contact with the rod. This suggests that the tendency to recruit kinematic information may be difficult to override.

By including incongruent reaching events, we were able to assess the tendency to recruit kinematic information when this information is incompatible with the target object. Our incongruent events were perceptually identical to the congruent events up until the moment that the hand made contact with the toy. Thus, differences in action anticipation were due to attention to the relationship between the kinematics of the observed action and the target objects orientation. This paradigm allowed us to assess infants' tendency to use kinematic information on incongruent trial events by examining infants' propensity for generate predictions to the distractor object. We show that when infants observed events where hand pre-shaping is incongruent with the target, infants, nevertheless, generate predictions to the target. We suspect that this may be because the incongruent reaches that infants observe always result in the hand grasping one of the two toys. After a demonstration of this actor's preference, infants may override their processing of the kinematic cue to generate a target prediction. If the reach was never completed, we may not have found such a strong propensity to generate target predictions. Future work is needed to examine this possibility.

Action Anticipation Following Immediate Experience

Following immediate reaching experience, we found that infants generated rapid predictions to both congruent and incongruent cues. Furthermore, we found that the amount of reaching performed during behavioral testing and the extent to which their own grasping behavior matched the observed action, did not correlate with gaze latency. Our findings also indicated that there were not differences in infants' global attention to the action observation events. Infants across both conditions (reach first vs. observe first) attended to the action observation videos for similar amounts of time and distributed their attention to the target object, hand, and distractor object AOIs similarly. This suggests that infants' visual attention to the events was comparable but that the motor behavior task may have primed infants to recruit the information in the action observation videos differently. These findings suggest that immediate experience reaching changes attention to (and use of) kinematic cues. Furthermore, this change may not be due to an overt shift in visual attention to others' movements. We speculate that action priming may prime attention to the goal structure of others' actions (rather than drawing attention to the specifics of how an actor moves). We suspect that infants in our study are shifting their attention toward the goal structure of others' actions following action priming because these infants reliably anticipate the target object on incongruent trials. While our findings primarily speak to the speed of infant's visual anticipations, it could be that action priming facilitates more rapid interpretation of the action in terms of the actor's goal or that action priming leads infants to rapidly perceive the actor-goal relation (even in the face of incongruent kinematic information).

The sensorimotor system is organized hierarchically (see Rosenbaum et al., 2004; Grafton and Hamilton, 2007 for review) and as such actions can be described at multiple levels. One interpretation of our reach first condition data could be that immediate action experience may prime a motor representation higher than kinematics. This would be in line with our finding that infants who receive action experience before observation, do not recruit kinematic cues in the same way that infants spontaneously recruit kinematic information. However, it is also possible that infants recruit kinematic information in addition to higher representations of the action goal (or recruit them concurrently) and this leads infants to be able to override their sensitivity to incongruent kinematic cues. Future research is needed to evaluate whether this could be the case.

Research suggests that experts (e.g., expert golfers, soccer players, etc.) tend to pay less attention to the kinematics of their own actions and more attention to their goal. Indeed, when acting, experts' performance suffers when they attend to the specific movements involved in their action (Beilock et al., 2002; Beilock and Gray, 2012). Similar effects have been found with young infants learning to coordinate their visual and manual actions in sequences. Gerson and Woodward (2013) trained 8-months-old infants on how to pull a cloth to obtain an out of reach toy by either highlighting the means (cloth) or the goal (toy). They found that infants learned more rapidly and sustained this learning throughout training if the training emphasized the goal of the action rather than the means needed to achieve the action (Gerson and Woodward, 2013). Given the close link between action execution and action observation across the lifespan (Kontra et al., 2012), it's possible that devoting considerable attention to the fine details of movement either during movement or immediately prior to observing someone else could make it more difficult to see the goal structure of an action sequence—particularly early in life. In line with this idea, research has also shown that the experience of coordinating visual and manual actions immediately before observing others act, facilitates attention to others' goals—not to the manner in which arms move through space (Krogh-Jesperson and Woodward, in preparation; Sommerville et al., 2005; see Woodward et al., 2009 for review). When considered in combination with our reach first condition findings, our work provides converging evidence for this claim. Future research should manipulate action tasks to highlight either the goal or the manner used to achieve the goal and assess effects on action anticipation.

Limitations

While these results suggest that there are differences across conditions in how reliably infants generate anticipatory predictions to the target, we did not find significant differences in overall gaze latency scores. This suggests that while infants are on average generating predictions to the target before the hand enters the target AOI (in all conditions except when observing incongruent trials in the observe first condition), overall prediction speeds are not significantly different across conditions. This raises a number of questions about the extent to which action priming changes action prediction. Our findings suggests that priming may change the relative speed of action prediction—that is, action priming may help infants reliably generate predictions ahead of hand movement particularly when faced with incongruent kinematic cues. Whereas, infants spontaneous behavior (i.e., observe first condition) suggests that they are likely following the hand's motion (as they do not generate saccades to the target before the hand enters the target AOI) when faced with incongruent kinematic cues.

One reason that we see no overall differences across conditions may be because there is substantial individual variability in infants' action prediction speed that is unaccounted for—possibly due to differences in general cognitive abilities (e.g., inhibitory control or speed of processing). Indeed, generating a prediction to the target requires the capacity to inhibit looking at the moving hand. This capacity may be underdeveloped at 13 months and limit the range of latency scores. Future research should examine the factors that could contribute to the large variability found across conditions.

CONCLUSION

The current study provides novel insight into the link between action experience and action anticipation. Many studies suggest that action experience (Sommerville and Woodward, 2005; Sommerville et al., 2005; Woodward et al., 2009; Gerson and Woodward, 2014) is at the center of action understanding. This past research tested whether action experience changes infants' high-level understanding of actions (i.e., that actions are structured by goals; e.g., Flanagan and Johansson, 2003; Sommerville and Woodward, 2010). Our data suggest that comparing these timescales can provide us new information about the mechanism that facilitates rapid anticipatory shifts in attention. We show that infants' immediate experience changes their recruitment of kinematic cues: following a simple reaching task, infants generated rapid predictions to the target object, regardless of kinematic cue congruency. This is different from how infants spontaneously recruit kinematic information. Without immediate reaching experience, infants appear to use kinematic information to generate predictions and they recruit their own ability to execute this specific motor skill.

In conclusion, these findings provide novel evidence to suggest that different types of action experience (e.g., lifetime vs. immediate) could prime infants to recruit motor cues in different ways. Indeed, our findings suggest that immediate experience may prime attention to action goals rather than kinematics. We suggest that this harmonizes with studies of adult skill expertise and infant action understanding. Together these findings raise new questions about the role that the motor system and action hierarchies may play in the development of action anticipation abilities.

AUTHOR CONTRIBUTIONS

CF and AW contributed to the study design and concept. CF collected the data, performed data analysis, and interpreted findings under the supervision of AW. CF drafted the manuscript and AW provided critical revisions.

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SUPPLEMENTARY MATERIAL

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Eighteen-month-olds' memory interference and distraction in a modified A-not-B task is not associated with their anticipatory looking in a false-belief task

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Infants' performance in non-verbal false-belief tasks is often interpreted as if they have understood false beliefs. This view has been questioned by a recent account that explains infants' performance in non-verbal false-belief tasks as the result of susceptibility to memory interference and distraction. We tested this alternative account by investigating the relationship between infants' false-belief understanding, susceptibility to memory interference and distraction, and general cognitive development in 18-month-old infants ($N = 22$). False-belief understanding was tested in an anticipatory looking paradigm of a standard false-belief task. Susceptibility to memory interference and distraction was tested in a modified A-not-B task. Cognitive development was measured via the Mental Scale of the Bayley Scales of Infant Development. We did not find any relationship between infants' performance in the false-belief task and the A-not-B task, even after controlling for cognitive development. This study shows that there is no ubiquitous relation between susceptibility to memory interference and distraction and performance in a false-belief task in infancy.

Keywords: false belief task, memory interference, infancy, distraction, inhibitory control

Introduction

The proposal that infants are able to understand other agents' false beliefs has been a source of lively debate over the last decade (Onishi and Baillargeon, 2005; Ruffman and Perner, 2005; Heyes, 2014; Scott and Baillargeon, 2014). In traditional false-belief tasks, children explicitly reason about an agent's future behavior based on the agent's false belief, which is indicated by the children's verbal response (Wimmer and Perner, 1983). In the seminal "Maxi" task, Maxi puts the chocolate in the blue cupboard and leaves the room. While he is away, his mother enters the room and puts the chocolate in the green cupboard. Children are asked where Maxi will look for his chocolate after his return. Children demonstrate their false-belief understanding by indicating that Maxi will look for the chocolate in the blue cupboard. At around 4 years of age, children pass this type of task (Wellman et al., 2001).

The idea that children do not understand false beliefs before the age of 4 has been challenged by studies reporting that infants and toddlers are able to pass false-belief tasks if one uses tasks in which children react spontaneously and are not asked questions (see Onishi and Baillargeon, 2005, for the starting point of this debate). In an anticipatory looking task (Southgate et al., 2007), toddlers observed a hand puppet placing a ball in one of two boxes and an observing agent subsequently retrieving the ball in two familiarization trials. In order to reach into the box, the agent had to open one of two windows in a barrier. Each window was directly above the corresponding box. In a subsequent belief-induction trial, two different conditions were administered. The hand puppet placed the ball in the first box, which was observed by the agent in both conditions. Then, the hand puppet transferred the ball to the second box, which was observed by the agent in only one condition. Finally, the hand puppet took the ball out of the second box, which was not observed by the agent in both conditions. Accordingly, the agent held two different false beliefs regarding the location of the ball. Before the agent reached into one of the boxes, the toddlers' eye gaze was measured. The majority of toddlers anticipated that the agent would reach for the ball in the location where she believed it to be. This type of task has also been employed with 18-month-olds (Thoermer et al., 2012). Although, here, the mean looking times revealed that infants did not look longer at the window that indicated false-belief understanding than at the other window, infants who did look longer at the correct window were more likely to pass standard false-belief tasks at 4 years of age. These findings of toddlers' false-belief understanding are especially informative because action prediction is often seen as being more cognitively demanding than an evaluation of past behavior (Gredebäck and Melinder, 2010; Daum et al., 2012; Verschoor et al., 2013).

The mentalistic interpretation of infants' performance in false-belief tasks has been controversial from the outset (e.g., Ruffman and Perner, 2005). However, the criticism only extended to single paradigms that reported evidence of infants' false-belief understanding. Recently, this criticism has been articulated more comprehensively (Heyes, 2014). According to this view, young children's performance in false-belief tasks is susceptible to low-level explanations for the following reasons: First, infants look longer at situations which they perceive to be novel (Olson and Sherman, 1983). For example, in Onishi and Baillargeon's (2005) study, the agent reached into a green box, where she had not seen the object being transferred. Infants' looking time was longer in this trial than in a trial in which the agent reached into a yellow box, where she had last seen the objects. Instead of attributing beliefs, infants might simply react to the novelty of the combination of person, place of the object, and reaching action. Second, infants' memory might be affected by retroactive interference: If two events occur one after another, the memory of the latter event might interfere with the memory of the former. For example, an agent witnesses an object being placed into box A and then leaves the scene. The object is then transferred to box B before the agent reappears. The subsequent reappearance of the agent interferes retroactively with the memory of the transfer of the object into box B. Thus, infants might themselves believe that the object is in box A and expect the agent to look at box A. Third, disruptive elements of false-belief tasks might distract infants' attention and therefore their memory.

The same argument might be applied to false-belief studies using anticipatory looking tasks. The ringing sound in Southgate et al.'s (2007) study, for example, might have distracted infants when the ball was being transferred from the first box to the second box (for the role distraction in imitation tasks, see Beisert et al., 2012). The agent's head turn toward the boxes after the ball has been transferred might interfere retroactively with the memory of the transfer of the ball. Both processes would lead to the infants' belief that the ball was still in the first box. Likewise, a deficit in working memory is fundamental to the A-not-B task because infants still look for a toy at location A even though they have observed the experimenter hiding the toy at location B. Although infants at the end of the first year of life master this task in the standard version, they fail if a delay is introduced between the hiding of the toy and the searching for the toy at location B (Diamond, 1985). Both proactive and retroactive interference might lead to this error. The repeated successful retrieval of the toy at location A might interfere proactively with the memory of the new location of the toy at B. Additionally, the delay between hiding the toy and searching for the toy might interfere retroactively with the memory that the toy is at location B. Thus, if a deficit in working memory is responsible for infants' seemingly successful performance in a false-belief task, then we would expect that infants who fail in the A-not-B task in the B trials will succeed in the false-belief task.

In the present study, we therefore tested whether infants' working memory is related to their performance in a false-belief task. We used an analogous version of Southgate et al.'s (2007) false-belief task and analyzed infants' anticipatory looking via eye tracking. According to our knowledge, there are two infant studies suggesting that infants acknowledge the actors' mental states in analogous videos. First, in Southgate et al.'s (2007) study, the majority of 25-month-olds anticipated that the actor directs her action to the box where she has last seen the object. Second, in Thoermer et al.'s (2012) study, 18-month-old performed at chance level in this task, but a correct anticipation at 18 months of age predicted passing the standard change-of-location task at 48 months of age. Another study with adult participants showed that adults with Asperger syndrome anticipated less reliably the reach of the actor according to her belief than adults without Asperger syndrome (Senju et al., 2010). We aimed at testing an age group with equal rates of passers and non-passers in the false-belief task. Southgate et al. (2007) reported that 85% of 25-month-old infants passed this test, while Thoermer et al. (2012) reported that only 55% of 18-month-olds passed. We opted to test 18-month-olds in order to increase the variance in infants' performance, which is essential when comparing it to the performance in the A-not-B task.

A modified version of the A-not-B task was used in order to test infants' working memory (Diamond, 1985) and retroactive interference (Heyes, 2014). After an object was hidden at one location and before the infants could reach for an object, a delay was introduced by putting a shield between the locations and the infants. This delay was reported to test infants working memory. For example, if landmarks indicate at which location a toy is hidden (location A or B), then infants do not err even after longer delays (Diamond, 1983). Additionally, lesions in the dorsolateral prefrontal cortex of macaques (Diamond and Goldman-Rakic, 1989) negatively affects their performance in the delayed A-not-B task and this region is typically associated with higher executive functions such as working memory (Stern et al., 2001). The delay is also believed to introduce retroactive interference: Putting the shield between the infant and the hidden object weakens the memory for the event that happened before, namely, the object being hidden at one location (Heyes, 2014). We further controlled for infants' cognitive development by employing the Mental Scale of the Bayley Scales of Infant Development (BSID-II).

Materials and Methods

Participants

Participants were 22 eighteen-month-olds ($M = 18$ months; 2 days, SD = 0;08; age range: 17;14–18;15, 14 girls). Thirty-nine additional infants were tested but excluded from the final sample due to fussiness and lack of interest during the false-belief task ($n = 15$), the A-not-B task ($n = 9$), or the Mental Scale of the BSID-II ($n = 2$). Further reasons were procedural errors ($n = 6$), failing to meet the inclusion criterion in the false-belief task ($n = 4$), interference by the parent ($n = 1$), or equipment failure ($n = 1$). Although the attrition rate is high, it is analogous to similar studies on false-belief understanding in this age range (e.g., Southgate et al., 2007; Buttelmann et al., 2009). The experiment was conducted in accordance with the ethical standards laid down in the Declaration of Helsinki and the standards of the local ethics committee of the University of Leipzig.

Material

The false-belief task was presented and gaze was measured using a Tobii 1750 near infrared eye tracker with an infant add-on (precision: 1°, accuracy: 0.5°, sampling rate: 50 Hz). A 9-point infant calibration was used. Viewing distance was approximately 80 cm. In the A-not-B task, a wooden panel (40 cm × 10 cm) and two plastic cups were used. An upright board (height = 25 cm, width = 45 cm) obscured infants' view of the cups. A maximum of sixteen cubes (3 cm × 3 cm × 3 cm) could be retrieved by the infants and put into a xylophone box, resulting in a series of tones.

Design

All infants were tested in three tasks: the false-belief task, the A-not-B task, and the BSID-II. The order of the false-belief task and the A-not-B task was counterbalanced and the BSID-II was conducted last.

Procedure

False-Belief Task

In the false-belief task, infants viewed videos, which presented two familiarization trials and one test trial. In all videos, an actor sat behind a board that contained a left and a right window. He wore a white visor cap and moved his head as if he were following the displayed actions closely in order to increase the impression that he was being attentive. Infants also watched a second similar video, which was presented before or after the false-belief task. However, this video was beyond the scope of the present research question and is not reported here.

The task was analogous to Southgate et al.'s (2007) false-belief II task: An opaque box was placed in front of each of the two windows described above. In the familiarization trials (see **Figure 1A**), the actor witnessed a ball being hidden by a human hand (henceforth called "operating hand") in one of the two boxes. The duration of this sequence was 10 s. Then, in an anticipation phase, which was similar across trials and tasks, a chime sounded and a still image was presented, with both windows first being illuminated (1,000 ms) and then not illuminated (1,750 ms). During the anticipation phase it was measured whether infants fixated the two windows. Each area of interest was 7.55 cm × 5.44 cm (height × width) which equals a visual angle of 5.4° × 3.9°. The actor then reached through the window on the side where the ball was located and opened the box (duration = 6 s). In the test trial (**Figure 1B**), the ball was again hidden in one box (duration = 10 s). Then, a telephone started ringing and the actor turned around. While he was looking away, the operating hand transferred the ball from one box to the other and after that, removed the ball from the second box (duration = 30 s). Then, the telephone stopped ringing, and the actor turned back and the next anticipation phase started.

We only analyzed infants' looking behavior in the test trial if infants met the inclusion criterion applied by Thoermer et al. (2012). Infants' looking time to the correct window had to be

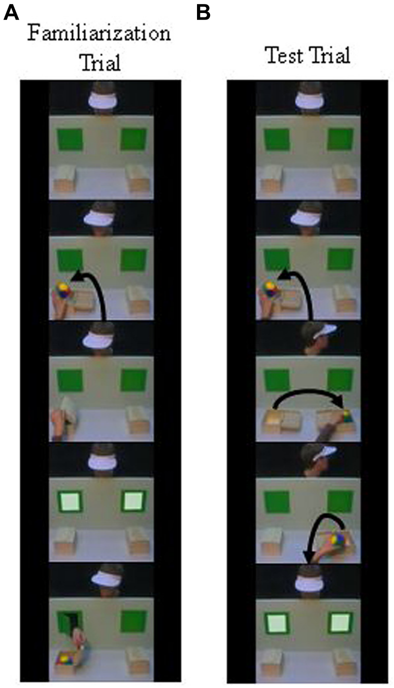

FIGURE 1 | Successive frames from the videos of one of the familiarization trials (A) and the test trial (B) for the change-of-location task.

longer than infants' looking time to the incorrect window in at least one familiarization trial. It should be noted that the same pattern of result showed when we used the inclusion criterion (i.e., toddlers had to direct their first fixation in the second familiarization trial to the correct window) applied by Southgate et al. (2007).

A-not-B Task and BSID

A modified version of the A-not-B task was designed for 18-month-olds (Diamond, 1985). Infants sat on their parents' lap facing the experimenter who sat at the opposite side of table. The experimenter hid a small cube under one of two cups. He then hid the cups behind the occluder for 5 s and finally placed them within the infants' reach. If the infants successfully retrieved the cube, they could put it in the xylophone box. After four successful retrievals from location A, the hiding place was switched to location B. The experiment ended when infants found the cube at location B. Finally, infants' cognitive development was assessed using the Mental Scale of the BSID (2nd edition, Bayley, 1993).

Coding and Reliability

In the false-belief task, infants' looking behavior was analyzed for 2,750 ms after the anticipation phase began. The first fixation on one of the two windows lasting more than 200 ms was identified and categorized as (a) anticipatory fixation that was congruent with the actor's false belief, resulting in a score of 1, or (b) anticipatory fixation that was incongruent with the actor's false belief, resulting in a score of 0. Additionally, the duration of all fixations on both windows during the anticipation phase was assessed and transformed into two sum scores (i.e., one sum score for each window). The proportion of mean looking time at one window was calculated by dividing the looking time at one window by the sum of looking times at both windows.

In the A-not-B task, the coding began when infants had retrieved the cube in four successive trials from location A and the cube was hidden at location B. We counted the number of trials in which infants searched at location A before they finally searched at location B.

The reliability rating of the A-not-B task by a second independent rater was excellent ($r = 0.92$, intraclass correlation coefficient). Infants' performance in the BSID was analyzed according to the standard procedure as described in the BSID manual.

Results

False-Belief Task

Infants' first fixation on the location that corresponded to the actor's false belief (7 out of 22 infants, $M = 32\%$) did not differ from the chance level ($p = 0.13$, binomial test)[1]. Analyses of the mean looking time of all fixations on the first box (where the agent has seen the ball being transferred) and the window above and as well as the second box (where the agent has not seen the ball being transferred) and the window above during the anticipation phase of the test trial did not result in any statistically significant effect [$M_{\text{first box}} = 533$ ms, SD = 479 ms, $M_{\text{second box}} = 913$ ms, SD = 682 ms, $t(21) = 1.77$, $p = 0.09$]. The infants' first anticipatory look to the side where the actor last saw the ball and proportion of looking the side where the actor last saw the ball correlated ($r = 0.77$, $p < 0.001$). Further analyses of possible moderating variables such as mean looking time toward the videos before the anticipation phase, referential looks toward the actor's head, and number of correct anticipatory looks during the familiarization trials did not reveal any statistically significant findings.

A-not-B Task and BSID

The mean number of incorrect searches at location A was 1.4 (SD = 1.7, range 0–5). Nine infants did not perform an incorrect search at location A, six infants searched at location A one time, two infants each searched at location A two, four, and five times, and one infants searched at location A three times. Infants' mean IQ score in the BSID was 93.3 (SD = 10.3, range 79–117). Four infants received a score below 85, 17 infants received a score within 85 and 115, and one infant received a score above 115. In order to assess whether infants who were excluded performed worse in the A-not-B task than infants who were included in the study we compared their performance. We did not find a difference between both mean scores, $M(\text{excluded}) = 1.4$ (SD = 1.6), $t < 1$.

Relationship between Tasks

There was no statistically significant relationship between the false-belief task and the A-not-B task for the toddlers' first fixation in the false-belief task ($r = -0.02$, $p = 0.92$, Spearman rank correlation, see **Figure 2** for group differences between infants who anticipated correctly and incorrectly in the false-belief task) or for the proportion of mean looking time of fixations on

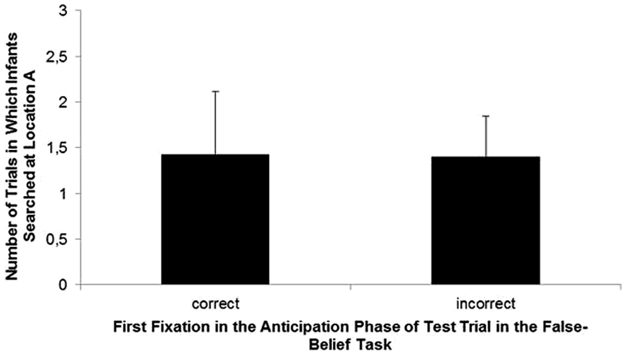

FIGURE 2 | Number of incorrect searches at location A in the A-not-B task for infants whose first fixation in the false-belief task was directed to the location where the actor last saw the ball (correct) and whose first fixation was directed to the location where the actor did not last see the ball (incorrect).

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[1] A similar result was obtained when applying the original coding criterion of Southgate et al. (2007), who coded an anticipatory look to one location if the infant fixated on the AOI for more than 20 ms.

the first box – where the agent has seen the ball being placed ($r = 0.11$, $p = 0.63$, Spearman rank correlation). This remained after controlling for cognitive development measured in the BSID ($r = -0.06$, $p = 0.78$; $r = -0.15$, $p = 0.49$, Spearman rank correlation).

Discussion

The present study revealed no correlation between a non-verbal false-belief task and a modified version of the A-not-B task. The lack of correlation remained after controlling for infants' cognitive development. Accordingly, the present study provided no evidence for the assumption that a deficit in working memory is related to infants' success in a non-verbal false-belief task (Heyes, 2014). This null result is especially informative because the scenario in the false-belief tasks was suggested to resemble the A-not-B task (Heyes, 2014) and a considerable proportion of infants failed in both tasks, which opened up the possibility that performance in both tasks correlated.

The absence of evidence of a relationship between performance in a working memory task and a false-belief task is not evidence of the absence of this relationship. Accordingly, this study does not straightforwardly refute the proposal that low-level explanations apply to false-belief tasks for infants. There are at least two possible explanations for the lack of relationship between the two tasks in the present study. A first explanation is based on specific characteristics of the tasks in this study, which might have reduced the correlation between the false-belief task and the A-not-B task. The critical variables might have been the infants' age, the criterion for anticipatory looking, and the stimuli used in the false-belief task. Whereas in the original study, 25-month-olds were tested (Southgate et al., 2007), we chose 18-month-olds in order to obtain more variance in their anticipatory looking. Previous findings have shown that 18-month-olds' looking behavior is not random in this task, but that the false-belief-like looking pattern (i.e., gaze to the window according to the agent's false belief) is related to their explicit false-belief understanding at the age of 4 years (Thoermer et al., 2012). Next, the criterion for an anticipatory fixation on one of the two windows was that it lasted more than 200 ms. We used this criterion because fixations with shorter duration appeared to be random and not directed to the window. However, when applying the original criterion by Southgate et al. (2007) of more than 20 ms, the correlation between the false-belief task and the A-not-B task remained statistically not significant. Additionally, although we matched the stimuli closely to the original stimuli used in Southgate et al.'s (2007) study, there were minor differences. The agent in the present study was male, while the agent of the Southgate et al. (2007) study was female. In the present study, a human hand transferred the ball from one location to the other, whereas in Southgate et al.'s (2007) study, a hand puppet resembling a polar bear transferred the ball. However, we do not think that these differences affected the infants' working memory, and therefore do not believe them to be responsible for the lack of correlation between performance in the false-belief task and the A-not-B task. Finally, we tested infants' false-belief understanding in an anticipatory-looking task which represents only one measure to test infants' false-belief understanding. We did not test infants' false-belief understanding in a violation-of-expectation task. There is a structural difference between both tasks because in anticipatory-looking tasks infants have to predict an agent's action whereas in violation-of-expectation tasks, infants have to evaluate an executed action. It remains an open question whether working memory and distraction is the key to understand infants' performance in false-belief tasks in violation-of-expectation tasks.

A second explanation is based on a mentalistic interpretation of infants' performance in the false-belief task. If infants do attribute false beliefs to others, then it is not surprising that this ability is not closely related to their working memory. Working memory might be a prerequisite for remembering the story line of a false-belief scenario. The mere memory, however, does not imply insight into the mental states of others. This notion was supported by a meta-analysis showing that early executive functions predict later false-belief understanding but not vice versa (Devine and Hughes, 2014).

The idea that young children are able to infer others' mental states is thought-provoking and should be tested more rigorously in the future. Improving the false-belief scenarios is one strategy to test this question (Heyes, 2014). In the present study, we used another strategy by correlating an established false-belief task with the A-not-B task, which tests inhibitory control and working memory. This strategy has been applied in previous studies on the relationship between non-verbal belief tasks and other tasks on inhibitory control, which were identified as being closely related in standard verbal false-belief tasks (for an overview, see Devine and Hughes, 2014). These studies revealed mixed findings. Three- and 4-year-olds' performance in the Dimensional Card Change Sorting task and a non-verbal false-belief task showed no relationship (Low, 2010). In contrast, 18-month-olds' performance in a detour task (i.e., infants had to open a box with a transparent window presenting a toy by touching a knob attached to the side of the box) and a non-verbal false-belief task using a violation-of-expectation paradigm did show a relationship (Yott and Poulin-Dubois, 2012). The latter finding is surprising because non-verbal false-belief tasks were designed to eliminate inhibitory control demands (Baillargeon et al., 2010). However, we were unable to find this relationship between the A-not-B task and a false-belief task in an unexpected transfer scenario. The present findings might indicate that predictive eye gaze is less affected by infants' inhibitory control than looking times in violation-of-expectation paradigms. A possible reason could be that predictive eye gaze is a more automatic response than continuous looking to an event, and therefore predictive eye gaze is less targeted by higher cognitive processes such as inhibition. It is clear, however, that the relationship between false-belief understanding in infancy and executive functions including working memory and inhibitory control should be further investigated.

The present study replicated Thoermer et al.'s (2012) finding that 18-month-olds as a group do not perform above chance level when anticipating an agent's action based on the agent's false belief. Southgate et al. (2007) demonstrated that the majority of 25-month-olds pass this test which shows that between 18 and 25 months of age infants develop the ability to anticipate others' action based on the others' false beliefs. The fact that children who passed the false-belief test at 18 months of age were more likely to pass a standard false-belief test at 48 months of age indicates that infants at 18 months of age do not perform at random, but that some 18-month-olds are sensitive to another's false belief. In the present study, we showed this successful performance in 18-month-olds is not predicted by distraction or memory interference as measured by the modified A-not-B task.

In sum, the present study revealed no relationship between performance in a false-belief task using an anticipatory looking paradigm and a modified version of the A-not-B task even after controlling for cognitive development. Accordingly, this study finds no evidence in support of a relationship between working memory and false-belief understanding in infancy.

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