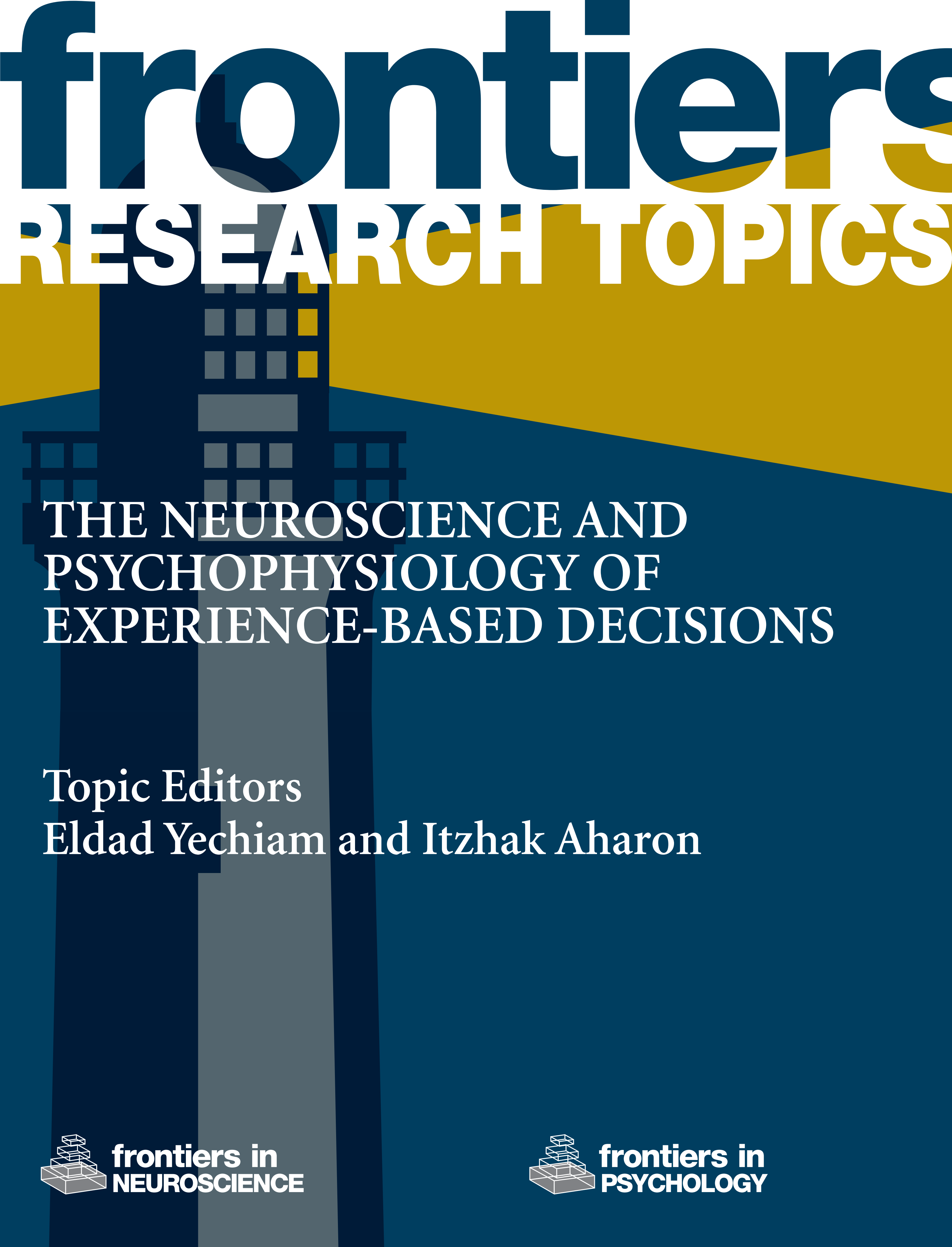

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THE NEUROSCIENCE AND PSYCHOPHYSIOLOGY OF EXPERIENCE-BASED DECISIONS

Topic Editors
Eldad Yechiam and Itzhak Aharon

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THE NEUROSCIENCE AND PSYCHOPHYSIOLOGY OF EXPERIENCE-BASED DECISIONS

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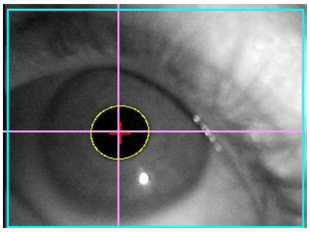

In experience-based decisions people learn to make decisions by sampling the relevant alternatives and getting feedback. The study of experience-based decisions has recently revealed some robust regularities that differ from how people make decisions based on descriptions. For example, people were found to underweight small probability events in experience-based decisions, while overweighting them in decisions based on descriptions (i.e. where the participants have full information about the outcome distributions but no feedback). This is now commonly referred to as the description-experience gap.

In parallel to the recent advancement in Decision Science, neuroscientists have for a long while used the experience-based decisions paradigm for analyzing brain-behavior interactions. For example, phenomena such as the feedback-based Error-Related Negativity (fERN) in event-related potentials and the role of non-declarative knowledge in selecting advantageously were discovered using experience-based tasks.

The goal of the current Research Topic is to combine two sources of knowledge concerning experience-based decisions: State of the art models in decision science, and neuroscientific and psychophysiological approaches that shed light on the working of the brain in these decisions.

Also relevant are process-based analyses of fractions of behavior in these types of decisions. We consider original empirical work and theoretical analyses of existing datasets.

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The neuroscience and psychophysiology of experience-based decisions: an introduction to the research topic

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Experience-based decisions can be defined as decisions emanating from direct or vicarious reinforcements that were received in the past. For example, in a typical setting a person initially faces blank buttons and needs to press any of them without prior information concerning the selection outcomes. Upon pressing a button the participant receives monetary outcomes (e.g., "you won $5") and then, based on this experience, makes another selection. Quite often hundreds of trials of this sort are administered. The outcomes of the two alternatives are usually sampled from different payoff distributions (e.g., a button producing a fixed payoff of $5 could be contrasted with a button producing risky payoff, such as wining $9 or $1 with equal likelihood). This allows examining the decision response to different incentive structures without explicit information concerning their statistical properties.

The current Research Topic aims to integrate various works in this area that have been conducted in Decision science and Neuroscience. The study of experience-based decisions has recently revealed some robust regularities that differ from how people make decisions based on descriptions (i.e., where the participants have full information about the outcome distributions but no feedback). For example, people were found to underweight small probability events in experience-based decisions, while overweighting them in decisions based on descriptions. This is now commonly referred to as the description-experience gap (Hertwig and Erev, 2009). In parallel to the recent advancement in Decision Science, neuroscientists have for a long while used the experience-based decisions paradigm for analyzing brain-behavior interactions. For example, phenomena such as the feedback-based Error-Related Negativity (fERN) in event-related potentials (Gehring and Willoughby, 2002) and the role of non-declarative knowledge in selecting advantageously were discovered using experience-based tasks. The goal of the current Research Topic was to combine these two disciplinary sources concerning experience-based decisions.

As expected, several works in this Research Topic explored the "underweighting rare event" tendency. Zhang and Maloney (2012) propose a logit model for this tendency as well as some other robust biases, and also suggest that the underweighting tendency may be driven by basic properties of neural transmission. Upton et al. (2012) propose that underweighting rare events may underlie some of the differences found between neuropsychological populations and controls in complex tasks such as the Iowa Gambling task. By contrast Glöckner et al. (2012) do not replicate the underweighting phenomena in decisions from sampling both in behavior as well as in eye point of gaze. Finally, Nevo and Erev (2012) investigate the immediate aftermath of a rare event and highlight a phenomenon whereby surprising events trigger a change in the participants' response.

Other authors focused on the issue of consistent preferences in experience-based tasks. Yechiam and Telpaz (2011) demonstrate consistency between tonic (at rest) arousal and risk taking, and show that it is more prominent in tasks with losses. In an important critique, Marchiori and Elqayam (2012) present some boundaries for consistency in risk taking. Ert (2012) retorts by arguing that most of these boundaries have been demonstrated in decisions from description, while in experience-based decisions consistency of individual differences is more robust. Relating to this, Warren and Holroyd (2012) show that the rapid fERN phenomena, which demarcates the rapid frontal cortical sensitivity to negative/positive outcomes, is larger in a condition involving active learning similar to an experience-based task, than in a condition involving passive learning.

Wang et al. (2012) examine the issue of whether choices in an experience-based task are guided by unconscious motivations, as evidenced by advantageous choices in the absence of conscious awareness of the difference between outcomes. Their results suggest a role for unconscious motivations. Such findings are very often interpreted as denoting dual processes or systems. Investigating the influence of dual processes, Hawes et al. (2012) focus on cognitive strategies in a complex decision task and their neural correlates, and their result demonstrate a combination of bottom-up experience-based learning and abstract learning. Sela et al. (2012) focus on an inhibition-related dual process and show that weak transcranial stimulation in the left hemisphere has the ability to affect risk taking, stressing the role of balance between theta activity in the two hemispheres. Finally, Warren and Holroyd (2012) propose two neuromodulatory systems in learning and decision making but stress the context-specific nature of the conditions for the activation of these two systems. For instance, changing the task context from gender to color provided sufficient conditions for differentially activating the two systems.

Finally, several authors examined the effect of social versus private environments, a research area often addressed by both decision and neuroscience models. Grygolec et al. (2012) show that in an experience-based task both the striatal and behavioral response to risk greatly differs in a social versus private setting. Investigating a similar domain, de Bruijn and von Rhein (2012) find that the context in which a person makes a decision with other people greatly determines how others' payoffs are perceived and the frontal mechanisms activated upon them. In a related work, Fahrenfort et al. (2012) show that sharing in a public good game prompts activation of neural systems associated with reward (striatum), but also empathy (anterior insular cortex and anterior cingulate cortex). Finally, Marchiori and Warglien's (2011) study demonstrates that a neurally inspired model can explain changes in participants' responses to different social dilemmas.

We believe that the current Research Topic led to some transfusion of ideas between the two disciplinary sources of Decision science and Neuroscience in key issues related to experience-based decisions (though see our concluding paper for some gaps that remain unresolved). Reflecting on one emergent theme, it appears that brain-behavior relations are quite unstable and may form or unform in different contexts. Contexts that facilitate the relation between frontal processes and behavior, and have been discussed in this Research Topic, include the availability of active choice, feedback, and losses. This sheds light on why experience-based tasks, which typically include these three components, are quite often used in neuropsychological assessment batteries for evaluating brain dysfunctions.

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On the value of experience-based decisions in studying constructs of risk taking

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Does risk taking behavior reflect intrinsic or constructed preferences? This question is deeply rooted in psychology and decision science, but is still the subject of a lively debate. The current paper suggests that the degree of support for the idea of consistent constructs of risk taking might be contingent upon the methodology used in the experiment. Specifically, it addresses the properties of two main paradigms that have been used to study this question: decisions from description and decisions from experience (Hertwig et al., 2004). The first paradigm attends to "explicit risk taking" extracted from self-reports of risky behaviors and/or tasks in which subjects are asked to choose between descriptions of different outcomes and their associated probabilities. The second paradigm deals with "implicit risk taking." It focuses on experience-based tasks in which people make repeated choices between options without knowing their exact payoffs and probabilities. Instead, they have to learn them from experience.

Interestingly, while description-based studies typically find risk taking to be mostly situation-specific, experience-based studies show evidence of consistent individual differences, and seem able to distinguish populations associated with risk taking behaviors from controls. The current paper will first overview some evidence showing the difference between the paradigms in suggesting stable constructs of risk, and then will address properties of these paradigms that may contribute to the discrepancies.

EVIDENCE FOR INDIVIDUAL DIFFERENCES IN RISK TAKING FROM DESCRIPTION-BASED AND EXPERIENCE-BASED TASKS

Until recently, the search for stable constructs of risk taking has mainly focused on explicit tasks, such as self-report questionnaires and description-based tasks. The results from those studies, however, showed mainly individual inconsistencies (e.g., Schoemaker, 1990), suggesting that risk taking is mostly situation-specific. For example, it might be reversed, depending on whether individuals are choosing between gains or between losses (Kahneman and Tversky, 1979), it seems to depend on the exact response mode (e.g., choice vs. pricing, see Lichtenstein and Slovic, 1971), and it varies across different life domains such as financial, health, and recreational (Weber et al., 2002; Hanoch et al., 2006). Strikingly, even minor changes in the question format might reverse preferences among alternatives. For example, when people are asked whether they would accept a risky gamble that has a positive expected value they tend to reject it, yet when they are asked to "choose between" that gamble, and a sure zero payoff, they tend to prefer the gamble (Ert and Erev, 2008). These results might lead to the conclusion that behavior does not depend on stable individual constructs of risk taking; rather, it depends mainly on situational factors.

However, this conclusion seems inconsistent with another line of research that focuses on experience-based tasks. In these tasks, the risks associated with each option are not described to the decision maker. Rather, it is only through experiencing the different options that the individual can get a sense of what actions might be riskier. Two well-known examples are the "Iowa gambling task" (IGT) and the "balloon analog risk task" (BART). In the IGT, the decision maker repeatedly selects among four decks of cards. Each deck is associated with a gain but also a loss, sometimes a large one. Two decks have positive expected value and therefore are considered "advantageous." The other two decks are "disadvantageous" since they are associated with negative expected value. Decisions are made from experience: participants do not know the outcomes of each deck and have to learn them through realizing the outcomes of their selection following each choice. Initially, the IGT was found to be effective in differentiating individuals with bilateral damage to the ventromedial prefrontal cortices (VMPC) from control subjects (Bechara et al., 1994)[1]. This deficit was reflected in the task by higher selection of disadvantageous decks. Later studies showed that the IGT also seems useful in distinguishing control subjects from risk taking populations such as chronic drug abusers (Yechiam et al., 2005), prisoners (Yechiam et al., 2008), and traffic offenders (Lev et al., 2008).

In the second popular task, the BART, people pump "air" into a virtual balloon; each time they pump, a fixed sum is added to their account, but if the balloon pops before they cash out, they receive nothing. The common measure of risk is the number of pumps the subject tries before cashing out. Evidence indicates that the BART score could be a good predictor of self-reported unhealthy risk behaviors (Lejuez et al., 2002), and that it can differentiate controls from drug users and cigarette smokers (Lejuez et al., 2003).

The picture emerging from studies of the experience-based paradigm suggests that behavior is affected by stable individual differences that account for risk taking behaviors. Taken together, the evidence from the different paradigms suggests that the researcher's conclusion regarding the role of stable individual differences in risk taking might vary substantially according to whether a description-based task or an experience-based task was used in the study. The next section suggests potential reasons contributing to the apparent discrepancy between the conclusions from the two paradigms.

EXPLAINING THE DISCREPANCIES BETWEEN EXPERIENCE-BASED AND DESCRIPTION-BASED TASKS IN ADDRESSING INDIVIDUAL RISK TAKING

Before addressing the different properties of each paradigm, it might be constructive to note that typical evidence from personality

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[1] Ventromedial prefrontal cortices lesions are associated with a syndrome in which individuals have normal IQ and reasoning ability, but demonstrate excessive risk taking in their decision-making behavior.

research suggests some support for both the situational and the individual trait views. Mischel and Shoda (1995) note that "the fact that the average cross-situational coefficients are typically low but non-zero is now widely accepted" (p. 247). Support for the effect of individual differences is suggested by the finding that the typical correlations across situations are consistently above zero. However, the large variation across situations suggests that situational factors may either mask such inherent tendencies, or at least interact with them in a way that results in apparently different behaviors (see also Weber and Johnson, 2008).

It is natural to assume that the role of situational factors will become more apparent when such factors receive more attention (e.g., when they are more salient). In description-based tasks, the situational factors are central and therefore are salient part of the description (e.g., the case of accepting/rejecting an attractive gamble vs. choice between sure zero and the gamble). In particular, they seem to be much more salient than in experience-based decisions in which the options are not described. Recently, Ert and Yechiam (2010) examined the possibility that individual differences in risk taking emerging from decisions from experience might differ from supposedly equivalent individual differences in decisions from description. Recall that a main finding in the decisions from description literature is the reversal of risk taking between the gain and loss domains, typically referred to as the "reflection effect." For example, while choosing between a sure $600 and a gamble that gives equal chances of winning $1200 or $0, most people choose the certain amount. Yet, in a choice between a sure loss of $600 and a gamble providing an equal chance of losing $1200 or $0, most people prefer the risky gamble (Kahneman and Tversky, 1979). Ert and Yechiam (2010) tested this prediction with a simple form of an experience-based task in which, instead of getting descriptions of the certain amount and the gamble, people chose repeatedly between two undescribed options, one that always yields 600 (−600 in the loss problem) and another that yields either 1200 (−1200 in the loss problem) or 0 with equal probability. The authors found that the aggregate proportion of risk taking replicated the reflection effect, showing higher risk taking in the loss domain. However, the analysis of choice at the individual level showed a significant *positive* correlation of 0.63 between the gain and loss domains, contradicting the reflection effect. This observation suggests that people who prefer certainty in the gain domain also prefer certainty while choosing between losses. In another study, Yechiam and Ert (2011) gave participants descriptions of these same problems. The aggregate results once again revealed higher risk taking in choice between losses, consistent with the reflection effect. However, the analysis at the individual level showed no correlation between choices in the gain and loss domains. One interpretation of these results is that in the experience-based choice, the framing of gambles has only a small effect, so the tendency to take risks over certain payoffs emerges at the individual level. However, this tendency might be masked or canceled out by the saliency of the framing in the description-based task.

The observation that description-based tasks might be more sensitive to framing effects than experience-based tasks may possibly relate to Langer's (1989) notion of mindfulness vs. mindlessness. Mindful decisions are explicit ones in which the decision maker considers the properties of the problem. When the decision maker operates mindlessly, she tends not to think about the properties of the problem, at least not explicitly. It is natural to assume that experience-based decisions are more mindless than description-based ones. Interestingly, while intuition suggests that to extract individual differences one would possibly like to encourage the individual to think deeply about the task, evidence suggests that such thinking might actually bias the decision maker to consider irrelevant data. Therefore, the decision maker may be more likely to exhibit her inherent tendencies while acting mindlessly than while acting mindfully. Moreover, while operating mindfully, the decision maker might avoid (or approach) risks for a variety of strategic reasons that could also interfere with her inherent tendencies. In line with this argument, Koritzky and Yechiam (2010) found that experience-based tasks are less sensitive than description-based ones to social-desirability effects. When participants were instructed to make a "good impression," they tended to avoid risks in description-based tasks more than under a control condition in which the instructions were neutral. Behavior in the experience-based task, however, was unaffected by the instruction to behave strategically, perhaps because it is relatively hard to pinpoint the kind of behavior that is expected to make a good impression in such tasks.

Additional evidence supporting the existence of stable constructs of risk taking comes from studies in neuroscience, showing activities in brain areas that are related to risk taking. Interestingly, many of those studies seem to use experience-based tasks in addressing the constructs of risk taking behavior. Some studies use the aforementioned IGT and BART (Rao et al., 2008; Lawrence et al., 2009), while others use different tasks that are also experience-based in nature (Critchley et al., 2001; Preuschoff et al., 2006; Gianotti et al., 2009). This observation also suggests the potential usefulness of experience-based tasks in studying individual differences.

CONCLUSION

In a recent review of studies of individual differences in decision-making, Appelt et al. (2011) highlighted the importance of a standardized approach to studying individual differences, and the value of categorizing the existing measures into meaningful classes that share similar properties. The current analysis suggests that one such meaningful categorization is the differentiation between description-based and experience-based tasks. Evidence suggests that experience-based tasks tend to be more successful in revealing consistent individual differences than description-based tasks. A potential reason for this relative success could be that experience-based tasks involve more mindless than mindfulness decisions and thus they are less sensitive to the influence of situation-specific factors. The relative success of experienced-based tasks in addressing individual differences suggests reasons for optimism regarding our understanding of the role of individual differences in risk taking. The high variety of experience-based tasks that are currently in use seem to call for comparative evaluations of those tasks to better understand the contribution of each task beyond and above the others. Such analyses may facilitate standardization and could further clarify the exact constructs that the different tasks aim to address.

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On surprise, change, and the effect of recent outcomes

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The leading models of human and animal learning rest on the assumption that individuals tend to select the alternatives that led to the best recent outcomes. The current research highlights three boundaries of this "recency" assumption. Analysis of the stock market and simple laboratory experiments suggests that positively surprising obtained payoffs, and negatively surprising forgone payoffs reduce the rate of repeating the previous choice. In addition, all previous trails outcomes, except the latest outcome (most recent), have similar effect on future choices. We show that these results, and other robust properties of decisions from experience, can be captured with a simple addition to the leading models: the assumption that surprise triggers change.

Keywords: fourfold response pattern to recent outcomes, positive and negative recency, the very recent effect, I-SAW, volume of trade

Analyses of financial markets reveal that the volume of trade tends to increase after sharp price increase, and also after sharp price decline (Karpoff, 1988). Higher volume of trade implies that owners are more likely to sell, and potential buyers are more likely to buy. Thus, the data suggest a fourfold response pattern to recent outcomes: Owners appear to exhibit negative recency after obtained gains (behave as if they expect a price decrease after a large price increase), but positive recency after a loss (expect another decrease after a large decrease). Potential buyers appear to exhibit the opposite pattern: positive recency after a large forgone gain (expect another increase after a large gain that they missed), and a negative recency after a forgone loss (expect a price increase after a price decrease).

Previous studies of decisions from experience appear to reflect a simpler effect of recent outcomes. Most studies document a robust positive recency effect (Estes, 1976; Barron and Erev, 2003; Barron and Yechiam, 2009; Biele et al., 2009): People tend to select the alternative that led to the best outcome in the previous trials[1]. This pattern is consistent with the law of effect (Thorndike, 1898), brain activity (Schultz, 1998), and is assumed by most learning models (e.g., Bush and Mosteller, 1955; Rescorla and Wagner, 1972; Erev and Roth, 1998; Fudenberg and Levine, 1998; Selten and Buchta, 1998; Camerer and Ho, 1999; Dayan and Niv, 2008; Marchiori and Warglien, 2008; Erev and Haruvy, in press).

The natural explanation for this apparent inconsistency between the stock market pattern and previous studies would be that many factors affect the behavior in the stock market, and the basic properties of human learning are only a small part of these factors. This explanation is consistent with the leading models of the stock market data. According to these models the effect of price change on the volume of trade is a product of an interaction between asymmetric traders (e.g., different interests, different knowledge etc.).

The current analysis focuses on a less natural explanation of the inconsistency. It considers the possibility that the financial data reflect an important behavioral regularity that was ignored by basic learning research. Our interest in this possibility was triggered by the recent demonstration that the insights obtained in basic learning research could be used to justify the prediction of the 2008 sub-prime crises in the financial markets (Taleb, 2007; Hertwig and Erev, 2009). Yet, the goal here is different. Rather than trying to predict the behavior of the stock market, we try to build on the robust stock market pattern in order to improve our understanding of basic learning processes. The attempt to achieve this goal led us to focus on the role of surprising outcomes. Specifically, we hypothesize that "surprise-trigger-change"[2]. Our definition of surprise is similar to the definition implied by the classical Rescorla–Wagner model: Surprise is assumed to increase with the gap between the expected and the observed outcomes. The surprise-trigger-change hypothesis is consistent with the stock market data: Large price changes are surprising, and for that reason they increase trade (change implies trade).

In addition, the surprise-trigger-change hypothesis can explain the fact that most learning studies document positive recency: These studies focus on the main effect of the recent payoff over the different outcomes, and do not examine this effect contingent on the level of surprise[3]. Thus, their results are consistent with

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[1] Several studies highlight interesting exceptions to this regularity. One example is the evidence for negative recency in prediction tasks (Barron and Yechiam, 2009). Ayton and Fischer (2004) show that negative recency is more likely to emerge in expectations of sequences of natural events.

[2] Previous studies of the effect of surprise (Mellers et al., 1997) show that surprising outcomes are overweighted. The main additions of the current hypothesis are the assertions that (1) surprising outcome have the same effect on the implicit decision of whether to think again during learning, and that (2) without this overweighting the common implicit decision is "not to think again."

[3] One contributor to the tendency to focus on the main effect and ignore the level of surprise is the fact that most basic learning studies focus on situations in which the feedback was limited to the obtained payoffs (and the computation of the net

a natural abstraction of the surprise-trigger-change hypothesis that implies a positive recency effect in most cases, and allows for the possibility of a negative recency effect after surprising outcomes.

Another nice feature of the surprise-trigger-change hypothesis involves its consistency with brain research. Analysis of the neural activation in the dopaminergic system reveals correlation between activation level and prediction error (Schultz, 1998). The current hypothesis suggests that the detection of prediction error, implies surprise, and increases the probability of a change.

The first part of the current paper tests the surprises-trigger-change hypothesis in simple binary choice experiments. The analysis continues with an exploration of the implications of the current results to the modeling of learning.

EXPERIMENT 1: THE SURPRISE-TRIGGER-CHANGE HYPOTHESIS

METHODS

Experiment 1 focuses on repeated play of the two problems presented in **Table 1**. The experiment used the "clicking paradigm" described in **Figure 1**.

The participants were 48 Technion students. Each participant faced each problem ("game") in a block of 100 trials. The order of the two problems was balanced over participants. The participants received a show-up fee of 30 Shekels (about $8) and could win more, or lose part of this amount in the experiment. The exact addition to the show-up fee was the outcome (in Shekels) in one randomly selected trial.

The experiment was run on personal computers. The experimental instructions (see left-hand side of **Figure 1**) were presented on printed sheet of paper and the participants could read them at all times. As the instructions indicate, the participants did not receive a description of the incentive structure. They were simply told that the experiment includes several multi-trial games, and their task (in each trial, in each game) is to select between the two keys. It was explained that their choices will determine their trial's payoff, and that they will receive immediate feedback after each trial. In addition, the instructions explain that the different games involve different payoffs, and that the subjects will be informed when a new game starts.

Notice that both problems involve a choice between the *status quo* (payoff of 0 with certainty), and a two-outcome risky prospect. The more surprising (less likely) outcome is the best outcome (+10) in Problem 1, and the worst outcome (−10) in Problem 2.

RESULTS OF EXPERIMENT 1

The results (c.f. **Table 1**) reveal the fourfold pattern predicted by the surprise-triggers-change hypothesis. In problem 1 (when the high payoff, +10, is rare and surprising) the participants exhibited positive recency after an *S* choice, but negative recency after an *R* choice. The positive recency effect is reflected by a higher rate of switches to *R* after high forgone payoff (23%) than after low forgone payoff (6%). The negative recency effect is reflected by a lower rate of repeated *R* choices after high obtained payoff (60%) than after low obtained payoff (79%).

In problem 2 (when the low payoff, −10, is rare and surprising) the participants exhibited negative recency after an *S* choice, but positive recency after an *R* choice. The negative recency effect is reflected by a lower rate of switches to *R* after high forgone payoff (21%) than after low forgone payoff (31%). The positive recency effect is reflected by higher rate of repeated *R* choices after high obtained payoff (84%) than after low obtained payoff (69%).

Analysis of individual participants reveals that this pattern is robust: 24 of the 36 participants that were faced with all

Table 1 | The two new problems studied in Experiment 1, and the main results.

Problem (*N*)		**Recent events**		**Experimental results**			**The predictions of I–SAW**		
		Recent choice	**Recent payoff from *R***	**Contingent *R*-rate**	**Implied recency effect**	***R*-rate over all trials**	**Contingent *R*-rate**	**Implied recency effect**	***R*-rate over all trials**
1 (48)	*S*: 0 with certainty	*S*	High: +10	0.23	+	0.29	0.25	+	0.41
	R: (10, 0.1; −1)		Low: −1	0.06			0.11		
		R	High: +10	0.60	–		0.81	–	
			Low: −1	0.79			0.82		
2 (48)	*S*: 0 with certainty	*S*	High: +1	0.21	–	0.57	0.18	–	0.59
	R: (1, 0.9; −10)		Low: −10	0.31			0.20		
		R	High: +1	0.84	+		0.89	+	
			Low: −10	0.69			0.75		

The contingent R-rates are the proportions of R choices as a function of the recent choice and the recent payoff from R. The implied recency effect is the sign of the difference between the R-rates after high and low payoffs from R given the same recent choice. When the recent choice is S, the recent payoffs from R are the recent "forgone payoffs," and the contingent R-rate is the proportion of switches from S to R. When the recent choice is R, the recent payoffs from R are the recent "obtained payoffs," and the contingent R-rate is the proportion of repeated R choices. N is the number of subjects.

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effect of surprise is difficult), and/or situations that do not involve low probability outcomes. Another contributor is the fact that the assumption that surprise triggers change dramatically complicates parameter estimation with the leading statistical methods.

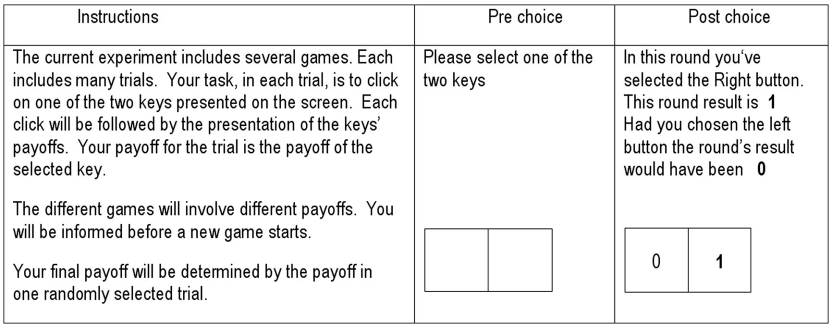
eight "recent outcomes by recent choice" contingencies[4] are better described by the fourfold hypothesis than by the positive recency hypothesis. This ratio (24/36) is significant larger than half ($p < 0.05$ in a sign test).

The aggregate *R*-rates were only 29% in Problem 1 when the expected value of *R* is positive, and 57% in Problem 2 when the expected value of Option *R* is negative. This result is consistent with the assertion that decisions from experience reflect underweighting of rare events (Barron and Erev, 2003).

Figure 2 presents the mean *R*-rates as a function of time. It reveals robustness of the main results over time.

REANALYSIS OF PREVIOUS STUDIES

The surprise-trigger-change hypothesis implies an important boundary for the fourfold recency pattern documented above. It suggests that this pattern will not emerge when the possible outcomes are equally likely; when the outcomes are equally likely, they are equally surprising, and the probability of a change is expected to be independent of the relative attractiveness of the



Instructions	Pre choice	Post choice
The current experiment includes several games. Each includes many trials. Your task, in each trial, is to click on one of the two keys presented on the screen. Each click will be followed by the presentation of the keys' payoffs. Your payoff for the trial is the payoff of the selected key. The different games will involve different payoffs. You will be informed before a new game starts. Your final payoff will be determined by the payoff in one randomly selected trial.	Please select one of the two keys	In this round you've selected the Right button. This round result is **1** Had you chosen the left button the round's result would have been **0** 0 **1**

FIGURE 1 | The instructions, and the screens in a study that uses the basic clicking paradigm. In the example the participant chose Right, won 1; and the forgone payoff was 0. The exact payoffs were determined by the game's payoff rule. Each of the games considered here focused on one of the problems listed in **Tables 1, 2,** or **3,** and included 100 trials. Each key was associated with one of the prospects. The assignment of prospects to buttons and the order of the problems were randomly determined for each participant.

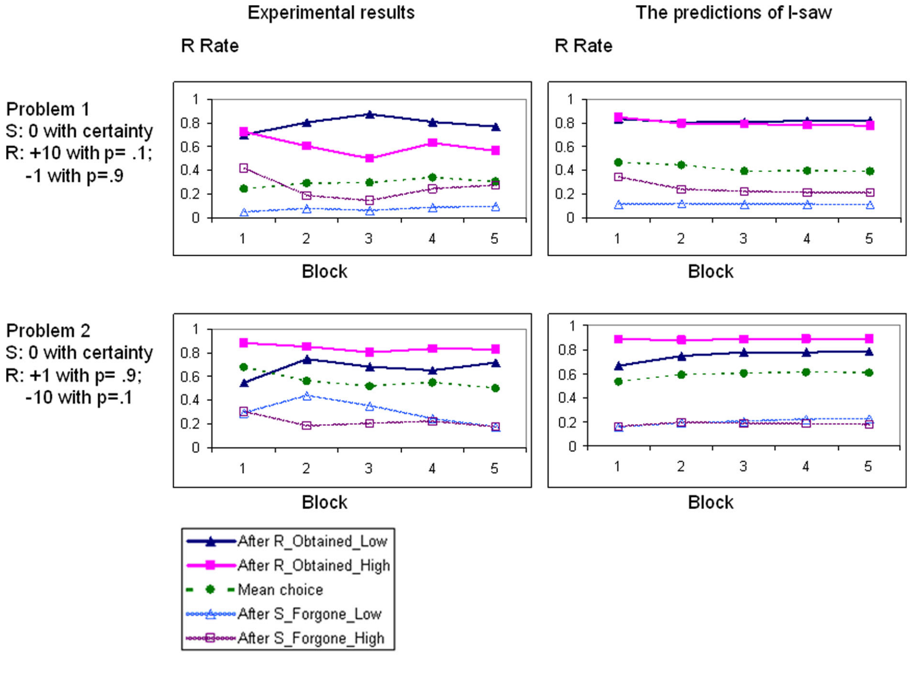


FIGURE 2 | The mean choice rates (over the 48 participants) in five blocks of 20 trials in Experiment 1. The left-hand graphs show the experimental results, the right-hand graphs show the predictions of the model. The *R* curve shows the aggregate *R*-rate (the mean choice rate of the risky option). The other four curves show the *R*-rate as a function of the choice and the outcome in the previous trial.

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[4] The remaining 12 participants did not face one or more of the eight contingencies. For example, 10 of them never experienced the payoff "+10" after selecting *R* (because they tended to select *S* and/or were unlucky).

recent payoff. In order to evaluate this prediction we reanalyzed data from previous studies that used the current paradigm to examine repeated choices between a safe prospect and a gamble that yields two equally likely outcomes. **Table 2** summarizes the contingent choice proportions documented in the study of six "50–50" problems. Problems 3 and 4 were studied in Haruvy and Erev (2002) and Grosskopf et al. (2006). Problems 5–8 were studied in Erev et al. (2008). The results are consistent with the current hypothesis. A strong positive recency effect was documented in all six problems (Problems 3–8). On average, the rate of risky choices is 58% after high payoff, and 38% after low payoff.

THE VERY RECENT EFFECT

Additional analysis of the positive recency effect documented in Problems 3–8 reveals that it is limited to the very recent outcome: The choice rate of the alternative that led to the best payoff in the most recent trial is 60%, and the choice rate of the alternative that led to the best payoff in the trial before the most recent is only 50% (the rate expected under the assumption of "no recency effect").

EXPERIMENT 2: A ROBUSTNESS TEST

METHODS

Experiment 2 was designed to evaluate the robustness of the current results. It uses Experiment 1's procedure with the exception that each participant was presented with 12 different problems. The participants were 28 Technion students. The 12 problems are presented in **Table 3**. These problems were randomly selected and studied in Erev et al. (2010a) under distinct information conditions.

RESULTS OF EXPERIMENT 2

The results, summarized in **Table 3**, replicate the surprise-trigger-change pattern documented in Experiment 1. Problems 9–15 in which the high payoff occurs with small probability (0.1 or less) are similar to Problem 1: The participants exhibited positive recency after an *S* choice, but negative recency after an *R* choice. The positive recency effect is reflected by the observation that the mean switch rate from *S* to *R* over these seven problems was higher after the high forgone payoff (26%) than after low forgone payoff (6%). The negative recency effect is reflected by the observation that the mean rate of repeated *R* choice over these seven problems

Table 2 | Six 50–50 problems that were examined in previous research.

Problem (*N*)		**Recent events**		**Experimental results**			**The predictions of I–SAW**		
		Recent choice	**Recent payoff from *R***	**Contingent *R*-rate**	**Implied recency effect**	***R*-rate over all trials**	**Contingent *R*-rate**	**Implied recency effect**	***R*-rate over all trials**
3 (10)	*S*: 10 with certainty	*S*	High: +21	0.58	+	0.63	0.27	+	0.58
	R: (21, 0.5; 1)		Low: +1	0.33			0.21		
		R	High: +21	0.79	+		0.85	+	
			Low: +1	0.59			0.81		
4 (10)	*S*: −10 with certainty	*S*	High: −1	0.39	+	0.45	0.19	+	0.42
	R: (−1, 0.5; −21)		Low: −21	0.21			0.15		
		R	High: −1	0.56	+		0.79	+	
			Low: −21	0.53			0.73		
5 (45)	*S*: 0 with certainty	*S*	High: +1000	0.44	+	0.48	0.23	+	0.50
	R: (1000, 0.5; −1000)		Low: −1000	0.24			0.17		
		R	High: +1000	0.71	+		0.83	+	
			Low: −1000	0.55			0.77		
6 (45)	*S*: 1000 with certainty	*S*	High: +2000	0.35	+	0.40	0.23	+	0.50
	R: (2000, 0.5; 0)		Low: 0	0.15			0.17		
		R	High: +2000	0.74	+		0.83	+	
			Low: 0	0.49			0.77		
7 (45)	*S*: 400 with certainty	*S*	High: +1400	0.40	+	0.45	0.23	+	0.50
	R: (1400, 0.50; −600)		Low: −600	0.17			0.17		
		R	High: +1400	0.73	+		0.83	+	
			Low: −600	0.55			0.77		
8 (45)	*S*: 1400 with certainty	*S*	High: +2400	0.47	+	0.49	0.23	+	0.50
	R: (2400, 0.5; 400)		Low: +400	0.19			0.17		
		R	High: +2400	0.79	+		0.83	+	
			Low: +400	0.52			0.77		

Problems in 3 and 4 were studied by Haruvy and Erev (2002), Problems 5–8 were studied by Erev et al. (2008). The format of the table and the meaning of the variables are the same as in ***Table 1****.*

Table 3 | The 12 problems studied in Experiment 2. The format of the table and the meaning of the variables are the same as in Table 1.

Problem (*N*)		**Recent events**		**Experimental results**			**The predictions of I–SAW**		
		Recent choice	**Recent payoff from *R***	**Contingent *R*-rate**	**Implied recency effect**	***R*-rate over all trials**	**Contingent *R*-rate**	**Implied recency effect**	***R*-rate over all trials**
9 (28)	*S*: 7 with certainty	*S*	High: +16.5	0.40	+	0.45	0.34	+	0.47
	R: (16.5, 0.01; 6.9)		Low: +6.9	0.04			0.07		
		R	High: +16.5	0.94	–		0.82	–	
			Low: +6.9	0.95			0.91		
10 (28)	*S*: −9.4 with certainty	*S*	High: −2	0.15	+	0.26	0.18	+	0.30
	R: (−2, 0.05; −10.4)		Low: −10.4	0.06			0.08		
		R	High: −2	0.70	–		0.69	–	
			Low: −10.4	0.80			0.80		
11 (28)	*S*: −4.1 with certainty	*S*	High: +1.3	0.27	+	0.54	0.28	+	0.44
	R: (1.3, 0.05; −4.3)		Low: −4.3	0.06			0.09		
		R	High: +1.3	0.86	–		0.84	–	
			Low: −4.3	0.94			0.87		
12 (28)	*S*: −18.7 with certainty	*S*	High: −7.1	0.29	+	0.38	0.24	+	0.37
	R: (−7.1, 0.07; −19.6)		Low: −19.6	0.06			0.10		
		R	High: −7.1	0.85	–		0.78	–	
			Low: −19.6	0.87			0.82		
13 (28)	*S*: −7.9 with certainty	*S*	High: +5	0.20	+	0.31	0.23	+	0.37
	R: (5, 0.08; −9.1)		Low: −19.6	0.06			0.10		
		R	High: +5	0.86	+		0.78	–*	
			Low: −19.6	0.84			0.81		
14 (28)	*S*: −25.4 with certainty	*S*	High: −8.9	0.22	+	0.45	0.28	+	0.47
	R: (−8.9, 0.08; −26.3)		Low: −26.3	0.07			0.11		
		R	High: −8.9	0.89	–		0.85	–	
			Low: −26.3	0.90			0.86		
15 (28)	*S*: 11.5 with certainty	*S*	High: +25.7	0.29	+	0.30	0.18	+	0.31
	R: (25.7, 0.1; 8.1)		Low: +8.1	0.07			0.09		
		R	High: +25.7	0.81	+		0.72	–*	
			Low: +8.1	0.78			0.77		
16 (28)	*S*: −15.5 with certainty	*S*	High: −8.8	0.42	+	0.68	0.30	+	0.73
	R: (−8.8, 0.6; −19.5)		Low: −19.5	0.19			0.27		
		R	High: −8.8	0.91	+		0.91	+	
			Low: −19.5	0.75			0.88		
17 (28)	*S*: 2.2 with certainty	*S*	High: +3	0.13	–	0.47	0.19	–	0.64
	R: (3, 0.93; −7.2)		Low: −7.2	0.15			0.23		
		R	High: +3	0.85	+		0.90	+	
			Low: −7.2	0.68			0.77		
18 (28)	*S*: 25.2 with certainty	*S*	High: +25.2	0.14	–	0.52	0.18	–	0.65
	R: (26.5, 0.94; 8.3)		Low: +8.3	0.32			0.24		
		R	High: +25.2	0.86	+		0.91	+	
			Low: +8.3	0.82			0.77		
19 (28)	*S*: 6.8 with certainty	*S*	High: +7.3	0.08	–	0.50	0.13	–	0.57
	R: (7.3, 0.96; −8.5)		Low: −8.5	0.23			0.18		
		R	High: +7.3	0.92	+		0.91	+	
			Low: −8.5	0.77			0.72		
20 (28)	*S*: 11 with certainty	*S*	High: +11.4	0.09	–	0.57	0.15	–	0.64
	R (11.4, 0.97; 1.9)		Low: +1.9	0.19			0.25		
		R	High: +11.4	0.94	+		0.92	+	
			Low: +1.9	0.71			0.77		

was lower after the high obtained payoff (84%) than after low obtained payoff (87%).

Problems 17–20 in which the low payoffs occur with small probability (0.1 or less) are similar to Problem 2: The participants exhibited negative recency after an *S* choice, and positive recency after an *R* choice. The negative recency effect is reflected by the observation that the mean switch rate from *S* to *R* over these four problems was lower after the high forgone payoff (11%) than after low forgone payoff (22%). The positive recency effect is reflected by the observation that the mean rate of repeated *R* choice over these four problems was higher after the high obtained payoff (89%) than after low obtained payoff (75%).

Finally, Problem 16 is which the high and low outcomes occur with moderate probability is similar to Problems 3–8: The participants exhibit positive recency after *R* and after *S* choices.

A QUANTITATIVE SUMMARY

In order to clarify the implications of the surprise-trigger-change hypothesis we chose to quantify it within a simplified variant of the explorative sampler model that provides the best predictions of the results in the first Technion choice prediction competition (Erev et al., 2010a). The model is described below.

THE INERTIA SAMPLING AND WEIGHTING MODEL[5]

The model distinguishes between three response modes: exploration, exploitation, and inertia. Exploration implies random choice. The probability of exploration, by individual *i*, is 1 in the first trial, and ε_i (a trait of *i*) in all other trials.

During exploitation trials, individual *i* selects the alternative with the highest estimated subjective value (ESV). The ESV of alternative *j* at trial $t > 1$ is:

$$\text{ESV}\,(j,t) = (I - w_i)\,(\text{S\_}Mean) + w_i\,(\text{G\_}Mean) \quad (1)$$

where S_Mean (sample mean) is the average payoff from Alternative *j* in a small sample of μ_i similar previous experiences (trials), G_Mean (grand mean) is the average payoff from *j* over all $(t-1)$ previous trials, and μ_i and w_i are traits. The assumed reliance on small samples was introduced to capture the observed tendency to underweight rare events (Barron and Erev, 2003). The similarity based sampling rule was added to capture discrimination between different states of nature (Gonzalez et al., 2003)[6].

The μ_i draws are assumed to be independent (sampling with replacement) and biased toward the most recent experience (Trial $t-1$). A bias occurs with probability ρ_i (a trait) and implies draw of Trial $t-1$. When a bias does not occur (probability $1-\rho_i$) all previous trials are equally likely to be sampled[7]. The motivation behind this assumption is the "very recent effect."

Inertia is added with the assumption that the individuals tend to repeat their last choice. The exact probability of inertia at trial $t+1$ is assumed to decrease when the recent outcomes are surprising. Specifically, if the exploration mode was not selected, the probability of inertia is:

$$P\,(Inertia\ at\ t+1) = \pi_i^{Surprise(t)} \quad (2)$$

where $0 < \pi_i < 1$ is a trait that captures the tendency for inertia. As in Rescorla and Wagner (1972) we assume that surprise increases with the gap between the expected and the realized outcomes. The exact value of the gap is computed under the assumption the agents compare the realized outcomes to two estimates (or expectations): One estimate is based on the most recent outcome, and one is based on the mean payoff. Thus, the gap is the mean of four differences:

$$Gap(t) = \frac{1}{4}\left[\sum_{j=1}^{2}\left|obtained_j(t-1) - \text{obtained}_j(t)\right| + \sum_{j=1}^{2}\left|G\_mean_j(t) - obtained_j(t)\right|\right] \quad (3)$$

where $\text{Obtained}_j(t)$ is the payoff obtained from *j* at trial *t*, and $\text{G\_mean}_j(t)$ is the average payoff obtained from *j* in the first $t-1$ trials (the grand mean). The surprise at *t* is normalized by the mean gap (in the first $t-1$ trials):

$$Surprise(t) = Gap(t)\big/\big[Mean\_Gap(t) + Gap(t)\big] \quad (4)$$

The mean gap at *t* is a running average of the gap in the previous trials [with Mean_Gap(1) = 0.00001]. Specifically,

$$Mean\_Gap(t+1) = Mean\_Gap(t)(1 - 1/r) + Gap(t)(1/r) \quad (5)$$

where *r* is the expected number of trials in the experiment (100 in the current study).

Notice that the normalization (Eq. 4) is necessary to capture the intuition that a multiplication of all the nominal payoffs by a positive constant will not increase surprise in the long term. In addition, normalization keeps the value of Surprise(t) between 0 and 1, and the probability if inertia between π_i [when Surprise$(t) = 1$] and 1 [when Surprise$(t) = 0$].

An interesting justification for this gap-based abstraction comes from the observation that dopamine neurons activation increases with prediction error (Schultz, 1992, 1998; Montague et al., 1996, 2004; Caplin and Dean, 2007). The current abstraction of surprise is a quantification of this observation; in the current context, the present quantification outperforms all the other quantifications that we have considered (the choice prediction competition described below suggest that it is not easy to find a better quantification).

The traits are assumed to be independently drawn from a uniform distribution between the minimal possible value (allowed by the model) and a higher point. Thus, the estimation focused on estimating the upper points (five free parameters). The estimation

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[5] Computer programs (in SAS and Matlab) that derive the predictions of the current model can be downloaded from http://sites.google.com/site/gpredcomp/7-baseline-models.

[6] The current implementation of the model is simplified with the assumption that all previous trials are equally similar. The simplification assumption has to be modified to address learning in dynamic settings.

[7] This assumption implies that the sampling probability is independent of the outcome (of the sampled experiences). The assumed independence implies underweighting of rare events, and distinguishes the current models from the "representativeness heuristic" that can lead to overweighting of rare (low base rate) events (see Erev et al., 2008).

used a grid search procedure. Best fit implies the following trait distribution: $\varepsilon_i \sim U[0,0.24]$, $w_i \sim U[0,1]$, $\rho_i \sim U[0,0.12]$, $\pi_i \sim U[0,1]$, and $\mu_i = 1, 2, 3$, or 4.

The right-hand columns in **Tables 1–3** and **Figure 2** present the predictions of inertia sampling and weighting (I–SAW) with these distributions. These exhibits reveal that I–SAW reproduces the main behavioral tendencies. For example, I–SAW correctly captures the direction (sign) of the recency effect in 38 of the 40 contingencies (20 games × 2 possible recent choices). The correlation between the 20 observed and predicted mean choice rates is 0.85, and the correlation between the 80 observed and predicted contingent choice rates is 0.94.

We believe that the most important contribution of I–SAW is the demonstration that the surprise-trigger-change assumption is sufficient to capture direction of the recency effect in the current setting. It is not necessary to assume expectations concerning specific sequential dependencies (e.g., the expectation that $+10$ in Problem 1 is more likely after -1); nor is it necessary to relax the assumption that good outcomes increases the tendency to choose the reinforced alternative again.

COMPARISON WITH THE EXPLORATIVE SAMPLER MODEL

Inertia sampling and weighting differs from the explorative sampler model that motivates it in four ways; the changes include two simplification assumptions, and two additions. The first simplification involves the probability of exploration. The explorative sampler assumes a continuous decrease in the probability of exploration with time. Specifically, $P(Explore_t) = \varepsilon^{\frac{t-1}{t+T^{\delta}}}$ where T is the expected length of the experiment, and δ is a free parameter that captures the sensitivity to the length of the experiment. This assumption is simplified in I–SAW with the assertion that $P(\text{Explore}_t) = 1$ if $t = 1$, and ε_i otherwise. The main motivation for the simplification is the current focus on learning with complete feedback that reduces the importance of exploration (the explorative sampler, in contrast, was designed to address learning when the feedback in limited to the obtained payoff). A second motivation is the observation that the simplification assumption saves a parameter, and does not reduce the fit of the current data.

A second simplification concerns with the recalled subjective value of the objective outcomes. The explorative sampler allows for the possibility of a non-linear function in the spirit of prospect theory (Kahneman and Tversky, 1979) that implies diminishing sensitivity. This assumption is simplified in I–SAW with the implicit assumption that the recalled values are the objective payoffs. This simplification assumption saves a parameter, and does not reduce the fit.

The main addition, introduced in I–SAW, is the surprise-trigger-change assumption. In order to evaluate the significance of this assumption we evaluated a simplified variant of I–SAW that does not include this addition (the inertia trait, π_i, is set to zero). The results reveal that with this constraint, I–SAW predicts positive recency in all 40 cases (and for that reason in capture the direction of the recency effect in only 31 of the 40 cases). In addition, this constraint reduces the correlation between the observed and predicted contingent R-rates from 0.94 to 0.77.

The second addition is the individual differences assumed in I–SAW. This addition does not increase the number of free parameters and was introduced to capture the consistent individual differences documented in recent learning studies (see Yechiam et al., 2005). Elimination of this addition has limited effect on the fit of the statistics discussed above.

POTENTIAL GENERALITY AND ALTERNATIVE MODELS

Recall that the current paper is based on the assertion that similar learning processes drive behavior in simple laboratory experiments and in the stock market. This assertion has directed our choice of model. That is, I–SAW is meant to be more than an *ad hoc* summary of the current results; it tries to summarize the basic properties of decisions from experience, and should be able to provide useful prediction of behavior in a wide set of situations. In order to evaluate this optimistic "generality hypothesis" it is constructive to consider the results of a recent choice prediction competition that was organized by Erev et al. (2010b).

The competition was conducted after the completion of the first draft of the current paper (which included the data and the presentation of I–SAW), and focused on the prediction of behavior in four-person two-alternative Market Entry games. In each trial of these games, each player has to decide between a safe option and risky entry to a market in which the payoff can decrease with the number of entrants. Notice that the set of individual decision tasks considered above is a subset of the class of market entry games (the subset in which the payoffs from risky choice do not decrease with the number of other entrants).

The competition was based on two studies. Each study examined 40 games (randomly selected from the same population of games). Each game was played for 50 trials with immediate feedback concerning the obtained and the forgone payoffs. After the completion of the first study the organizers published the "introduction to the competition paper" (Erev et al., 2010b). This paper presents the results, and the best fit of these results with nine baseline models. The baseline models included the most popular models proposed to capture behavior in games (including: several versions of reinforcement learning, Erev and Roth, 1998; stochastic fictitious play, Fudenberg and Levine, 1998; EWA, Camerer and Ho, 1999) and I–SAW. The analysis of the fit of these models revealed a large advantage of I–SAW over the other models.

Immediately after the publication of the introduction paper, and before running the second study, the competition organizers challenged other researchers to participate in a competition that focuses on the prediction of the results of the second study. The call for participation in the competition was published in leading Email lists in psychology of decision making, cognitive psychology, behavioral economics, game theory, and reinforcement learning. To participate in the competition the potential competitors had to submit a model implemented in a computer program model that reads the parameters of the games as input, and derives the results as an output. The models were ranked based on their mean squared error. The participants were allowed to use improved versions of the baseline models.

Twenty-five teams participated in the competition. The submitted models included reinforcement learning, neural networks, ACT-R, and I–SAW like sampling models. The results reveal large advantage of sampling models that assume reliance on small samples and the current surprise-triggers-change rule. Indeed, all the 10 leading submissions belong to this class of models. The winner of the competition (Chen et al., 2011) is a variant of I–SAW that adds the assumption of bounded memory. The runner up (Gonzalez et al., 2011) quantifies the same assumptions in a refinement of the instance based learning model (Gonzalez et al., 2003).

It is important to emphasize that the advantage of I–SAW over the reinforcement learning models that were examined in the competition does not question that value of the reinforcement learning approach. Rather, this observation suggests that it is not easy to outperform I–SAW with the natural extensions of the popular reinforcement learning models. We hope that the publication of the competition and the current results will facilitate the exploration of the assumptions that have to be added to basic reinforcement learning models in order to capture decisions from experience. It seems that these assumptions will include sensitivity to recent choices (see similar observation in Lau and Glimcher, 2005).

In summary, the results clarify potential of simple learning models that assume reliance on small samples and surprise-trigger-change. Models of this type can be used to provide useful *ex ante* prediction in a wide set of situations. In addition, the competition suggests that additional research is needed to improve our understanding of the best quantification of these assumptions.

RELATIONSHIP TO MODELS OF PAVLOVIAN CONDITIONING

Comparison of I–SAW to the leading models of Pavlovian conditioning (including Rescorla and Wagner, 1972; Pearce and Hall, 1980) reveals one similarity, and one difference. The similarity involves the quantification of surprise by the difference between the expected and obtained outcomes. The difference involves the implication of surprise. The Rescorla–Wagner and similar models suggest that "surprise triggers learning," and the current analysis suggests that "surprise triggers change." This difference, however, does not imply an inconsistency: the Rescorla–Wagner model focuses on associative strength and do not have clear predictions for choice behavior. Our favorite interpretation of the effect of associative strength on choice behavior is based on Rescorla and Solomon (1967) two-process learning theory; this interpretation implies that the associative strength determines the similarity function that affects the sampling in I–SAW and similar models. We hope to address this and alternative explanations of the relationship between the current results and Pavlovian conditioning in future research.

CONCLUSION

The main implications of the current results are related to two of the main assumptions of basic learning research. The first assumption states that learning processes are extremely general and robust. They are common to different species (Shafir et al., 2008), underlay behavior in wide sets of situations (Skinner, 1938), and reflect basic properties of the brain (Schultz, 1998). The current analysis demonstrates the value this assumption. It shows that the apparent inconsistency between the recency effects documented in financial data and in basic learning research does not imply distinct behavioral tendencies. Examination of the sequential dependencies reveals that the fourfold recency pattern, suggested by the financial data, is a robust property of basic learning processes.

The second assumption involves the abstraction of the robust properties of learning. Most leading models assume a general positive recency effect. The current results highlight three boundaries of this effect. Two boundaries are the negative recency parts of fourfold recency pattern: Positively surprising outcomes were found to reduce the likelihood of repeated choice of the reinforcing prospect, and surprising unattractive forgone payoffs were found to increase the tendency of a switch to the prospect that led to the worst payoffs. A third boundary is suggested by the very recent effect. The current results suggest that the most recent trial has larger effect than previous experiences, but all previous experiences have an approximately the same effect independently of their recency.

The current analysis suggests that the distinct effects of recent outcomes can be captured with simple models that share two main assumptions: reliance on small samples of past experiences, and surprise-triggers-change. I–SAW, the model proposed above, is one abstraction of these assumptions. One explanation for the success of I–SAW and similar models here and in the choice prediction competition (Erev et al., 2010b), is related to the dynamic features of natural environments. The positive recency assumption is useful (likely to be selected by consequences) when the recent outcomes are best predictors of the next outcomes. But positive recency is not likely to be effective if the outcomes are determined by a Markov process with small number of distinguishable states. The reliance on the outcomes obtained in similar (and not necessarily recent) experiences, and high sensitivity to surprises, can be more effective in these settings. Thus, it is possible that the success of sampling based models reflects the ecological importance of learning in environments with relatively small number of distinguishable states.

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The role of risk aversion in non-conscious decision making

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To what extent can people choose advantageously without knowing why they are making those choices? This hotly debated question has capitalized on the Iowa Gambling Task (IGT), in which people often learn to choose advantageously without appearing to know why. However, because the IGT is unconstrained in many respects, this finding remains debated and other interpretations are possible (e.g., risk aversion, ambiguity aversion, limits of working memory, or insensitivity to reward/punishment can explain the finding of the IGT). Here we devised an improved variant of the IGT in which the deck-payoff contingency switches after subjects repeatedly choose from a good deck, offering the statistical power of repeated within-subject measures based on learning the reward contingencies associated with each deck. We found that participants exhibited low confidence in their choices, as probed with post-decision wagering, despite high accuracy in selecting advantageous decks in the task, which is putative evidence for non-conscious decision making. However, such a behavioral dissociation could also be explained by risk aversion, a tendency to avoid risky decisions under uncertainty. By explicitly measuring risk aversion for each individual, we predicted subjects' post-decision wagering using Bayesian modeling. We found that risk aversion indeed does play a role, but that it did not explain the entire effect. Moreover, independently measured risk aversion was uncorrelated with risk aversion exhibited during our version of the IGT, raising the possibility that the latter risk aversion may be non-conscious. Our findings support the idea that people can make optimal choices without being fully aware of the basis of their decision. We suggest that non-conscious decision making may be mediated by emotional feelings of risk that are based on mechanisms distinct from those that support cognitive assessment of risk.

Keywords: decision making, consciousness, risk aversion, post-decision wagering, confidence

INTRODUCTION

Decision making refers to a process of forming preferences, selecting and executing an action from alternatives, and evaluating and predicting rewarding or aversive outcomes. Whether we can make accurate and optimal decisions without full conscious awareness of the basis for the decision remains controversial, while evidence for non-conscious processing itself has been established in the perceptual domain [e.g., implicit memory and priming (Kouider and Dehaene, 2007)]. Some evidence suggests that neuropsychological patients with damage to primary visual cortex lack visual phenomenal awareness, yet can successfully make many visually guided decisions (Stoerig et al., 2002; Persaud et al., 2007). Under certain circumstances, neurologically healthy subjects seem to make advantageous decisions without knowing why, for instance when they face a situation where the number of relevant parameters exceeds the limits of conscious working memory (Dijksterhuis et al., 2006).

Another possible instance of non-conscious decision making is reported in a number of studies using the Iowa Gambling Task (IGT). In the past decade, the IGT has been extensively used as a probe for decision making in situations that feature uncertainty, reward, and punishment, mimicking aspects of real life (Damasio, 1994; Bechara et al., 1997, 1999, 2000; Anderson et al., 1999; Fellows, 2004; Oya et al., 2005; Dunn et al., 2006). In the IGT, participants are faced with four decks of cards. In each trial, they choose one deck and draw a card from it. Each card is associated with a variable amount of monetary gain. In some trials, it is followed by a large amount of loss. In the long run, participants lose money on some decks, but win money on others. Yet the complexity of payoffs in the IGT prevents subjects from calculating the expected value associated with each deck, and subjects typically feel as though they are guessing when making their choices, especially early on in the task. Past studies of the IGT have reported an intriguing phenomenon, which motivated our study: subjects start to make advantageous card selections well before they can verbalize why they selected those decks (Bechara et al., 1997; Persaud et al., 2007). Remarkably, their autonomic response, as measured by skin conductance, also distinguishes good and bad deck selection before the subjects can verbalize the basis of their deck selection (Bechara et al., 1997), supporting the theory that emotional response informs complex decision making (Damasio, 1994; Bechara et al., 2000; but also, see Tomb et al., 2002; Dunn et al., 2006). Though an intriguing finding, the claim that decision making occurs in the absence of awareness in the IGT has been criticized on several grounds. In particular, Maia and McClelland (2004, 2005) have criticized the operational definition of "non-conscious," arguing that people may be vaguely aware of their strategy even though they do not say so with open-ended questions (Bechara et al., 1997). When subjects were probed every 10 trials by a set of questionnaires, which involves numerical rating of the goodness of each deck, direct estimation of the expected payoff of each deck, expression of the best strategy for the IGT, and so on, it was found that they started to make optimal choices at the same time as they started to show some form of conscious awareness (Maia and McClelland, 2004; Persaud et al., 2007).

However, these detailed questionnaires have themselves been criticized because they force subjects to introspect in an unnatural way during decision making (Koch and Preuschoff, 2007), thus undermining the methods for identifying implicit knowledge by prompting subjects to become aware when they otherwise would not (Bechara et al., 2005). To address this problem, Persaud et al. (2007) proposed an alternative measure of awareness, which is objective in that it does not rely on subjective ratings, and also indirect and less obtrusive compared to the detailed questionnaire used by Maia and McClelland (2004). In Persaud et al.'s post-decision wagering task, subjects indirectly reveal the confidence that they have in their decision by wagering high or low on the expected outcome of their choice. A correct choice followed by a high wager is taken as an index of conscious awareness. When probed with open-ended questions (Bechara et al., 1997), post-decision wagering replicated the original findings: subjects chose advantageously from the decks before they showed any evidence of conscious awareness as revealed by post-decision wagering. However, when probed with a more intrusive questionnaire (Maia and McClelland, 2004), advantageous deck choices and optimal post-decision wagers developed concurrently. These results reconcile the previous findings and underline the fact that detailed inquiry of conscious awareness can alter the very conscious access one intends to measure.

The validity of post-decision wagering as a probe of consciousness, however, has yet to be fully demonstrated (Koch and Preuschoff, 2007; Clifford et al., 2008a; Schurger and Sher, 2008; Dienes and Seth, 2010; Fleming and Dolan, 2010; Sandberg et al., 2010). The ensuing critiques have argued that there is a distinction between true performance without awareness on the one hand, and simply a reluctance, on the other hand, to gamble with weak sensory evidence despite full awareness (Clifford et al., 2008a). This second possibility is "risk aversion" (Koch and Preuschoff, 2007; Schurger and Sher, 2008), the well-known finding that people will often make a choice that has a lower expected value than some other option, if it also has less variance in its payoffs. This phenomenon is accounted for by assuming that people maximize utility rather than expected value, where utility is a concave function of value for risk-averse individuals (and convex for risk-seeking individuals) (Kahneman and Tversky, 1979; Rabin, 2000; Holt and Laury, 2002). Therefore, risk-averse subjects often turn down gambles with positive expected value, simply because the variance (or their belief about the variance) in payoffs is sufficiently high that their utility for the gamble is lower than an alternative option. In other words, subjects' wagering strategies may be a reflection of their attitude toward risk, and so sub-optimal wagering may be perfectly consistent with their preferences (Schurger and Sher, 2008). In fact, Dienes and Seth (2010) found correlation between risk aversion and the degree of non-conscious knowledge inferred from wagering. It is therefore critical to understand the role of risk aversion in post-decision wagering in order to fully dissect the role of non-conscious processes in decision making.

There are additional aspects in the task design of the IGT itself (Fellows, 2004; Dunn et al., 2006; Bossaerts et al., 2008), which preclude an unequivocal interpretation either for or against non-conscious decision making. Notably, the IGT has at most one onset of awareness and is essentially a one-shot experiment, where subjects are not allowed to practice the task and they are not informed of any critical information about the task structure (e.g., the possible payoff structure for each deck, when the task ends, etc.). In such a situation, people are known to exhibit ambiguity aversion (Ellsberg, 1963; Camerer and Weber, 1992; Rode et al., 1999; Hsu et al., 2005), which may or may not be related to non-conscious decision making. In the economics literature, ambiguity refers to situations where the probabilities of the different outcomes are unknown. Ambiguity aversion then refers to the fact that most people tend to avoid choosing options where the probabilities are unknown. It is important to note that risk aversion and ambiguity aversion are separate phenomena. Risk aversion describes an individual's aversion to variance in payoffs while ambiguity aversion describes an individual's aversion to unknown probabilities (lack of information about the likelihood of the outcomes).

In addition, due to the IGT's one-shot nature, subjects can notice which decks are good at most once during the experiment. This is statistically inefficient, yielding effects that are sometimes unreliable even in healthy normal controls (Dunn et al., 2006). While a previous study (Oya et al., 2005) applied a reinforcement learning algorithm to the IGT to solve some of these difficulties, it remains unclear how to incorporate risk aversion effects into reinforcement learning under the unconstrained parameters of the original IGT (Bossaerts et al., 2008).

The goal of our study was to test for non-conscious decision making while ruling out other explanations. Toward that aim, we modified the IGT in four important ways. First, we incorporated post-decision wagering to probe subjects' awareness indirectly in each trial (Persaud et al., 2007). Second, to improve statistical power, we repeatedly reshuffled deck-payoff contingencies once subjects noticed the contingency, resulting in multiple epochs of learning, and choice within each subject. Third, to eliminate ambiguity and heterogeneous priors about the task structure, we told subjects the structure of the game by detailing the distribution of payoffs from the four decks (but without identifying the location of the decks). This also allowed us to apply a formal Bayesian model to subjects' choices. Fourth, we measured each subject's risk aversion profile with a similar but explicit task where they were asked to wager on various gambles with different expected values and levels of risk (shown explicitly). We incorporated this measure of explicit risk aversion into the Bayesian model to predict subjects' wagering behaviors.

With our modified version of the IGT, we replicated the finding that there is a gap between when subjects start to choose optimally in the IGT and when they start to bet high in the post-decision wagering task (Persaud et al., 2007). Subjects wagered high much less often than predicted from the Bayesian model incorporating their risk aversion profiles. Thus, the discrepancy between good choice behavior yet poor wagering cannot be fully explained by risk aversion alone. We also found that risk aversion in our modified IGT and in the explicit task were uncorrelated. We suggest that risk aversion observed in our version of the IGT may reflect processes that are distinct from those at work when payoff probabilities are explicitly known. Such implicit risk aversion may arise from the feeling of risk (Loewenstein et al., 2001) under complicated real life situations where no explicit probabilities are available and may be an instance of a "somatic marker" that helps us navigate choices and plans in everyday life (Damasio, 1994).

MATERIALS AND METHODS

SUBJECTS AND EXPERIMENTAL PROCEDURE

We carried out two experiments, involving separate subject samples. Each experiment consisted of the two phases described below, but their order was counterbalanced.

Experiment 1

Sixteen students (six females) from the California Institute of Technology (Caltech) gave written informed consent according to a protocol approved by the Caltech IRB. The age of subjects ranged from 18 to 24 (mean = 21). Their psychological and economic background information was collected at the end of the experiment.

All participants first participated in 100 trials of a computerized version of the IGT (Bechara et al., 1994) with post-decision wagering (Persaud et al., 2007), followed by two versions of our learning task (**Figure 1A**) without knowledge of the task structure or the payoffs. Data from these prior tasks are not analyzed or presented in the present study, but it is important to note that they

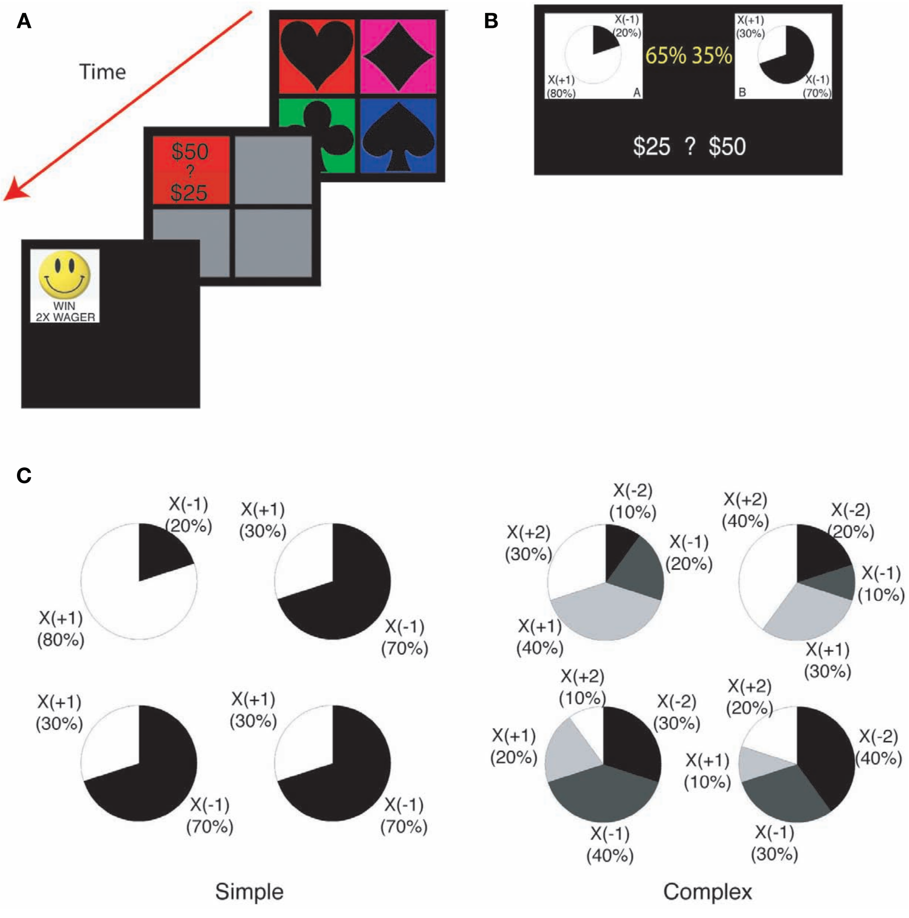

FIGURE 1 | Task structure. (A) The learning task with post-decision wagering. Four decks were presented to subjects on a computer display. After subjects chose a card, they wagered either $50 or $25. Subjects saw the outcome of the trial immediately after wagering. **(B)** The explicit risk aversion task. Identical payoff structures were used as in the learning task. The payoff structure was depicted with pie charts. The probability with which each pie chart would be selected was indicated by a yellow percentage. Subjects wagered either $50 or $25. **(C)** The payoff structures for four decks in the simple (left) and the complex (right) version of the tasks.

provided all subjects with a substantial and equal amount of prior background experience.

Each subject then underwent two phases of the experiment in the same fixed order:

Phase 1–Two versions of the *learning task with post-decision wagering*, after being informed of the payoff distributions from the different types of decks, 100 trials each.

Phase 2–Two versions of the *explicit risk aversion task* (**Figure 1B**), the first version with 50 trials of the "simple" gamble and the second with 100 trials of the "complex" gamble (**Figure 1C**, see below for details of different versions of the task).

Subjects were familiarized with the tasks and post-decision wagering through practice trials ($\sim$20 trials). Within each phase, the order of the two versions of the tasks was randomized across subjects. Questionnaires were given after each phase to make sure subjects understood the tasks.

Subjects were paid a fixed amount for their participation ($5), a fixed amount ($3) for the IGT, as well as a variable amount for their performance (mean = $5.34) in the learning and explicit tasks. For the learning task, subjects were paid the amount they earned, which was divided by 2000. For the explicit risk aversion task, subjects were paid at the end of their experiment, based on their earnings from one randomly selected trial.

Experiment 2

We conducted Experiment 2 with 20 naïve Caltech subjects. The tasks in Experiment 2 were identical to those in Experiment 1, with four important differences:

1) Subjects did not receive any prior background tasks (IGT or learning task), as they had in Experiment 1.
2) The two phases were done in a fixed order (Phase 2 first, then Phase 1), counterbalancing the order from Experiment 1.
3) Subjects underwent two *explicit risk aversion tasks*, 100 trials of the "simple" and 100 trials of the "complex" gamble. Unlike Experiment 1, here we paid subjects for every trial, in order to match the payment scheme with the learning task (see below for details).
4) All subjects were tested simultaneously in a social science experimental laboratory with many cubicles with computer terminals for each individual rather than individually as in Experiment 1.

In this experiment, subjects were paid a fixed amount for their participation ($10) in addition to a variable amount based on their performance in all four tasks (simple and complex versions of the explicit and learning tasks). Prior to each phase, subjects were familiarized with each task through 10 practice trials.

LEARNING TASK WITH POST-DECISION WAGERING

Subjects were given a $2000 loan of play money in the beginning and told that their goal was simply to earn as much play money as possible. In each trial, four decks with different colored symbols were presented on the display (**Figure 1A**). Subjects clicked on one of the decks using a mouse. After selecting a card, they wagered either $50 or $25 by clicking on the upper or lower half of the flipped card, respectively. After wagering, the payoff of the selected card was displayed as a multiplier for the wagered amount (X WAGER). For example, if a subject wagered $50 and got a $X(-2)$ payoff, they would lose $100 in that trial. Note that the final outcome (i.e., loss of $100) was not shown to the subjects. At the time of the payoff, the positive multiplier was associated with a happy icon and a positive laughter sound (070-who2.wav[1]) while the negative multiplier was associated with a sad icon and an obnoxious sound of shattered glass (truckcollide.wav[2]).

We randomized the spatial positions of the decks in each trial, thus forcing subjects to learn solely about the association between their appearance and their payoff. To encourage quick decisions relying on gut feelings, we instructed subjects to respond within 1.5 s after the deck presentation. If they did not move the mouse within this time interval, we randomized the deck positions again ($<$5% of trials). If they moved the mouse to one of the decks but failed to click on it, we regarded the deck under the mouse cursor as their choice ($<$5% of trials). We did not impose any time pressure for wagering responses.

We employed two learning tasks differing in complexity. In the simple version of the task, the payoff was either $X(+1)$ or $X(-1$; **Figure 1C** left). The expected payoff was positive (+0.6) for one deck and negative (−0.4) for the other three decks. In the complex version of the task (**Figure 1C** right), the possible payoffs were $X(+2)$, $X(+1)$, $X(-1)$, and $X(-2)$. The expected payoff was positive (+0.6) for two decks and negative (−0.6) for the other two decks. In the complex version, one positive, and one negative deck had high variance (2.44) and the others had low variance (1.84). We refer to positive (or negative) decks as "good" (or "bad") decks.

The theoretical expected earnings over 100 trials with random deck choice are $-281.25 for the simple version and $0 for the complex version. In Experiment 1, subjects earned $781 ± 474 (mean ± SD) in the simple version and $747 ± 346 in the complex version, and in Experiment 2, subjects earned $345 ± 347 in the simple version and $891 ± 408 in the complex version, confirming that subjects performed well above-chance ($p < 10^{-6}$ for both versions in both experiments, one-tailed t-test).

Subjects were told that the optimal strategy is (1) to initially explore the four decks while wagering $25 and (2) to exploit the good deck while wagering $50 once they notice which deck is most likely to give a positive payoff. 35 out of 36 subjects discovered the good deck and then repeatedly chose from it (**Figure 2A**)[3]. After six to eight consecutive choices from a good deck, we showed a text message, "Game Restarted," on the display to notify the subject that the deck-reward contingencies were reassigned and that the subject should explore again (red bars in **Figure 2A**). The number of consecutive choices required for each reassignment was randomly chosen from six to eight to reduce subjects' anticipation for the next reassignment and to have sufficient trials to observe the evolution of wagering behavior (**Figure 2B**).

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[1] http://www.moviewavs.com/

[2] http://download848.mediafire.com/

[3] We observed one subject who purposely chose from a bad deck every few trials. This subject told us after the experiment that he tried to beat our game by occasionally selecting a bad deck after selecting the good deck a few times in a row.

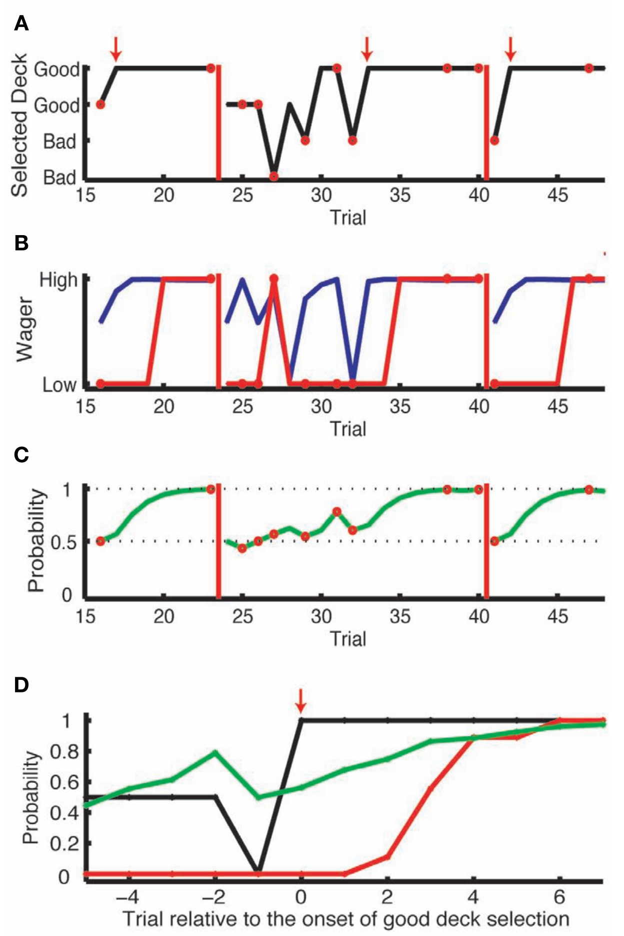

FIGURE 2 | Results from one subject in the complex learning task. **(A)** The history of card selection. Initially, the subject sampled from four decks, then discovered the good deck and stuck with this deck until the reshuffle (red vertical bars). Small red arrows indicate the trial where the subject started to choose from the good deck consistently, which we define as "the onset of good deck choice." The red circles indicate the trials where the subject received a negative payoff. **(B)** The history of actual wagering (red) and the predicted probability of a high wager based on the explicit task results (blue). **(C)** The Bayesian probability for an objectively good deck [the good deck in the upper row in **(A)**] being a good deck. As the evidence accumulates, this probability updates from 0.5 (the Bayesian prior). It increases when this good deck is selected with a positive outcome or when other decks are selected with a negative outcome. **(D)** The aligned results of nine onsets of consecutive good deck selection from this subject. The probability of good deck selection (black) and wagering high (red) are aligned at the onsets (shown as the red arrow). The green line is the Bayesian probability of the chosen deck being a good deck.

EXPLICIT RISK AVERSION TASK

To measure each subject's risk aversion, we employed a standard technique from experimental economics. In each trial, we showed two or four pie charts for the simple or the complex version of the risk aversion task, respectively (**Figure 1B**). These pie charts are identical to the payoff distribution charts from the instructions for the learning task (**Figure 1C**). The goal was to mimic the information structure from the learning task as closely as possible in order to maximize the predictive power of the risk aversion model from one task to the other. During the wagering stage, the learning task can be thought of as being equivalent to the risk aversion task, except that in the learning task the subjects estimate the probabilities (indicated explicitly here in yellow in **Figure 1B**) based on their previous card draws. For example, in the simple version of the risk aversion task, if the good and bad decks have explicitly stated probabilities of 70% and 30% respectively, this would correspond to a situation in the learning task, where the subject draws a card from a deck they believe to be good and is (subjectively) 70% sure that the chosen deck is good (a good deck is a deck with positive expected payoff). In reality, its unlikely that subjects assign explicit probabilities to the decks in the learning task. But they may behave "as if" they are tracking the Bayesian probabilities (Hampton et al., 2006).

The probabilities assigned to the pie charts in the explicit task ranged from 0.25 to 0.70 for the simple version and from 0.35 to 0.85 for the complex version. There was no time restriction. The order of the simple and complex versions was randomized across subjects. In this explicit task, the subjects' goal was again to maximize their payoff.

In Experiment 1 and 2, we implemented two ways of payment in this explicit task. In Experiment 1, we randomly picked one of the 150 trials from the explicit tasks (combining simple and complex versions), selected one of the pie charts according to their probabilities, then selected one of the possible payoffs from that pie chart according to the probabilities in the chart, and finally multiplied the chosen payoff by the subject's wager. Subjects were shown this procedure on the display animation and understood this procedure during practice sessions for both versions of the explicit task. In Experiment 2, we gave subjects a $2000 loan of play money in the beginning and we told them that the goal was simply to earn as much play money as possible. We gave trial-by-trial feedback (with the same sound and icon as in the learning task), accumulated the total amount of play money and paid subjects the amount they earned which was divided by 2000.

BAYESIAN UPDATING TO ESTIMATE SUBJECTIVE PROBABILITY

We computed the Bayesian probability of the chosen deck being the good deck using a Bayesian model (**Figure 2C**). Briefly, this model computes the probability of each deck being the good deck, given the distribution of payoffs from each type of deck (good or bad) and the actual history of positive and negative payoffs to the subject. The probabilities for all four decks were updated after each choice. We describe the details of our Bayesian model and assess how well our assumptions are justified in the Appendix.

The Bayesian model of learning that we used was chosen for its simplicity and descriptive power in other learning research (Ghahramani, 2001; Daw et al., 2005; Hampton et al., 2006; Brodersen et al., 2008). We compared our Bayesian model with the prevailing cognitive models (Busemeyer and Stout, 2002), including a variant of reinforcement learning, and showed that our model is superior in predicting choices and wagers. We describe the details of the model comparison in the Appendix.

PREDICTING WAGERING BEHAVIOR IN THE LEARNING TASK AND DATA FITTING

In the explicit task, the probability of subjects wagering high increases with the probability for the good deck in a sigmoidal manner (**Figures 3C,D,G,H**, blue curves). Combining this psychometric function in the explicit task with the Bayesian probabilities computed in each trial, we tried to predict the probability of a high wager in the learning trials. If the subjects were learning the probabilities like Bayesians (even roughly) then their choice characteristics in the explicit risk aversion task should help predict their wagering behavior in the learning task.

We used local regression to obtain smooth psychometric curves shown in **Figures 3C,D,G,H** and **4G,H**. We used the Locfit package (Loader, 1999) included in the Chronux Toolbox[4] (Mitra and Bokil, 2008) in MATLAB. We used a Gaussian kernel and a binomial local likelihood fitting family. To stabilize the fit, we defined the probability of a high wager as 0 at a good deck probability of 0. For each subject, we optimized the smoothing width using a cross-validation method by (1) randomly dividing the dataset into halves, a training and a test data set, (2) obtaining the best fit to the training set for each of the different smoothing widths, and (3) computing the squared difference between the fitted curve and the actual data from the test set, which was not used during curve fitting. We repeated the above cross-validation procedure 10 times and chose the smoothing width that minimized the overall error for the test set. For **Figures 3C,D,G,H**, we averaged the derived smoothed curves across subjects.

RISK AVERSION INDEX AND RISK-SENSITIVITY INDEX

We defined a risk aversion index (RAI) as the point (x-axis in **Figures 3C,D,G,H**) where the probability of a high wager (y-axis) reaches 0.5. We derived the RAI from the fitted curve for each subject. We also defined a risk-sensitivity index (RSI) as the steepness of the fitted curve as follows:

$$\mathrm{RSI} = \frac{\begin{array}{c}(\text{Probability of high wager at } p = 0.75)\\ -(\text{Probability of high wager at } p = 0.25)\end{array}}{0.75 - 0.25}$$

Due to the nature of the task and noise in the learning task, traditional models of risk aversion (Kahneman and Tversky, 1979; Rabin, 2000; Holt and Laury, 2002) did not fit the data well. Our measures of risk aversion are simple but do a better job of characterizing subjects' risk aversion, as demonstrated by the high within-subject correlations between the simple and complex versions of the explicit tasks as well as those of the learning tasks (see Results).

RESULTS

LEARNING TASK WITH POST-DECISION WAGERING

In our novel learning task, the deck-payoff contingency switched after subjects repeatedly selected cards from a deck with positive expected value (a "good" deck). In each trial, subjects first selected a card from one of four decks, and then wagered either \$50 or \$25. Immediately after wagering, subjects saw their payoff as a multiplier of the wager amount, that is, either $X(+2)$, $X(+1)$, $X(-1)$, or $X(-2)$. The total amount of the payoff (i.e., the wagered amount times the multiplier) was not shown explicitly on the display (**Figure 1A**).

We show a typical subject's behavior for deck selection and wagering in **Figures 2A,B**. Initially, the subject sampled from several decks, then settled on the good deck. He stuck with this deck until the reshuffle. As for wagering, he started off wagering low but eventually wagered high after several selections from the good deck (red line). After the reshuffle, he returned to wagering low. Interestingly, his actual wagering behavior lagged behind his theoretically predicted wagering behavior (blue line), which incorporated his risk aversion as measured in the explicit task (see below). This lag is consistent with non-conscious optimal choice, and we will return to this point later.

To analyze when subjects started to wager high, in **Figures 2D** and **3A,B,E,F**, we aligned card selection and wagering to the onset of good deck selection. **Figure 2D** shows that the exemplar subject never wagered high (the red line) before he found the good deck. On subsequent draws from the good deck, the subject increasingly wagered high, and by the sixth card the subject was always wagering high. **Figures 3A,B** (Experiment 1, $n = 16$) and **Figures 3E,F** (Experiment 2, $n = 20$) show similar trends at the group level in both the simple and complex versions of the learning task in both experiments. Subjects wagered high (the red lines) on less than 100% of the trials even after repeatedly choosing from the good deck (up to seven cards after the onset of good deck selection).

This alone does not yet prove that subjects were choosing the advantageous good deck(s) without conscious awareness; it merely suggests that subjects needed to build up to a certain level of confidence in their selection before making a high wager. We therefore used a Bayesian model to estimate subjects' beliefs about which decks were the good ones and then used those beliefs to predict the subjects' wagering behavior. The model's prediction was based on the past history of outcomes for the subjects as well as their risk aversion.

EXPLICITLY MEASURING RISK AVERSION

To measure risk aversion, we asked subjects to wager \$50 or \$25 in a situation where the probability of the chosen deck being good or bad was *explicitly* available (the explicit risk aversion task, **Figure 1B**). Note that in the learning task (**Figure 1A**), subjects might never have had an explicit representation of this probability, even if they computed it implicitly in order to guide choice and wagering.

The resulting psychometric curves for high wagers in the explicit task are shown by the blue curves in **Figures 3C,D,G,H**. As an example, for the simple version of the explicit task in Experiment1, subjects wagered high more than 90% of the time when the probability of being a good deck exceeded 0.65. They wagered high only 50% of the time when the explicit probability of being a good deck was 0.55, consistent with published risk aversion results from experimental economics (Kahneman and Tversky, 1979; Rabin, 2000; Holt and Laury, 2002).

We then analyzed how often subjects wagered high in the learning task as a function of the Bayesian probability of the chosen deck being the good one (**Figures 3C,D,G,H**, red curves). When making their wagering decisions in the learning task, subjects' psychometric curves shifted to the right, suggesting that they became more risk-averse. Furthermore, the curves became flatter, suggesting that

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[4] http://chronux.org/

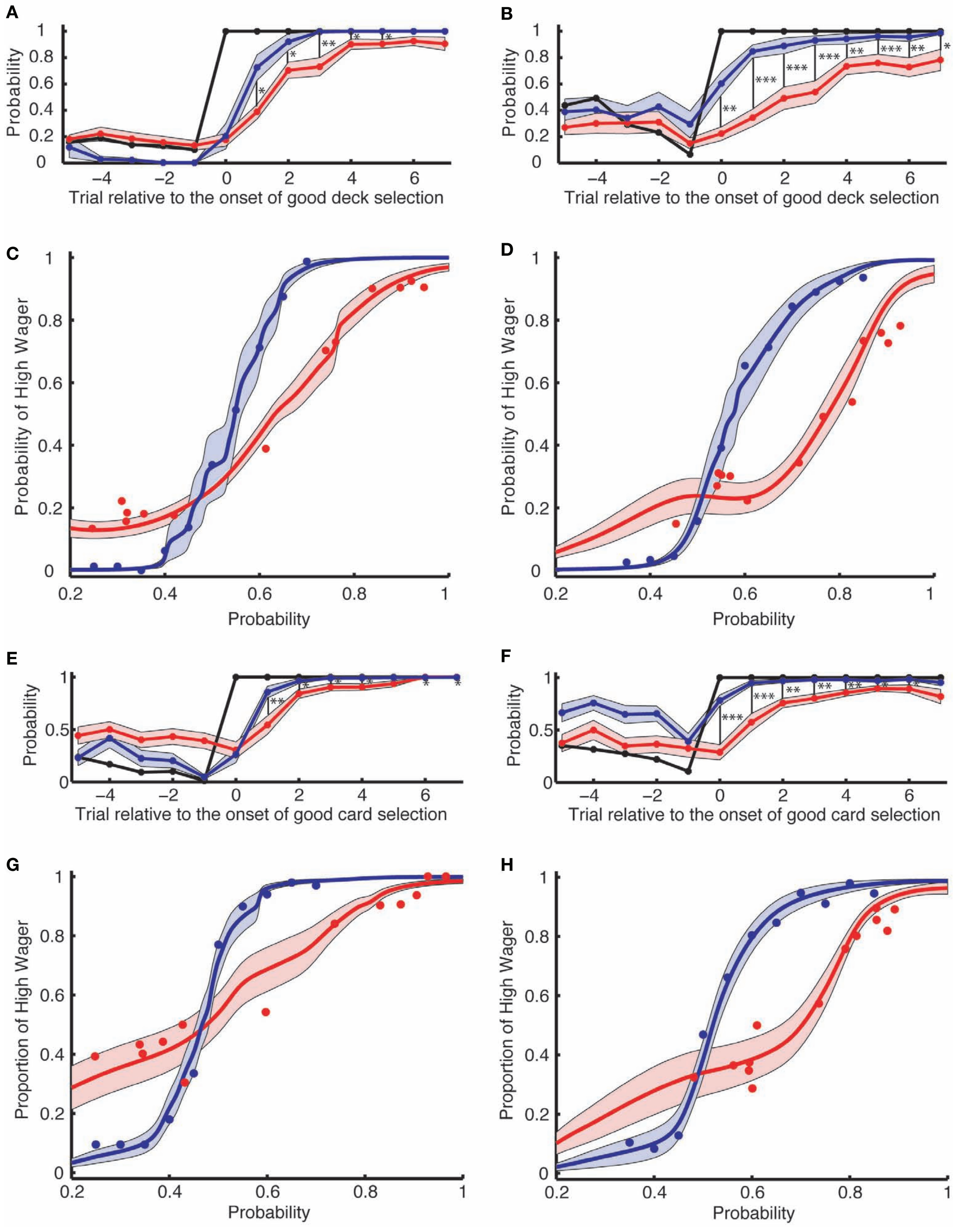

FIGURE 3 | Wagering behavior in the learning task cannot be completely accounted for by the risk aversion measured in the explicit task [(A–D): Experiment 1; (E–H): Experiment 2]. (A,B,E,F) The actual probability of a high wager (red) is aligned across multiple onsets of good deck selection [**(A,E)** for the simple version and **(B,F)** for the complex version of the learning task]. The *x*-axis denotes the trial relative to the onset of good deck selection. The probability of good deck selection (black) as well as the predicted probability of a high wager (based on the explicit task; blue) are also aligned at the onset of good deck selection. The black vertical bars indicate a significant difference between the predicted and actual probability of a high wager. *, **, and *** indicate significance levels of $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively. **(C,D,G,H)** The probability of a high wager as a function of the explicit probability in the risk aversion task (blue) and as a function of the Bayesian probability in the learning task (red) for the simple **(C,G)** and for the complex **(D,H)** versions of the tasks. The curves are obtained by averaging individually fitted curves using local regression. Shading denotes 1 SEM across subjects.

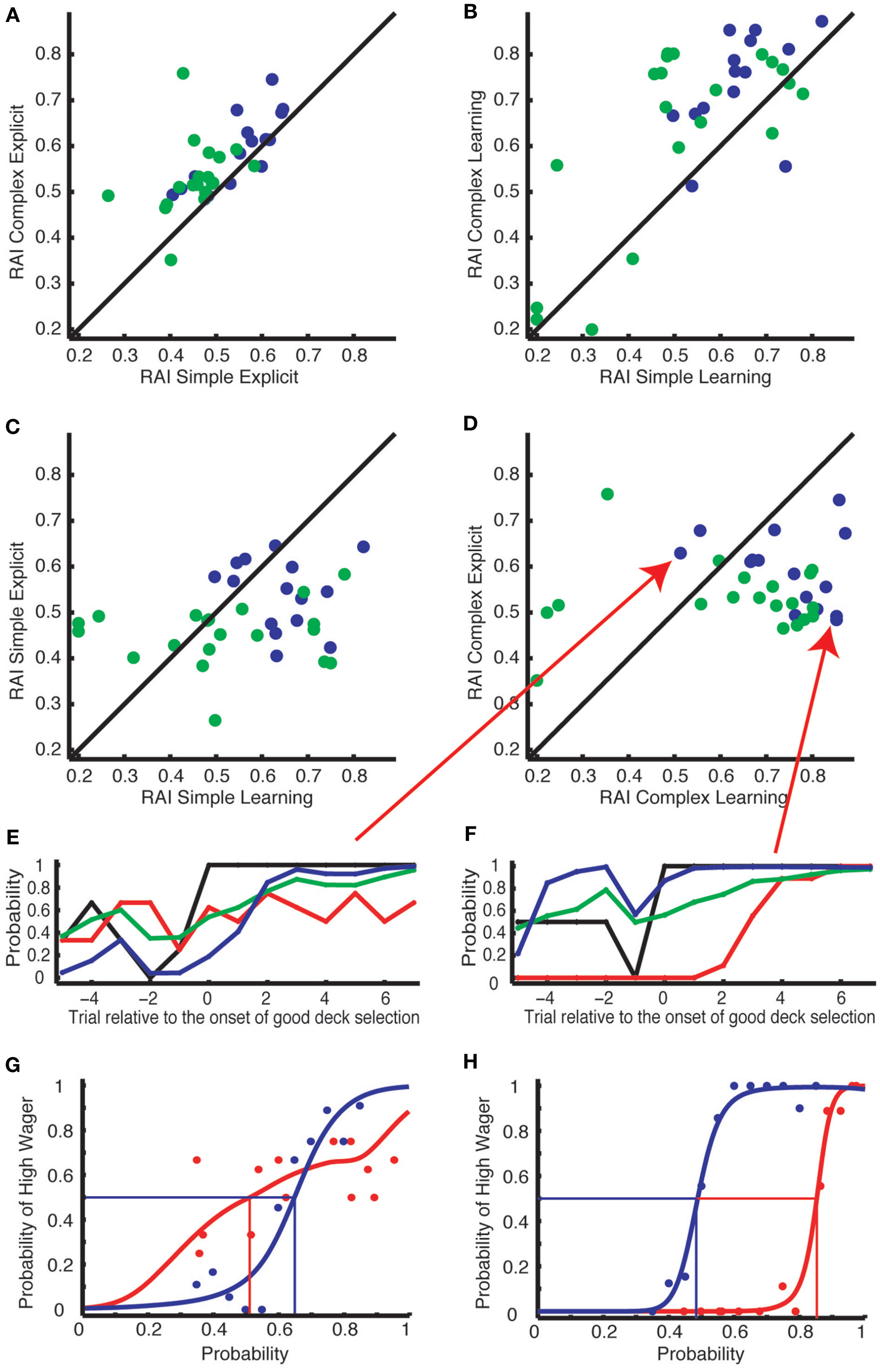

FIGURE 4 | Subject-specific risk aversion indices (RAI) are correlated between the simple and complex versions of the tasks, but not between the explicit and learning tasks. **(A,B)** RAI was highly correlated between the simple (*x*-axis) and complex (*y*-axis) versions within the explicit tasks **(A)** and within the learning tasks **(B)**. **(C,D)** RAI was uncorrelated across the learning (*x*-axis) and the explicit task (*y*-axis) in either the simple **(C)** or the complex **(D)** versions. Blue dots represent subjects from Experiment 1 and green dots represent subjects from Experiment 2. **(E–H)** The results from two exemplar subjects indicated by the red arrows in **(D)**. Their behaviors are presented in the same format as in **Figures 3A–D**. **(E,G)** A subject who preferred to wager high in the learning but not in the explicit task. **(F,H)** A subject who showed extreme risk aversion only in the learning task.

subjects were less sensitive to the payoffs during the learning task. To quantify these effects, we computed two indices for each subject: a RAI and a RSI. RAI represents the explicit probability of the deck being "good" at which subjects wagered high in 50% of the trials. RAI approaches 1 if subjects are risk-averse (i.e., those who wager high only when they are sure to win). If subjects are risk-neutral, RAI is 0.45 (due to the negative expected payoffs for the random choice strategy) for the simple and 0.5 for the complex versions of the task. In Experiment 1 (**Figures 3C,D**), RAI was higher in the learning tasks ($\text{RAI} = 0.633$ for the simple and 0.775 for the complex) than in the explicit risk aversion tasks ($\text{RAI} = 0.548$ for the simple and 0.576 for the complex, paired t-test, $p = 0.007$ for the simple, and $p = 0.002$ for the complex). In Experiment 2 (**Figures 3G,H**), for the complex version, RAI was higher in the learning tasks ($\text{RAI} = 0.702$) than in the explicit tasks ($\text{RAI} = 0.520$, $p = 0.045$). For the simple version, RAI in the learning task (0.476) was not different from that in the explicit task ($\text{RAI} = 0.467$, $p = 0.15$). RSI is the slope of the curve, representing the sensitivity to the change in probability. In Experiment 1, RSI was smaller in the learning tasks ($\text{RSI} = 1.12$ for the simple and 0.70 for the complex) than in the explicit tasks ($\text{RSI} = 1.97$ for the simple and 1.78 for the complex, paired t-test, $p < 10^{-5}$ for both the simple and the complex versions). In Experiment 2, RSI was also smaller in the learning tasks ($\text{RAI} = 1.06$ for the simple and 0.949 for the complex) than in the explicit tasks ($\text{RAI} = 1.87$ for the simple and 1.83 for the complex, $p < 10^{-4}$ for both the simple and the complex versions).

Overall, the results from Experiment 1 and 2 were consistent although there was some difference in the simple version of the task. RAI in both the learning and explicit task was significantly lower in Experiment 2 than Experiment 1 (unpaired t-test, $p = 0.016$ for the learning and $p < 0.001$ for the explicit task; see Discussion). The RSI was not significantly different between the two experiments.

Looking at **Figure 3C** more closely, in the explicit task subjects wagered high in 100% of the trials where the probability of choosing from the good deck was 70%. However, in the learning task they wagered high in less than 65% of the trials where the Bayesian probability was at the same level. Our analysis reveals that this phenomenon is a combined effect of lower RSI (i.e., flatter psychometric curves) indicating an insensitivity to the payoffs, and higher RAI (i.e., rightward shift of the curves) indicating that subjects were more risk-averse during the learning task than the explicit task.

THE DELAYED ONSET OF AWARENESS COMPARED TO THE ONSET OF GOOD CARD CHOICE

We predicted the probability of a high wager for each trial in the learning task based on the actual payoff history in the learning task and the risk aversion profile in the explicit task (as in **Figures 3C,D,G,H**). First, we computed the Bayesian probability for each trial based on the history of payoffs (**Figure 2C**). Then, we derived the probability of a high wager by drawing a vertical line from the Bayesian probability (on the x-axis) in the risk aversion sigmoidal curve and finding the corresponding y-value. This was repeated for each trial (**Figure 2B**, blue curve). If there is a period of non-conscious decision making, we should see a gap between the actual and the predicted probability of high wagers even after taking into account each subject's risk aversion.

In **Figures 3A,B,E,F**, the blue curves show the proportion of trials in which subjects would have wagered high if they had explicitly been shown the Bayesian probability that they were choosing from the good deck. We see that subjects wagered high much less frequently in the actual gambling task (red) than predicted based on risk aversion and the Bayesian probabilities (blue). In both experiments, the gaps between the two curves were significantly different at most points: in Experiment 1 for the simple version, $p < 0.05$ for points from $+1$ to $+5$, $p = 0.055$ for $+6$, and $p = 0.088$ for $+7$; for the complex, $p < 0.05$ for all the points after 0, and in Experiment 2 for the simple, $p < 0.05$ for points from $+1$ to $+7$ except $+5$ ($p = 0.069$); for the complex, $p < 0.05$ for all the points from 0 to $+6$, and $p = 0.062$ for $+7$; two-tailed paired t-test, corrected for multiple comparisons for trial 0 to trial $+7$ with false discovery rate (FDR) of 0.05 (Benjamini and Hochberg, 1995).

Thus, even when we take into account the effects of risk aversion, we still find that subjects did not wager optimally. We conclude that we cannot fully explain the gap between choosing optimally and wagering high (Bechara et al., 1997; Persaud et al., 2007) based solely on risk aversion (Clifford et al., 2008a; Schurger and Sher, 2008; Dienes and Seth, 2010).

RISK AVERSION IN THE LEARNING TASK IS UNCORRELATED WITH THAT MEASURED IN THE EXPLICIT TASK

Even if risk aversion does not completely account for behavior in the learning task, we would expect to see a correlation between risk aversion measures in the two tasks, since it is generally assumed that risk aversion is an individual personality trait that should be fairly stable across tasks, especially over short periods of time (Harrison et al., 2005; Koch and Preuschoff, 2007). To check this assumption, we ran a correlation analysis on the risk aversion measures.

Within-subject RAIs were highly correlated between two levels of payoff complexity within the explicit tasks for Experiment 1 (**Figure 4A**, blue dots, Spearman correlation test:$\rho = 0.81$, $p = 0.00022$) and for Experiment 2 (green dots, $\rho = 0.58$, $p = 0.01$). This was also true within the learning tasks for Experiment 1 (**Figure 4B**, blue dots, $\rho = 0.6$, $p = 0.024$) and Experiment 2 (green dots, $\rho = 0.5$, $p = 0.026$). When we combined data from both Experiment 1 and 2, we found strong correlations within the explicit ($\rho = 0.72$, $p = 1.2 \times 10^{-6}$) and the learning tasks ($\rho = 0.5$, $p = 0.0028$). This reliable correlation is consistent with the assumption that risk aversion is a fixed factor specific to each subject. However, within-subject RAIs across the learning and the explicit tasks were uncorrelated in both levels of task complexity. Within the simple version, the correlation coefficient (ρ) was -0.24 ($p = 0.39$) in Experiment 1, 0.021 ($p = 0.93$) in Experiment 2 and 0.19 ($p = 0.28$) when we combined the data from Experiment 1 and 2 to increase statistical power (see **Figure 4C**). Within the complex version, we again found no correlation between the tasks ($\rho = -0.28$, $p = 0.31$ for Experiment 1; $\rho = -0.074$, $p = 0.76$ for Experiment 2; $\rho = -0.15$, $p = 0.39$ for combined; see **Figure 4D**). We show exemplar subjects who showed striking inconsistency between the learning and the explicit tasks in **Figures 4E–H**.

MEAN CHOICE-WAGER GAP IN THE LEARNING TASK IS UNCORRELATED WITH RAI MEASURED IN THE EXPLICIT TASK

To verify that risk aversion is uncorrelated between tasks, we further analyzed the correlation between RAI estimated from the explicit task (50% crossing points of the blue curves in **Figures 3C,D,G,H**) and mean choice-wager gap from the learning task (i.e., the mean difference between black and red curves from 0 to +7 in **Figure 2D**). RAI from the explicit task did not correlate with the mean choice-wager gap in the simple ($\rho = 0.021$, $p = 0.94$) or complex version ($\rho = -0.13$, $p = 0.65$) of Experiment 1 nor in the simple ($\rho = 0.18$, $p = 0.45$) or complex version ($\rho = 0.23$, $p = 0.34$) of Experiment 2.

We also analyzed the correlation between RAI and mean choice-wager gap both estimated from the learning task. Within the learning task, RAI was correlated with the mean choice-wager gap in the simple ($\rho = 0.55$, $p = 0.034$) and the complex version ($\rho = 0.83$, $p = 0.00012$) of Experiment 1 as well as in the simple ($\rho = 0.54$, $p = 0.014$) and the complex version ($\rho = 0.48$, $p = 0.033$) of Experiment 2.

Taken together, the gap between actual choice and wagering behavior in the learning task was not correlated with risk aversion estimated from the explicit task, while it was correlated with the risk aversion estimated from the learning task. This is consistent with the results presented in **Figure 4**.

COMPARISON BETWEEN THE SIMPLE AND COMPLEX VERSION OF THE TASK

We used a simple and a complex version of the task to allow easy or more difficult conscious access to the contingencies between decks and their expected outcomes (see **Figure 1C** and Materials and Methods for details). We expected to observe an increased period of non-conscious decision making in the complex version as the complexity of the payoff histories exceeds the capacity of conscious working memory (Bechara et al., 1997; Dijksterhuis et al., 2006). When we aligned all the variables at the onset of good deck selection (**Figures 3A,B,E,F**), the difference between the predicted and the actual probability of high wagers (i.e., the gap between the blue and red curves from trial 0 to +7) was larger in the complex version than in the simple version ($p = 0.0075$ for Experiment 1 and $p = 0.0013$ for Experiment 2). This is consistent with the idea that non-conscious decision making is likely to be induced when the task is more complex.

DISCUSSION

The original IGT has been cited as evidence for non-conscious decision making. However, due to its unconstrained nature, there may be alternative explanations other than non-conscious decision making. Here we reported evidence that casts doubt on several of those alternative explanations. To exclude explanations due to risk aversion and ambiguity aversion (Fellows, 2004; Dunn et al., 2006; Koch and Preuschoff, 2007; Clifford et al., 2008a,b; Schurger and Sher, 2008; Dienes and Seth, 2010; Fleming and Dolan, 2010; Sandberg et al., 2010), we modified the original IGT in several respects. In particular, we showed that risk aversion could not explain the entire effect of non-conscious decision making in our task. Furthermore, we found that risk aversion observed during the learning task was not correlated with risk aversion elicited during a similar gambling task with explicit probabilities. We suggest that these two types of risk aversion may map onto an emotional feeling of risk on the one hand, and an explicitly accessible representation of risk on the other hand.

In our learning tasks, subjects were able to discover the good decks and stick with them. However, as in Persaud et al. (2007), we found that it generally took several choice–outcome experiences from a good deck before subjects were willing to place high wagers on the outcomes. Interestingly, some subjects continued to wager low even after selecting from the good deck six to eight trials in a row. The reason for this reluctance to wager high could be that subjects were unaware of the deck-reward contingencies and selected cards using non-conscious decision making (Bechara et al., 1997; Persaud et al., 2007). Alternatively, subjects may have been risk-averse and not willing to wager high until they were confident enough that they were choosing from the good deck (Clifford et al., 2008a; Schurger and Sher, 2008). What we found partially supports both explanations: subjects showed strong risk aversion in our modified version of the IGT, that is, they showed RAI values significantly larger than risk-neutral in all the learning tasks except the simple version in Experiment 2. However, this did not account for all of the temporal gap between the onsets of optimal choice and advantageous wagering in the experiments. We conclude that people can choose advantageously without full awareness of why they do so, at least to some extent.

By carrying out two independent experiments on two pools of naïve subjects ($n = 16$ and 20), we replicated most of the findings. With two different experiments, we ruled out some of the potential artifacts, including the effects of (1) the extent of prior practice, (2) the order of the learning and explicit risk aversion task, (3) the presence of trial-by-trial feedback and payment, and (4) the testing environment (one-to-one experiment typical of psychophysics experiments and group experiments typical of experimental economics).

While most effects between the two experiments were similar, we observed two differences in the simple version of the task. First, in both the learning and the explicit task, the RAI was lower for Experiment 2 than Experiment 1. The lower levels of risk aversion in Experiment 2 would be expected when paying subjects for many trials rather than one, but we cannot rule out the possibility that the other experimental changes played a role as well. Second, the RAI was not different between the explicit and learning tasks in the simple version in Experiment 2 (**Figure 3G**). This could be because the simple version of the task itself may not be optimal to induce the effects that we were looking for. This interpretation is consistent with past studies (Bechara et al., 1997; Dijksterhuis et al., 2006), suggesting that evidence for non-conscious decision making is more evident in complex tasks where subjects rely less on conscious working memory.

NON-CONSCIOUS DECISION MAKING AND POST-DECISION WAGERING

In this study, we applied post-decision wagering to assess if advantageous decision making can occur non-consciously. While our wagering procedure asked subjects to simply bet high or low, we do not believe that subjects' confidence level is all or nothing, as is sometimes assumed in perceptual consciousness. In fact, we believe that confidence is graded and more or less continuous on a trial-by-trial basis, which is the basis of our Bayesian model.

Over the last decades, convincing evidence for non-conscious processing has been established in at least two ways. First, while showing complete lack of detectability/discriminability (e.g., chance performance or $d' = 0$) of stimuli with a direct task that assesses awareness of the stimuli, robust non-conscious processing has been shown with indirect measures, such as behavioral priming effects and neurophysiological signals (for a review, see Hannula et al., 2005; Kouider and Dehaene, 2007). Second, above-chance behavioral performance can be considered to be non-consciously mediated if the level of conscious confidence, reported in a forced manner, is completely uncorrelated with performance (Kolb and Braun, 1995; Kunimoto et al., 2001; Persaud et al., 2007). Non-conscious processing in our task has been established via the second method with conscious confidence indirectly assessed with post-decision wagering.

Recently, the nature of post-decision wagering as a way to assess conscious confidence has been intensely debated (Koch and Preuschoff, 2007; Clifford et al., 2008a; Schurger and Sher, 2008; Dienes and Seth, 2010; Fleming and Dolan, 2010; Sandberg et al., 2010). Some emphasize the advantage of post-decision wagering (Koch and Preuschoff, 2007; Persaud et al., 2007). It is highly intuitive and easy to administer, even for children (Ruffman et al., 2001) or animals (Kornell et al., 2007; Kiani and Shadlen, 2009), compared to confidence ratings. As post-decision wagering indirectly assesses conscious confidence, it is less likely to alter task performance than direct confidence ratings, which might affect performance because it forces subjects to introspect in an unnatural way (Koch and Preuschoff, 2007). Furthermore, the monetary incentives ensure that subjects are motivated to reveal all the information they have for their advantageous decisions (Persaud et al., 2007).

Others have pointed out disadvantages with post-decision wagering (Clifford et al., 2008a; Schurger and Sher, 2008; Dienes and Seth, 2010; Fleming and Dolan, 2010; Sandberg et al., 2010). Post-decision wagering may be subject to economic context, which might influence conscious confidence. For example, risk aversion may lead to different wagering behavior even when the underlying conscious confidence is the same. In fact, using backward masking in sensory psychophysics, Fleming and Dolan (2010) showed that risk aversion discouraged high wagers. Furthermore, Sandberg et al. (2010) have suggested that other meta-cognitive measures such as a perceptual awareness scale could improve our ability to detect weak conscious confidence.

In our study, we chose post-decision wagering for the assessment of conscious confidence because we can use the same wagering task during both learning and explicit risk aversion tasks and we can directly examine the role of risk aversion on an individual basis across two very similar tasks. Future work is needed to see whether non-conscious, advantageous decision making can be confirmed with other methods, such as allowing subjects to bet on a continuous scale rather than just high or low.

ADVANTAGES OF OUR MODIFIED VERSION OF THE IGT

It has been argued that the task design of the IGT confounds several factors known to play an important role in decision making (Fellows, 2004; Sanfey and Cohen, 2004; Dunn et al., 2006), which undermined previous attempts to demonstrate non-conscious decision making. We sought to avoid these confounds by modifying the original IGT in several important ways. First, we incorporated post-decision wagering to indirectly measure subjects' conscious awareness of the deck-payoff contingency in every trial (Persaud et al., 2007). Second, we introduced a reshuffling procedure to observe multiple episodes of learning and choice within a single subject, resulting in greater statistical power. Such a feature is desirable not only for behavioral studies like ours, but also for neurophysiological experiments (Fukui et al., 2005; Oya et al., 2005). In fact, despite its wide application in behavioral studies, the IGT, which can induce at most a single onset of awareness, has been used only in a few imaging studies in good part due to this statistical limitation. Third, we addressed the concern about heterogeneous priors on the task structure by explicitly telling the subjects the distributions of payoffs from the four decks and letting them practice the task. This also helped to eliminate the effects of ambiguity aversion, which have been shown to cause subjects to avoid gambles with unknown probabilities (Ellsberg, 1963; Camerer and Weber, 1992; Rode et al., 1999; Hsu et al., 2005). This improvement was also critical for our Bayesian modeling analysis. If subjects did not know anything about the task structure we could still have used a reinforcement learning algorithm (Oya et al., 2005), but it is unclear how to combine such a model with risk aversion (Bossaerts et al., 2008). In fact, the model comparison (see Appendix) suggests that our Bayesian model with knowledge of the task structure performs better in predicting subjects' behavior than the one without this knowledge and other related reinforcement learning models (Busemeyer and Stout, 2002).

In fairness to alternative explanations, our experiment did not explicitly measure subjects' beliefs about the different deck probabilities, and so we cannot rule out the possibility that subjects' beliefs were non-Bayesian. Although our novel gambling task eliminated ambiguity about the task structure, subjects still had to learn and estimate the probabilities of selecting from a good deck and were thus facing compound lotteries with potentially inaccurate probabilities. In the learning task, there is the potential for individual differences in learning rates, in differential memory for positive versus negative payoffs, in ability to keep the payoff distributions described in the instructions in working memory, and in the discounting of past outcomes, etc. These individual differences would have only affected the learning task but not the explicit task, which could account for the divergence in risk aversion between the tasks. We did observe that the psychometric curves relating the probability of a high wager to the probability of being a good deck (**Figures 3C,D,G,H**) were flatter in the learning than in the explicit tasks. Though we described it as evidence that subjects become less risk sensitive, alternative accounts are also possible. In the learning task, inaccurate estimation of the probabilities could result in an observed insensitivity to risk. Further experiments will be needed to address these issues.

MULTIPLE MECHANISMS FOR DECISION MAKING UNDER RISK

The behavioral and neural correlates of decision making under risk have been extensively investigated and it has been shown that components of risk, such as variance of probability and reward, influence the activity of midbrain dopamine neurons as well as the activation of ventral prefrontal, insular, and cingulate cortices (Bechara et al., 1999; Critchley et al., 2001; Smith et al., 2002; Fiorillo et al., 2003; Tobler et al., 2007; Christopoulos et al., 2009). Interestingly, Huettel et al. (2006) have argued that decision making under risk and under ambiguity are supported by distinct mechanisms, with risk preference encoded in the posterior parietal cortex and ambiguity preference encoded in the lateral prefrontal cortex. In our study, we did not observe significant correlation between risk aversion in the learning and explicit tasks. It is even more intriguing because the tasks were so similar and they were done in the same session, with very similar stimuli and identical payoffs. Importantly, the high correlations of risk aversion between the simple and complex versions of the task within each of the learning and the explicit task ruled out that the non-significant correlations were due to subjects' confusion, or a lack of statistical power.

Inconsistency between risk aversion in the learning and the explicit tasks (**Figure 4**) suggests the possibility of two separable psychological processes for the computation of risk: one process may depend on an explicit and verbally accessible representation of risk (since this is how the risk information was provided in the first place), while the other process may depend on an emotional feeling of risk based on experienced outcomes that need not be accessible to explicit verbal report (Loewenstein et al., 2001). Our findings suggest a description–experience gap between risk in explicit and implicit tasks. Recently, some studies have demonstrated this description–experience gap. FitzGerald et al. (2010) showed that the risk of learned options is correlated with activity in the anterior cingulate cortex while the risk of described options is correlated with activity in the bilateral anterior insula cortices. Erev et al. (2010) found that decisions from description were predicted best by different models than those that predicted decisions from experience.

Distinctive processes for risk computation have been suggested in recent studies in normal subjects (Hertwig and Erev, 2009), as well as with lesion patients and psychiatric populations. When normal subjects learn probabilities from experience, they can show a reversed risk preference compared to when they are notified of the risk through description of the probabilities (Hertwig and Erev, 2009). Patients with damage to the ventromedial prefrontal cortex can cognitively assess appropriate behaviors but cannot act accordingly in real life, a dissociation which is in part replicated in the IGT (Anderson et al., 1999; Krajbich et al., 2009). Pathological gamblers are obsessed by risky gambles (Holden, 2001; Potenza et al., 2001). With some drug treatments, their risk aversion can be enhanced to a level higher than in healthy controls (Brañas-Garza et al., 2007), however, their pathological behaviors are prone to relapse in real life (Holden, 2001). Interestingly, these clinical populations are capable of computing risks cognitively. However, they fail to choose appropriately in everyday life, possibly because of an inability to implement risk mechanisms based on emotional feelings (Loewenstein et al., 2001).

While Dienes and Seth (2010) found correlation between risk aversion and the degree of non-conscious knowledge inferred from wagering, we did not get an analogous result. We believe that our two separate risk models described above could explain this discordance. For tasks that do not involve learning and emotional feeling of risks, such as those employed by Dienes and Seth, the explicit risk mechanism is likely at work. Obviously, further studies are needed to test these ideas.

Taken together with these other results, the present findings suggest that these two processes for risk computation may be subserved by distinctive neuronal mechanisms within the prefrontal cortex (Tobler et al., 2007; Christopoulos et al., 2009), posterior cingulate cortex (McCoy and Platt, 2005), and insula or components of the basal ganglia (Preuschoff et al., 2006). Whether emotional experiences (Damasio, 1994; Bechara et al., 1997, 2000) guide subjects in our learning task in a non-conscious manner is an important open question for future studies.

AUTHOR CONTRIBUTIONS

Shuo Wang, Ian Krajbich, Ralph Adolphs, and Naotsugu Tsuchiya designed research; Shuo Wang performed research; Shuo Wang, Ian Krajbich and Naotsugu Tsuchiya analyzed data; and Shuo Wang, Ian Krajbich, Ralph Adolphs, and Naotsugu Tsuchiya wrote the paper.

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APPENDIX

BAYESIAN INFERENCE MODEL: ASSUMPTION AND VALIDATION

We constructed a Bayesian inference model to estimate the probability of each deck being the good deck. This estimated probability would be a good proxy of how actual subjects would feel about each deck (1) if subjects have perfect memory of the payoff structure and can keep track of the Bayesian probability associated with each deck (assuming the Markov property) and (2) if subjects understand and utilize the structure of the gambling task. Further, (3) if subjects were to select the deck and to wager on the chosen card based on the Bayesian probability, we should be able to predict the choice and the wager behavior well.

We quantified the performance of the Bayesian model in their ability to predict subjects' choices and wagers on a trial-by-trial basis using signal detection theory (SDT; Macmillan and Creelman, 2005).

For prediction of a choice in a given trial, we say that the model made a correct prediction (i.e., hit) when it assigned the highest Bayesian probability to the deck that the subject actually chose in that trial. If the model assigned the highest probability to an unselected deck, we regarded it as a false alarm. Further, we regarded the assigned highest probability as the confidence the model had in each prediction. By shifting the threshold for this confidence of the model from zero to one, we were able to construct ROC curves, which quantify how successfully the model could predict subjects' behavior. For the following analysis, we computed the area under the ROC curve, which we call A′ for short. A′ for the choice was 0.80 ± 0.13 (mean ± SD) for the simple version and 0.80 ± 0.11 for the complex version in Experiment 1, and 0.77 ± 0.13 for the simple version and 0.74 ± 0.14 for the complex version in Experiment 2.

For prediction of wagering in a given trial, the model always predicts a high wager with a confidence expressed as the assigned probability for the chosen deck. Again, by shifting the confidence threshold, we constructed ROC curves and computed A′ for the wager prediction. A′ for the wagering was 0.87 ± 0.11 for the simple version and 0.77 ± 0.13 for the complex version in Experiment 1, and 0.84 ± 0.12 for the simple version and 0.82 ± 0.16 for the complex version in Experiment 2. Although it is far from perfect (i.e., $A' = 1$; $p < 0.0005$), A′ was significantly higher than chance [chance A′ would be 0.5, $A' > 0.5$ with $p < 10^{-6}$ (t-test)].

There could be several reasons why subjects' choices and wagers were sub-optimal. First, subjects may not remember the payoff structures and lose track of the Bayesian probabilities (assumption 1 was wrong). This may be the case for the complex version, but is highly unlikely for the simple version. Second, subjects might not have understood or utilized the task structure. We took great care to familiarize subjects with the procedures, showed them the payoff structures (Figure 1C) and even explained the optimal strategy (see Materials and Methods) prior to the experiment. In Experiment 1, there were three practice sessions before entering the final critical sessions. Still, it is possible that subjects may have adopted other strategies, such as the "gambler's fallacy"; A spurious belief such as "after three positive outcomes in a row, I tend to receive a negative outcome" might have affected their decisions, which we did not model.

Below, we describe our implementation of the Bayesian model. Assuming a subject satisfies assumptions 1 and 2, we can compute the Bayesian probability of each deck being the good deck as:

$$p_{i,t} = P(D_{i,t} = \text{Good}), \qquad i = 1, 2, 3, 4 \tag{A1}$$

Where $p_{i,t}$ denotes the probability of deck i being the good deck at trial t, and $D_{i,t}$ represents the state of deck i at trial t ($D_{i,t} = \text{Good}$ or $D_{i,t} = \text{Bad}$).

In the simple version of the learning task, there is only one good deck, thus the sum of $p_{i,t}$ across the four decks is equal to 1.

$$\sum_{i=1,2,3,4} p_{i,t} = 1 \tag{A2}$$

In the complex version, there are two good decks, thus the sum of $p_{i,t}$ across the decks is equal to 2.

$$\sum_{i=1,2,3,4} p_{i,t} = 2 \tag{A3}$$

After each trial, we update $p_{i,t+1}$ using the Bayesian updating rule based on the behavior and the outcome at trial t. We used a two-stage updating rule, first for the selected deck and then the other three unselected decks.

The Bayesian updating rule for the selected deck

We applied the Bayesian model to update the probability of deck i being a good deck at trial $t+1$ ($p_{i,t+1}$) based on the probability of deck i being a good deck at trial t ($p_{i,t}$) and the actual payoff (value) observed at trial t (V_t, representing the reward or loss the subject received at trial t) as follows:

$$\begin{aligned}
p_{i,t+1} &= P\left(D_{i,t+1} = \text{Good}\right) = P\left(D_{i,t} = \text{Good}|V_t\right)\\
&= \frac{P\left(V_t|D_{i,t} = \text{Good}\right) \cdot P\left(D_{i,t} = \text{Good}\right)}{P\left(V_t\right)}\\
&= \frac{P\left(V_t|D_{i,t} = \text{Good}\right) \cdot P\left(D_{i,t} = \text{Good}\right)}{\sum_i P\left(V_t|D_{i,t}\right) \cdot P\left(D_{i,t}\right)}\\
&= P(V_t|D_{i,t} = \text{Good}) * P(D_{i,t} = \text{Good}) \big/ (P(V_t|D_{i,t} = \text{Good})\\
&\qquad * P(D_{i,t} = \text{Good}) + P(V_t|D_{i,t} = \text{Bad}) * P(D_{i,t} = \text{Bad}))\\
&= P(V_t|D_{i,t} = \text{Good}) * P(D_{i,t} = \text{Good}) \big/ (P(V_t|D_{i,t} = \text{Good})\\
&\qquad * p_{i,t} + P(V_t|D_{i,t} = \text{Bad}) * (1 - p_{i,t}))
\end{aligned} \tag{A4}$$

The updating rule for the unselected decks

Following the update of $p_{i,t+1}$ for the selected deck, we updated $p_{i,t+1}$ for the other decks that were not selected at trial t. Following Eqs A2 and A3, we updated the probability of each unselected deck being a good deck at trial $t+1$ based on $p_{i,t}$ and the behavior and the outcome at trial t as follows:

(a) If the selected deck gave a reward (i.e., $V_t > 0$),

$$p_{i,t+1} = p_{i,t} - \frac{p_{i,t}}{\sum_{i=\{1,2,3,4\}, i \neq A_t} p_{i,t}} \cdot \left(p_{A,t+1} - p_{A,t}\right) \tag{A5}$$

where A_t represents the deck selected at trial t.

(b) If the selected deck gave a punishment (i.e., $V_t < 0$),

$$p_{i,t+1} = p_{i,t} + \frac{1 - p_{i,t}}{\sum\limits_{i=\{1,2,3,4\},\ i \neq A_i} \left(1 - p_{i,t}\right)} \cdot \left(p_{A,t} - p_{A,t+1}\right) \quad \text{(A6)}$$

At the beginning of the experiment as well as after the reshuffle of the deck-reward contingency, we reset $p_{i,t}$ to 0.25 and 0.5 for the simple and the complex versions, respectively.

Equations A4–A6 have the Markov property that only knowledge of the probabilities ($p_{i,t}$, $i = 1,2,3,4$), selected action (A_t), and the value of the action (V_t) from the current trial are needed to calculate the probabilities of the next trial ($p_{i,t+1}$, $i = 1,2,3,4$).

MODEL COMPARISON

We compared the performance of four other models to that of ours in predicting subjects' choices and wagers. Here, we used models that represent three popular conceptual variants in the decision making literature, especially the ones that were applied to the real data in the IGT (Busemeyer and Stout, 2002). We replicated Busemeyer and Stout's four models: a Strategy-Switching Heuristic Choice Model (Heuristic for short), a Bayesian-Expected Utility Model (Bayes_EU for short), an Expectancy–Valence Learning Model (this is essentially a reinforcement learning model, RL for short), and a Baseline Model. We followed the exact definition of these models and the readers can refer to (Busemeyer and Stout, 2002) for the details of these models. While these models used three free parameters, our Bayesian model did not have any free parameters to fit. However, our Bayesian updating rules and inclusion of the knowledge of the task structure constrains the model in a way that may not be suitable for different tasks other than ours. Thus, comparisons of the model based on the number of free parameters or residual error in fitting are not well suited. Thus, we relied on the predictive performance based on SDT (Macmillan and Creelman, 2005) as a framework for model comparison.

We tuned three parameters for a given set of the data (i.e., each subject had the simple and the complex version of the learning task, resulting in six free parameters) in each of these models carefully to ensure that the models were well fitted. We quantified whether each model could predict subjects' choice and wagering behavior using SDT as we did for our model. The results of the model comparison are shown in **Figure A1**.

As can be seen from the figure, three models from Busemeyer and Stout (2002), namely Baseline model, Heuristic model,

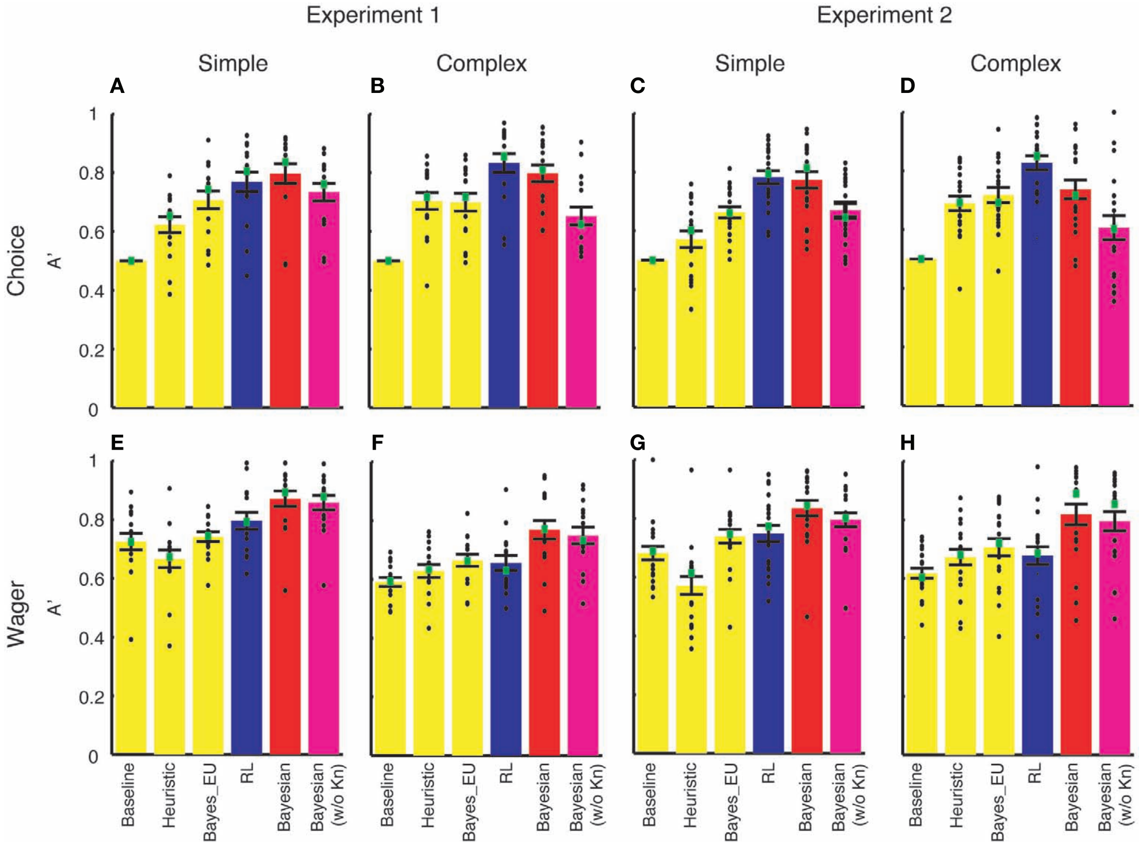

FIGURE A1 | Model comparison results of Experiment 1 (A,B,E,F) and Experiment 2 (C,D,G,H). A′ (*y*-axis) was computed to quantify how well each model (labeled on *x*-axis) can predict deck choice **(A–D)** and wagering behavior **(E–H)**. Simple **(A,C,E,G)** and complex **(B,D,F,H)** versions were analyzed separately. Each black dot represents A′ of an individual subject. Green squares denote the median of A′. Error bars denote 1 SEM across subjects. RL, Busemeyer and Stout's (2002) reinforcement learning model (blue bars); Bayesian, our Bayesian inference model (red bars); Bayesian (w/o K_n), a version of our Bayesian inference model without incorporating the knowledge of the task structure (magenta bars).

Table A1 | Comparisons of prediction performance for deck choice.

	B and S RL	Our Bayesian	*p*-Value
Exp 1 simple	0.77 ± 0.13	0.80 ± 0.13	$p = 0.16$
Exp 1 complex	0.83 ± 0.13	0.80 ± 0.11	$p = 0.17$
Exp 2 simple	0.78 ± 0.10	0.77 ± 0.13	$p = 0.69$
Exp 2 complex	0.83 ± 0.11	0.74 ± 0.14	$p = 0.0014$

Mean ± 1 SD.

Table A2 | Comparisons of prediction performance for wagering behavior.

	B and S RL	Our Bayesian	*p*-Value
Exp 1 simple	0.80 ± 0.11	0.87 ± 0.11	$p = 0.032$
Exp 1 complex	0.66 ± 0.10	0.77 ± 0.13	$p = 0.0015$
Exp 2 simple	0.75 ± 0.13	0.84 ± 0.12	$p = 0.0043$
Exp 2 complex	0.68 ± 0.13	0.82 ± 0.16	$p = 0.00022$

and Bayes_EU model, performed poorly in all cases and we will not describe them further. This trend is consistent with Busemeyer and Stout's (2002) model evaluation using G^2 measures.

For predicting deck choice (**Figures A1A–D**), Busemeyer and Stout's (2002) RL model (blue bars) performed similarly to our Bayesian inference model (red). For the details, see **Table A1**. We evaluated the significance of the difference with *p*-values from two-tailed paired *t*-tests.

For predicting wagering behavior (**Figures A1E–H**), the RL model performed significantly worse than our Bayesian inference model (red). For the details, see **Table A2**. We evaluated the significance of the difference with *p*-values from two-tailed paired *t*-tests.

Further, in all cases, our Bayesian inference model (red bars in **Figure A1**) outperformed a variant of this Bayesian model that does not incorporate knowledge of the task structure (magenta bars in **Figure A1**, paired *t*-test, $p < 0.05$ in all cases).

Taken together, we conclude that the RL model predicts choice behavior equally well or slightly better than our Bayesian inference model while it predicts wagering behavior much worse than our model in all cases.

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Comparing the Iowa and Soochow gambling tasks in opiate users

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The Iowa Gambling Task (IGT) is in many respects the gold standard for demonstrating decision making in drug using groups. However, it is not clear how basic task properties such as the frequency and magnitude of rewards and losses affect choice behavior in drug users and even in healthy players. In this study, we used a variant of the IGT, the Soochow Gambling Task (SGT), to observe choice behavior in opiate users and healthy decision makers in a task where reward frequency is not confounded with the long-term outcome of each alternative. In both opiate users ($n = 26$) and healthy controls ($n = 27$), we show that reward frequency strongly influences choice behavior in the IGT and SGT. Neither group showed a consistent preference across tasks for alternatives with good long-term outcomes, but rather, subjects appeared to prefer alternatives that win most frequently. We interpret this as evidence to suggest that healthy players perform better than opiate users on the IGT because they are able to utilize gain–loss frequencies to guide their choice behavior on the task. This challenges the previous notion that poorer performance on the IGT in drug users is due to an inability to be guided by future consequences.

Keywords: Iowa Gambling Task, Soochow Gambling Task, choice behavior, decision-making, opiate users, drug users

INTRODUCTION

Illicit drug use is a "risky" activity associated with negative consequences such as family and work disruption, overdose, addiction, and accidents from intoxication. Given such risks, an important question is why some people engage in this behavior. This question has prompted research into the thought processes underlying decisions under risk in drug users. Many findings indicate that drug users, when viewed as a group, are more sensitive to a range of rewarding stimuli and also less sensitive to loss (Rogers and Robbins, 2001; Bechara, 2005). In addition, drug users appear to have difficulty learning from past negative experiences to make more beneficial decisions in the future (Grant et al., 2000; Ersche et al., 2005; Brand et al., 2008). Of course, decisions involving risk are highly variable, and the type, value, and likelihood of rewards and losses can all influence choice. Thus, to understand why drug users take more risks, it is necessary to describe how factors related to learning, reward, and loss influence choice behavior. To this end, laboratory decision tasks allow a level of control not possible in the "real world," and several tasks are now widely used to study decisions under risk in drug users (CGT: Rogers et al., 1999; IGT: Bechara and Damasio, 2002; BART: Lejuez et al., 2002).

The Iowa Gambling Task (IGT; Bechara et al., 1997) is arguably the most popular decision task used in studies of clinical samples. Players choose from four "decks of cards" over a series of trials, with each selection resulting in a monetary reward and occasionally a monetary loss. A key feature of this task is that unbeknownst to the player, the decks vary in their win/loss frequencies and final outcomes. Players must make selections, experience the outcomes, and then develop their preferences through this experience. For a player to finish the IGT with a positive balance, the player must overcome an initial preference for decks that have large gains but large losses (with overall net losses), and switch their preference to decks that have relatively small rewards but less severe losses, ending with an overall net gain.

A typical finding in the IGT literature is that both drug users and healthy non-users prefer decks with net losses in the beginning stages of the task, but only healthy non-users shift their preference to the decks with the net gains as the task progresses (Bechara and Damasio, 2002; Stout et al., 2004, 2005). This finding suggests that drug users (unlike non-users) fail to learn from experience that the decks with large gains actually yield even larger losses, resulting in the negative expected value of the losing IGT decks. Instead, they continue to show a preference for losing decks either because they over-attend to the frequent large gains and under-attend to large losses, or because they are not attracted to the decks in which gains (and losses) are both smaller (Grant et al., 2000; Ersche et al., 2005).

To date, the most common method for analyzing IGT performance is by combining selections from decks with negative expected value (decks A and B) and decks with positive expected value (decks C and D; Bechara et al., 1994; Grant et al., 2000). However, pairing decks in this way obscures the influence of win frequency on IGT performance, because decks within each pairing differ in terms of win frequency. This issue was first described by (Chiu et al., 2008). In studies where IGT decks have been analyzed individually, drug users and non-users show a clear preference for decks with high frequency wins (Verdejo-Garcia et al., 2007). Drug users perform poorly because they prefer the high frequency win deck with higher risk (Deck B). Non-users start the task preferring this same deck, but as the task progresses, they typically shift their preference to the other high frequency win deck, which has relatively lower wins on every selection but also lower magnitude losses. So, although drug users and controls appear to prefer frequent win decks in the IGT, it is difficult to gage the strength of this factor's influence on decision making in each group because players have the option to switch from a high frequency win deck with negative expected value to a high frequency win deck with positive expected value. Would healthy decision makers develop a preference for decks with positive expected value in the IGT if a high frequency win alternative was not available?

To clarify the relative importance of expected value and win frequency on healthy decision makers' choices, Chiu et al. (2008) designed the Soochow Gambling Task (SGT). The key difference between the SGT and IGT is that both SGT decks with positive expected values have *lower frequency wins* than decks with negative expected values. Thus, in the SGT there is a negative correlation between expected value and win frequency which enables studying the relative influence of each factor on performance of the task. The selection patterns observed by Chiu et al. (2008) show that healthy players had no preference for decks with positive expected value, but rather, they preferred decks with high frequency wins despite those decks having negative expected value. In the SGT at least, healthy decision makers make what would be considered poor decisions overall, and win frequency appears to be a stronger influence than expected value. Applying the same interpretation to these findings as has been applied numerous times to the IGT; healthy decision makers appear insensitive to future consequences (Ahn et al., 2008; Chiu et al., 2008).

Why do healthy decision makers prefer high frequency win decks in the IGT and SGT? Research comparing descriptive and experienced based choices may provide some clues. In contrast to descriptive choices, where decision makers tend to *overvalue* low probability outcomes, decision makers tend to *undervalue* low probability outcomes when their decisions are based on feedback from past outcomes (Barron and Leider, 2009; Barron and Leider, 2009). That is, for experienced based choices, decision makers tend to prefer alternatives with a higher chance of being rewarded, even when the magnitude of the reward is smaller (Barron and Erev, 2003; see Rakow and Newell, 2010 for review). This may explain the pattern observed in the IGT and SGT, where both drug users and controls appear to prefer decks with the highest probability of winning (i.e., high frequency win decks). In the IGT, one high frequency win deck, Deck B, has negative expected value and the other, Deck D, has positive expected value. In the SGT, both high frequency win decks have negative expected value, which may explain why healthy players fail to develop a preference for decks with positive expected value as the task progresses.

Thus, the SGT can help to clarify the relative importance of factors such as expected value, win frequency and wins/loss magnitude on drug users' choices. And, given the difficulty of disentangling the influence of expected value, win frequency and sensitivity to risk in the IGT, a study that includes both the IGT and SGT will improve the accuracy in interpreting differences between drug users and non-users and broaden the available data upon which to base interpretations of decision characteristics in drug users. To maximize the possibility of seeing differences between drug users and controls in these two tasks, we examined opiate users in outpatient treatment rather than a group of milder drug users from the community. In both the IGT and SGT, we expected drug users to prefer high frequency win decks with high magnitude wins and losses, yielding overall losses in the IGT and in the SGT.

MATERIAL AND METHODS

SUBJECTS

We recruited 26 drug users ($M = 34.23$ years, $SD = 8.79$; male, 21) from Turning Point Alcohol and Drug Centre, a community outpatient service in inner Melbourne. These participants were either currently using illicit opiates (e.g., heroin) and/or taking prescribed opiate substitution medication (methadone, buprenorphine). Participants were asked to abstain from illicit drugs and alcohol for 12 h prior to the testing session (excluding opiate substitution medication). If participants reported using alcohol or drugs less than 12 h before the test session, or had a blood alcohol level reading above 0.05 mg/kg on arrival, their test session was postponed for at least 1 day. Test sessions were postponed for at least 2 days if participants arrived in a visibly intoxicated state or if they were experiencing acute withdrawal symptoms. We also recruited 27 control participants ($M = 35$ years, $SD = 10.44$; male, 22) using fliers and newspaper advertisements. Control participants had not used illicit drugs in the previous 6 months, had no history drug or alcohol problems, and had a blood alcohol level <0.05 mg/kg confirmed on arrival to the test session. Screening questions were used to ensure that participants from both groups had no history of psychosis. All participants provided written informed consent, and the Monash University Human Ethics Committee approved all study procedures.

Groups were matched on age, $t(51) = 0.29$, $p = 0.77$ and gender, $\chi^2(1, N = 53) < 0.01$, $p = 0.95$ (see **Table 1**), but drug users had lower education, $t(51) = 2.83$, $p < 0.01$, higher unemployment, $\chi^2(1, N = 53)$ 16.89, $p < 0.001$ and reported more incidences of head injury requiring hospitalization compared to non-users, $\chi^2(1, N = 53)$ 9.73, $p < 0.01$ (**Table 1**).

STUDY PROCEDURE

Participants from both groups underwent the same testing procedure in a single test session. During the initial part of the session, demographic characteristics, medical information, and substance use histories were recorded. A battery of computerized decision making tasks and a series of questionnaires followed. Testing took between 2 and 3 h for each participant, and was typically longer for drug users because their substance use histories were more extensive. Only a subset of the data collected is reported here.

CHARACTERIZATION OF PARTICIPANTS

Substance use

Lifetime substance use and frequency of use over 30 days prior to testing were recorded using the drug use section of the addiction severity index (ASI; Mclellan et al., 1980). We also determined alcohol related problems over the past 12 months (e.g., health, relationship, occupational, legal) using the Michigan Alcohol Screening Test (MAST; Selzer, 1971), and illicit drug related problems using the Drug Abuse Screening Test (DAST; Skinner, 1982). The MAST and DAST probe alcohol and drug related problems over

Table 1 | Summary of demographic, mood, personality, and substance use variables.

	Controls ($n = 27$)		Drug users ($n = 26$)	
	M (SD)	**%**	**M (SD)**	**%**
Age	35 (10.44)		34.23 (8.79)	
Gender (male)		81.49		80.67
Est. IQ (WTAR)	35.15 (8.23)		32.42 (10.22)	
Education (years)*	14.74 (2.93)		12.25 (3.46)	
Employed*		66.67		11.54
Head inj. requiring hospital*		3.70		38.46
Mood/anxiety dis.*		18.51		53.85
Anxiety (past week; HADS)*	5.41 (2.42)		9.73 (3.66)	
Depression (past week; HADS)*	3.11 (3.09)		7.50 (3.42)	
Impulsivity (Eysenck I7)*	5.41 (3.65)		10.46 (4.62)	
Antisociality (MMPI-PD)*	15.52 (4.50)		24.44 (6.31)	
Alcohol				
Past month use		59.26		59.26
Past month use (numb. days)	3.22 (5.77)		7.42 (9.12)	
Lifetime use (years)	11.70 (10.78)		13.69 (8.69)	
Problems (MAST)	0.44 (0.66)		8.23 (6.71)	
Tobacco				
Never		74.10		3.85
Quit		11.11		0
Current (occasional)		7.41		0
Current (daily)		7.41		96.15
Cannabis				
Past month use		0		42.31
Past month use (numb. days)	0		8.15 (11.75)	
Lifetime use (years)	1.74 (5.35)		8.81 (7.84)	
Amphetamine				
Past month use		0		23.10
Past month use (numb. days)	0		0.50 (1.14)	
Lifetime use (years)	0		5.04 (6.45)	
Heroin				
Past month use		0		73.10
Past month use (numb. days)	0		5.85 (6.44)	
Lifetime use (years)	0		9.35 (6.75)	
Prescr. Methadone (current)				
Past month use		0		46.15
Past month use (numb. days)	0		13.69 (15)	
Lifetime use (years)	0		1.96 (3.23)	
Parent hist. (sub. problems)*		3.70		50
Illicit drug problems (DAST)	0.30 (0.61)		14.54 (4.34)	

*$P < 0.05$.

the past 12 months through a series of questions requiring a yes/no response. Parental history of substance use problems was also recorded.

As expected, the opiate user's group scored higher on the DAST, $t(51) = -16.58$, $p < 0.001$ and MAST, $t(51) = -5.89$, $p < 0.001$ compared to the control group. They also used a range of drugs for longer and more frequently over their lifetime (including alcohol and tobacco; see **Table 1**) and were more likely to have a parent with a substance use problem, $\chi^2(1, N = 53)$ 14.60, $p < 0.001$.

ESTIMATED IQ, MOOD, AND PERSONALITY

We estimated participant IQ using the Wechsler Test of Adult Reading (WTAR; Wechsler, 2001). The WTAR requires participants to read a list of 50 words to the experimenter, with word difficulty increasing further down the list. The number of correctly pronounced words is a strong predictor of general IQ (Wechsler, 2001). We also determined recent symptoms of depression and anxiety over the previous week using the Hospital Anxiety and Depression Scales (HADS; Zigmond and Snaith, 1983). The HADS is self-administered and has 16 questions (8 for anxiety and 8 for depression). Each question has four response levels scored from 0 (e.g., not at all) to 3 (e.g., definitely). Total scores range from 0 to 21 for each subscale, with higher scores indicating greater anxiety/depression symptomatology. We also assessed "rash impulsivity" using the Eysenck Impulsiveness Scale of the Eysenck Impulsivity Venturesomeness and Empathy Scales (Eysenck et al., 1985). The Impulsiveness scale is self-administered, and requires participants to answer 19 yes/no questions. Scores range between 0 and 19, with higher scores indicating greater impulsive tendencies. We assessed antisocial tendencies using the Minnesota Multiphasic Personality Inventory, psychopathic deviate subscale (MMPI-PD; Butcher et al., 1989). The MMPI-PD is a self-administered questionnaire consisting of 50 true/false questions. Scores range between 0 and 50, with higher scores indicating greater antisocial tendencies.

Drug users and non-users had comparable WTAR scores, $t(51) = 1.07, p = 0.29$ but drug users reported higher symptoms of depression, $t(51) = -4.90$, $p < 0.001$ and anxiety, $t(51) = -5.09$, $p < 0.001$ (HADS) and were more likely to report a history of mood disorder compared to the control group, $\chi^2(1, N = 53)$ 7.19, $p < 0.01$. Drug users also had higher self-reported impulsivity (Eysenck I7), $t(51) = -4.43$, $p < 0.001$ and higher antisociality (MMPI-PD scale), $t(51) = -5.90$, $p < 0.001$.

DECISION MAKING TASKS: THE IGT AND THE SGT

In the IGT (Bechara et al., 1997), players select from four "decks of cards" over a series of trials. On each trial, players receive a monetary reward or loss following their selection, with the frequency and magnitude of wins and losses differing across decks. Players are not given any information about the decks. Instead, they must learn from experience to choose from the decks that will maximize net return overall. Decks A and B have a large fixed reward ($1.00), and occasional large losses ($2.5 to 12.50). Over 10 selections, these decks return a *net loss* of $2.50 (**Table 2**). Decks C and D return a relatively small fixed reward ($0.50) compare to decks A and B, but also relatively small occasional losses ($0.25 to $2.50). Over 10 selections, these decks return a *net reward* of $2.50 (**Table 2**). Therefore, in order to finish the game on a positive balance, participants must make a higher proportion of selections from decks C and D overall.

Most studies using the IGT assess the total proportion (or number) of "good" deck selections over the course of the task to evaluate performance. However, recent findings suggest that combining decks for analysis can mask important patterns unique to each deck (Dunn et al., 2006; Yechiam et al., 2008). For this reason, we focused on individual deck selections and did not combine decks based on long-term outcome as some previous studies have. Given that changes can occur in preference as player experience the payoffs of each deck, we also analyzed changes in the mean proportion of selections from each deck a function of task progression (blocks 1–6).

The SGT (Chiu et al., 2008) is also computerized, requiring players to choose from four "decks of cards" over a series of trials. Like the IGT, players are not given any information about the decks. Two decks (A and B) have a fixed *reward* every selection (A, $1.00; B, $0.50) and a fixed *loss* every five selections (A, $5.25; B, $3.25)[1]. Ten selections from these decks results in a net *loss* of $2.50 (**Table 2**). The two other decks (C and D) have a fixed *loss* every selection (C, $1.00; D, $0.50) and a fixed *reward* every five selections (C, $5.25; D, $3.25). Ten selections from these decks results in a net *reward* of $2.50 (**Table 2**). Thus, unlike the IGT, decks that win frequently in the SGT (A, B) have a negative long-term value. We used the same approach to analyze SGT selections as described above for the IGT.

For both tasks, players began the game with a starting balance of $20.00 and received any money earned above this balance at the end of the task (120 trials). Players could not lose any money. The total balance was updated on-screen after every selection and players were also provided with feedback about the net change in balance every 20 trials (6 blocks). Each trial was player-initiated, and there were no time restrictions. Decks were positioned on the computer screen, from left to right, randomly

Table 2 | The pay-off distributions of the Iowa Gambling Task and Soochow Gambling Task for the first 10 trials, adapted from Ahn et al. (2008).

IGT	A	B	C	D	SGT	A	B	C	D
Expected value of 10 trials	−$2.50	−$2.50	$2.50	$2.50	Expected value of five trials	−$2.50	−$2.50	$2.50	$2.50
Gain on every trial	$1.00	$1.00	$0.50	$0.50	Gain on every trial	$1.00	$0.50	−$1.00	−$0.50
Loss on each trial					Loss on each trial				
Trial 1								−$1.00	−$0.50
Trial 2								−$1.00	−$0.50
Trial 3								−$1.00	−$0.50
Trial 4								−$1.00	−$0.50
Trial 5						−$5.25	−$3.25		
Trial 6	−$1.50		−$0.25					−$1.00	−$0.50
Trial 7	−$2.00		−$0.75					−$1.00	−$0.50
Trial 8	−$2.50		−$0.50					−$1.00	−$0.50
Trial 9	−$3.00		−$0.50					−$1.00	−$0.50
Trial 10	−$3.50	$12.50	−$0.50	−$2.50		−$5.25	−$3.25		

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[1] Note that in contrast to the IGT, which presents wins and losses (when they occur) separately on each trial, in the SGT, only a net win or loss is presented.

across participants, and the order of tasks was counterbalanced between participants.

STATISTICAL ANALYSIS

Demographic, substance use, mood, and personality measures were compared between groups using two-tailed independent samples *t*-tests for continuous variables (e.g., age, education) and chi square tests for categorical variables (e.g., gender, employment status). We computed separate repeated measures ANOVAs for the SGT and IGT to analyze the mean proportion of selections from each deck (A, B, C, D) across the 6 task blocks (repeated measures). Group was included as a between-subjects factor in this analysis (drug users, controls). Paired samples *t*-tests were used to explore significant ($p < 0.05$) main effects of deck, and one-way ANOVAs to explore interactions between deck and group. Interaction effects involving the factor of task block were explored using repeated measures ANOVAs. Greenhouse–Geisser adjusted degrees of freedom (and *p* values) are reported when Mauchly's Test of Sphericity was significant.

To further explore the influence of win frequency, magnitude, and expected value on deck preference, we also examined Pearson's correlations between the number of selections from each deck in the IGT with the decks in the SGT across a combined sample of drug users and controls. We expected decks with similar win frequency and win/loss magnitude characteristics would be more strongly related than other decks in the same task, but not decks with the same expected values.

RESULTS

IGT AND SGT DECK SELECTIONS

We analyzed SGT selections to determine how deck preferences developed during the task in each group. We found a main effect of deck in the SGT, $F(3,153) = 9.17$, $p < 0.001$, but no interaction between deck and group, $F(3,153) = 0.17$, $p > 0.05$, deck and block, $F(15,765) = 1.24$, $p > 0.05$, or deck, block, and group, $F(15,765) = 1.12$, $p > 0.05$. This indicates that both groups developed similar preferences and did not change those preferences over the course of the task. Both groups overwhelmingly preferred high frequency win deck A (bad long-term outcome) to all other decks [deck B, $t(52) = 4.58$, $p < 0.001$, deck C, $t(52) = 3.05$, $p < 0.01$, deck D, $t(52) = 5.13$, $p < 0.001$; **Figure 1**]. We also found a trend for both groups to prefer high frequency win deck (deck B; bad long-term outcome) over low frequency win deck D (good long-term outcome), $t(52) = 1.85$, $p = 0.07$ (**Figures 1B,D**).

For the IGT, our aim was to replicate previous findings (Stout et al., 2004, 2005), both in terms of initial preferences in each group (deck B) and changes in preference during the task (no change in substance users, healthy controls switch to deck D). We found a main effect of deck, $F(3,153) = 25.20$, $p < 0.001$ and an interaction between deck and group, $F(3,153) = 4.58$, $p < 0.05$, and deck, block, and group, $F(15,765) = 1.66$, $p = 0.05$. This finding replicates previous studies in that drug users and controls developed different deck preferences and that these preferences changed during task in a group specific way (Grant et al., 2000; Verdejo-Garcia et al., 2007; Verdejo-Garcia and Perez-Garcia, 2007). Interesting

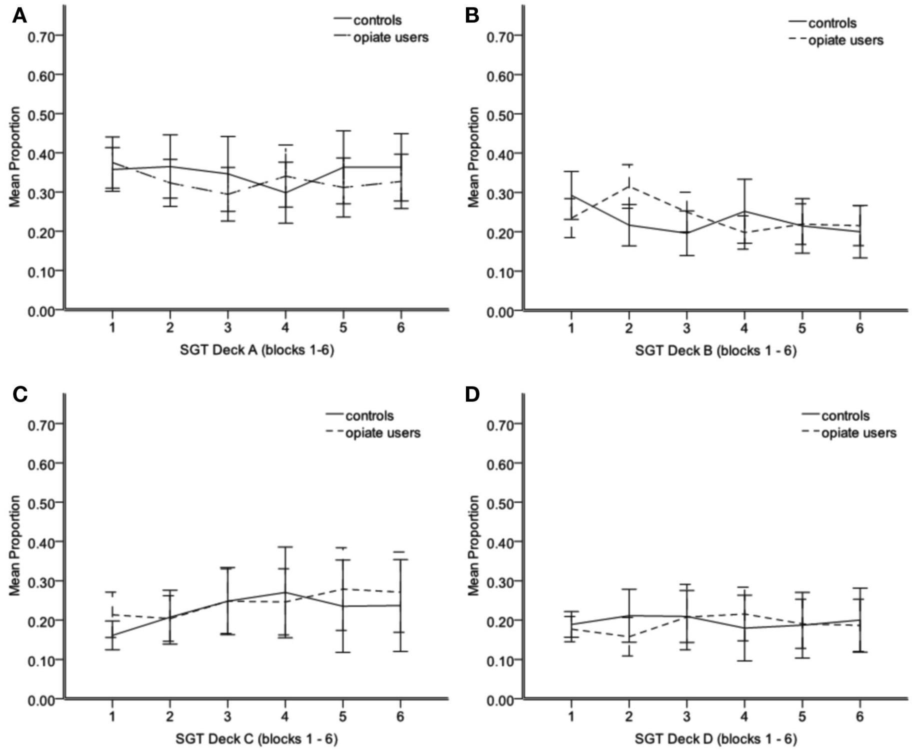

FIGURE 1 | Mean proportion of SGT selections from deck A (A) deck B (B) deck C (C) deck D (D) from blocks 1–6. Each block = 20 trials. Error bars 95% CI. *$P < 0.05$.

effects were in high frequency decks B and D. The controls made more deck D selections than opiate users $F(1{,}52) = 5.20$, $p < 0.05$ (**Figure 2D**). For controls, there was a significant increase in deck D selections across the task $F(5{,}130) = 2.74$, $p < 0.05$, suggesting learning in this group, whereas in opiate users there appears to be no change as the task progressed, $F(5{,}125) = 0.52$, $p > 0.05$. In contrast, controls made significantly fewer selections from deck B compared to opiate users $F(1{,}52) = 6.52$, $p < 0.05$, and although deck B selections appeared to decrease slightly across the task in controls and increase slightly in opiate users, this interaction was not significant [$F(5{,}255) = 1.813$, $p > 0.05$; **Figure 2B**]. deck A selections were comparable between groups, $F(1{,}52) = 0.02$, $p > 0.05$, as were deck C selections, $F(1{,}52) = 0.44$, $p > 0.05$ (**Figures 2A,C**).

CORRELATIONS BETWEEN IGT AND SGT DECK SELECTIONS

Consistent with the reasoning behind the SGT (i.e., deck expected value does not guide choice), selections from SGT decks with positive expected value (C, D "good decks") were not associated with selections from IGT decks with positive expected value (C, D "good decks"), $r(53) = 0.06$, $p > 0.05$ (**Figure 3B**). In contrast, we found correlations between decks with similar win frequency

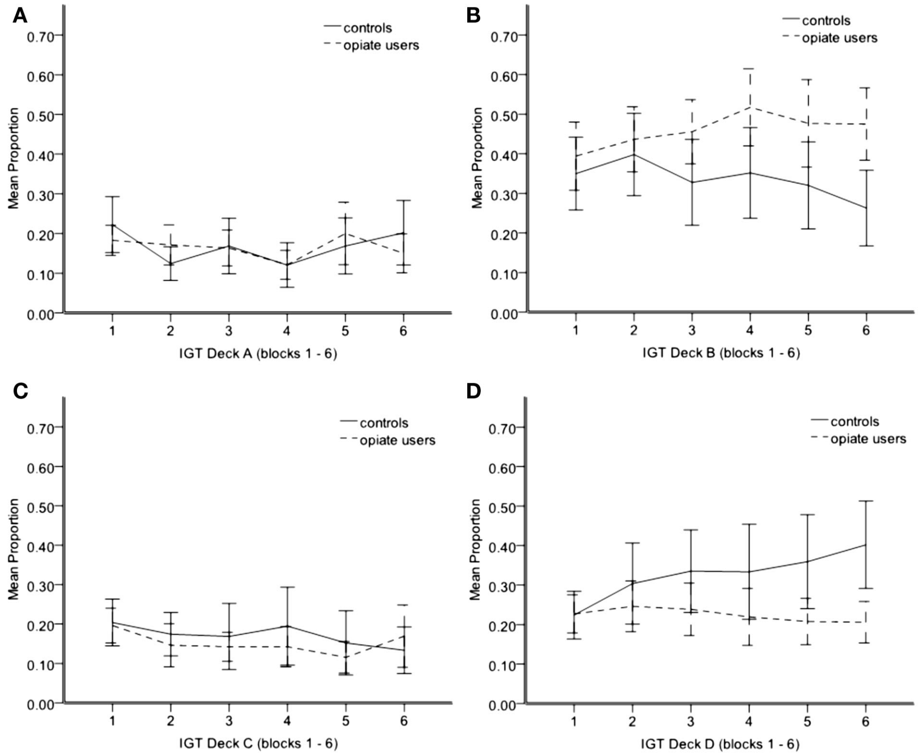

FIGURE 2 | Mean proportion of IGT selections from deck A (A) deck B (B) deck C (C) deck D (D) from blocks 1–6. Each block = 20 trials. Error bars 95% CI. $^*P < 0.05$.

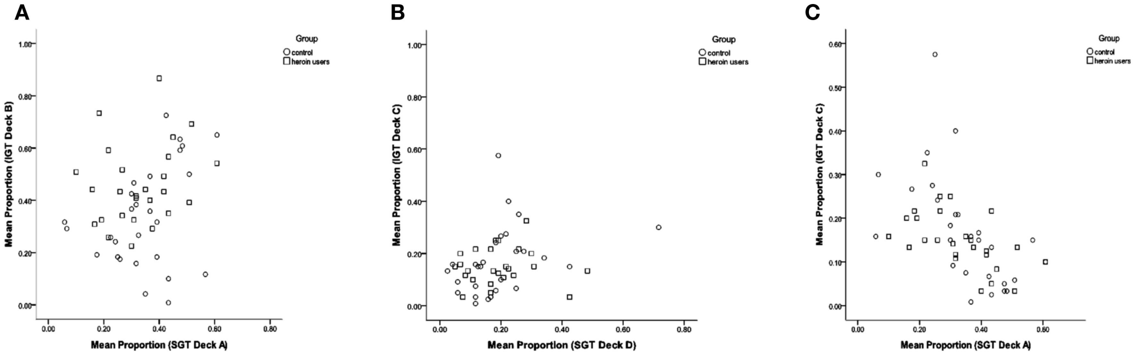

FIGURE 3 | Scatter plots showing the association between mean proportion of IGT and SGT selections for IGT deck B and SGT deck A (A) IGT deck C and SGT deck D (B) and IGT deck C and SGT deck A (C).

and win/loss magnitude characteristics. Participants who selected more from deck A in the SGT (high frequency win, high magnitude win/loss) also tended to select more from deck B in the IGT (also high frequency win, high magnitude win/loss), $r(53) = 0.251$, $p < 0.07$ (**Figure 3A**). In addition, participants who selected more from SGT deck A tended to make fewer selections from IGT deck C (low win frequency, low magnitude win/loss), $r(53) = -0.530$, $p < 0.001$ (**Figure 3C**). However, IGT deck D selections were not related to SGT deck B selections, despite both decks being high frequency win, low magnitude win/loss, $r(53) = 0.090$, $p > 0.05$.

DISCUSSION

Many studies have found that drug users perform poorly in the IGT, but it is unclear how the basic properties of this task are related to choice behavior. Our aim was to identify patterns of responding across the IGT and SGT in relation to each deck's expected value, its win frequency and win/loss magnitude. Our data indicate that opiate users and healthy controls are strongly influenced by win frequency, with both groups preferring high frequency win decks to low frequency win decks in the IGT and SGT.

Although the deck property of expected value has been the primary focus of most previous studies (Bechara et al., 1994, 1997, 2000) its influence on choice behavior was not obvious. Similar to Chiu et al. (2008) and Ahn et al. (2008), healthy controls preferred decks with positive expected value in the IGT, but negative expected value decks in the SGT. In addition, selections from decks with the same expected value were not correlated across the IGT and SGT. Thus, if expected value does influence choice behavior in healthy decision makers, as suggested in previous literature (Bechara et al., 1997), the effect does not appear to generalize from the IGT to the SGT.

One possibility raised by Chiu et al. (2008) is that controls prefer decks with positive expected value in the IGT because they do not have a lower win frequency. The SGT reveals that when behavior based on win frequency and expected value lead to different choices, win frequency is a stronger influence on choice behavior in this context (Ahn et al., 2008; Chiu et al., 2008). Our study confirms this finding and extends it to a group of drug users. Across both tasks, we found only one difference between opiate users and controls. In the SGT, both groups preferred SGT Deck A (high frequency win, high magnitude win/loss, negative expected value) and did not learn to maximize their earnings by shifting their preference to decks with positive expected value (C, D). In the IGT, both groups preferred Deck B early on (high frequency win, high magnitude win/loss, negative expected value), but only controls shifted their preference to Deck D in the later stages of the task (high frequency, low reward/loss magnitude).

To explain this pattern of results, we need to consider the win frequency and win/loss magnitude characteristics of IGT decks B and D. Deck D returns half the reward per selection compared to Deck B ($0.5 vs. $1), but has less harsh occasional losses ($2.50 vs. $12.50). Thus, it is likely that controls were motivated to shift their preference to Deck D after experiencing the large losses associated with Deck B. So why did not drug users also shift their preference from Deck B to Deck D? Previous studies suggest that drug users are more sensitive to rewarding stimuli and less sensitive to loss/punishment (Rogers and Robbins, 2001; Stout et al., 2004, 2005; Bechara, 2005). Thus drug users may have been relatively more attracted to the large rewards associated with Deck B, and less affected by this deck's large losses. This combination would reduce the likelihood of drug users shifting their preference to a lower paying deck with the same win frequency.

To understand why controls shifted their preference in the IGT but not in the SGT, it may help to consider IGT decks again. In the IGT, when players shift from Deck B to Deck D, they forgo 50% of the reward (per selection), but also get an 80% reduction in loss. In the SGT, when players shift from Deck A to Deck B, they forgo 50% of the reward, but only get a 38% reduction in loss. We can only speculate, but it could be that players are aware of this trade-off on some level and decide that it is not worth it in the SGT. This is fundamentally different to the suggestion that healthy controls learn the expected value of decks and shift their preference accordingly. Indeed, given that decision makers have been shown to undervalue low probability alternatives in experience-based choices (Barron and Leider, 2009; Barron and Yechiam, 2009), it is not surprising that players strongly preferred alternatives in both tasks that had the highest probability of winning. Furthermore, the correlation between high frequency win decks across the IGT and SGT found in this study, suggests that the strength of this preference is robust across related decision situations. This does not appear to be the case for the factor of expected value.

Of course, this is the first study to evaluate IGT and SGT performance together in drug users, so replication in a larger, more representative sample is required. Our sample of drug users also had high levels of head injury requiring hospitalization and high levels of anxiety and depression. These characteristics could reasonably affect decision processes, particularly the evaluation of reward and loss which appear to be important processes for understanding why choice behavior differs between drug users and non-users in the IGT Nevertheless, head injury, anxiety and depression are common characteristics in this population and in many respects inseparable from drug use disorders (Rogers and Robbins, 2001). We are encouraged however by our replication of previous IGT findings in cannabis users (Fridberg et al., 2010), which indicates that our sample was not unique in terms of their decision making abilities or tendencies.

In conclusion, given the importance of tasks such as the IGT for understanding decision making in clinical samples such as those in treatment for drug use, we know surprisingly little about how the basic properties of this task influence choice behavior. Our data indicated that opiate users and healthy controls are similarly influenced by win frequency across the IGT and SGT, but appear to value wins and losses differently, at least in the IGT. This may explain divergent choice behavior observed between groups later in the IGT. Future studies should determine how individual differences in the valuation of reward and loss affect choice behavior in this context.

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Neural network models of learning and categorization in multigame experiments

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Previous research has shown that regret-driven neural networks predict behavior in repeated completely mixed games remarkably well, substantially equating the performance of the most accurate established models of learning. This result prompts the question of what is the added value of modeling learning through neural networks. We submit that this modeling approach allows for models that are able to distinguish among and respond differently to different payoff structures. Moreover, the process of categorization of a game is implicitly carried out by these models, thus without the need of any external explicit theory of similarity between games. To validate our claims, we designed and ran two multigame experiments in which subjects faced, in random sequence, different instances of two completely mixed 2 × 2 games. Then, we tested on our experimental data two regret-driven neural network models, and compared their performance with that of other established models of learning and Nash equilibrium.

Keywords: neural networks, learning, categorization, regret, cross-game learning, mixed strategy equilibrium, repeated games

INTRODUCTION

In everyday life, interactive as well as individual decision problems very rarely repeat themselves identically over time; rather, the experience on which most human learning is based comes from the continuous encounter of different instances of different decision tasks.

The current paper proposes an experimental study in which subjects faced different instances of two interactive decision problems (games), making a step forward in the realism of the strategic situations simulated in the lab. Specifically, subjects played in sequence different completely mixed games[1], each obtained by multiplying the payoffs of one of two *archetypal* games for a randomly drawn constant. In each sequence, the perturbed payoff games of the two types were randomly shuffled. Thus, at each trial, subjects' task was twofold: recognize the type of the current game and act in accordance to this categorization.

In spite of its evident economic relevance, the topic of human interactive learning in mutating strategic settings has not received until now much attention, from both an experimental and modeling perspective.

One important stream of literature on this topic includes studies in which the experimental design is recognizably divided into two parts, according to which the repeated play of a stage game is followed by the repeated play of another one. The main goal of these studies is that of assessing the effects of learning spillovers (or *transfer*) from the first to the second part of the experiment (as in Kagel, 1995; Knez and Camerer, 2000; Devetag, 2005), also conditional to different environmental and framing conditions (as in Cooper and Kagel, 2003, 2008). In a different experimental paradigm, Rankin et al. (2000) propose a design in which players faced sequences of similar but not identical stag-hunt games, and whose goal is that of evaluating the basins of attractions of the risk- and payoff-dominant strategies in the game space.

Our experimental design distinguishes from those illustrated above for two key features. First, subjects played different instances of two different games, and, second, the instances of the two games occurred in random order, thus without inducing any evident partition in the experiment structure; at the beginning of our experiments, subjects were only told that they would have faced a sequence of interactive decision problems.

From the modeling perspective, a similarity-based decision process was for the first time formalized in the "Case-Based Decision Theory" (Gilboa and Schmeidler, 1995), according to which decisions are made based on the consequences from actions taken in similar past situations. Besides, the case-based approach was for the first time applied to game theory with the "fictitious play by cases" model proposed by LiCalzi (1995). This model addresses the situation in which players play sequentially different games, and the play in the current game is only affected by experiences with past similar games. In this vein, Sgroi and Zizzo (2007, 2009) explore neural networks' capability of learning game-playing rules and of generalizing them to never previously encountered games. The authors show that back-propagations neural network can learn to play Nash pure strategies, and use these skills when facing new games with a success rate close to that observed in experiments with human subjects.

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[1] Games with a unique Nash equilibrium in mixed strategies.

The contribution by Marchiori and Warglien (2008) has shown that, in repeatedly played completely mixed games, reinforcement learning models have limited predictive power, and that the best predictors, i.e., a fictitious play model and a neural network fed back by a measure of regret, have substantially the same accuracy. The current paper extends this research and shows that the added value of modeling learning by means of neural networks is that of capturing subjects' sensitivity to dynamic changes in the payoff structure. Specifically, we introduce a variant of the zero-parameter Perceptron-Based (PB0) model, which we call SOFTMAX-PB0, test these two neural network models on the data from our multigame experiments, and compare their performance with that of other established learning models and Nash equilibrium.

THE MULTIGAME EXPERIMENTS

The current paper proposes two multigame experiments, whose goal is that of improving our understanding of the processes of categorization in games. Eight groups of eight subjects each participated in the experiments, and each group played a different sequence of 120 games (see **Table A3** in Appendix). Within each group, half of the subjects were assigned the role of row player and the others that of column player; at each round, subjects assigned to different roles were randomly and anonymously paired. At the end of each round, subjects were provided with feedback about their and their opponents' actions and payoffs.

The experimental design is summarized in **Table 1**.

EXPERIMENT 1

Four groups of subjects played four game sequences built starting from two 2 × 2 constant-sum games (henceforth game A and game B; see **Table 1**). Game A and B payoffs were chosen in such a way that equilibrium probabilities for one player were not so different [respectively, $P(U) = 0.9$ and 0.7], whereas the other player was supposed to reverse his/her strategy [respectively, $P(L) = 0.1$ and 0.9]. Moreover, to get a balanced experimental design, payoffs in each cell of the two games where chosen to sum up to the same constant.

To build each sequence, 60 "type A" games were obtained by multiplying game A's payoffs for 60 randomly drawn constants[2] (normally distributed with mean 10 and SD 4). The same procedure was used to obtain 60 "type B" games[3]. Type A and B games were then shuffled in such a way that in each block of 10 trials there were five type A and five type B games in random order. Thus, in each block of 10 trials subjects could face the same number of type A and type B games.

Participants

Thirty-two students from the faculties of Economics, Law, and Sociology of the University of Trento (Italy) participated in Experiment 1. Subjects were paid based on their cumulated payoff in 12 randomly selected trials plus a show-up fee (see Experimental Instructions in Appendix).

Results

Figure 1 reports the relative frequency of *U* and *L* choices in blocks of 10 trials, separately for type A and B games.

Observed behavior in type A games is not well approximated by Nash equilibrium. Row players play Nash mixture in the first two blocks [for which $P(U) = 0.89$], but the proportion of *U* choices eventually converges to 0.74. As for the column players, play starts close to random behavior in the first block and converges to 0.33, higher than the 0.1 predicted by Nash's theory.

The predictive power of Nash equilibrium in type B games is also rather poor. In equilibrium, row players are supposed to choose action *U* with probability 0.7, whereas observed play converges to the relative frequency of 0.9. Column players are predicted to choose action *L* 90% of the times, but the observed proportion converges, from the third block, to about 0.4.

Table 1 | The two pairs of completely mixed *archetypal* games used for building the game sequences in the two experiments.

	Archetypal games					
	Game A			**Game B**		
Experiment 1	Player 2	*L*	*R*	Player 2	*L*	*R*
	Player 1			Player 1		
	U	17, 5	16, 6	*U*	5, 17	2, 20
	D	8, 14	17, 5	*D*	4, 18	11, 11
	Nash Eq.: $P(U) = 0.9$, $P(L) = 0.1$			Nash Eq.: $P(U) = 0.7$, $P(L) = 0.9$		
	Game A			**Game C**		
Experiment 2	Player 2	*L*	*R*	Player 2	*L*	*R*
	Player 1			Player 1		
	U	17, 5	16, 6	*U*	17, 5	15, 7
	D	8, 14	17, 5	*D*	15, 7	18, 4
	Nash Eq.: $P(U) = 0.9$, $P(L) = 0.1$			Nash Eq.: $P(U) = 0.6$, $P(L) = 0.6$		

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[2] Only positive values were considered.

[3] Thus type A and B games had, respectively, the same mixed strategy equilibrium of games A and B.

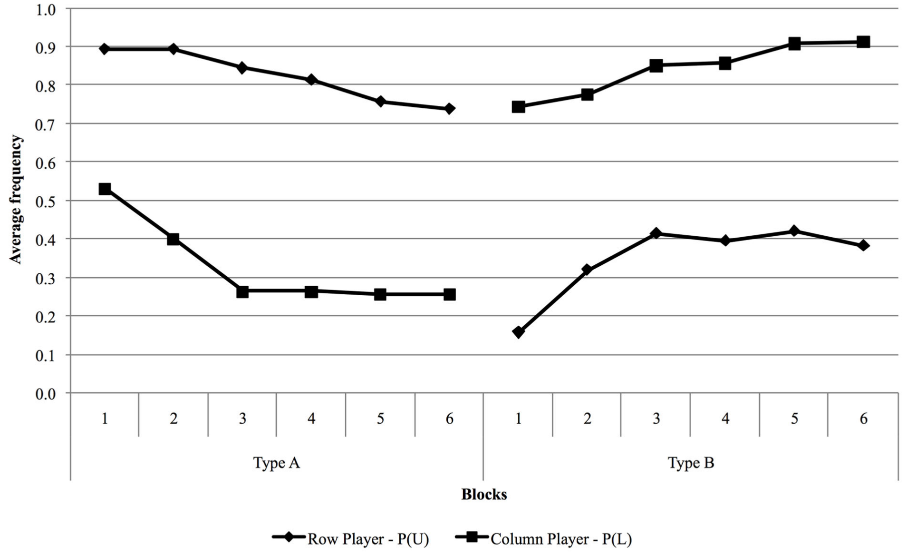

FIGURE 1 | Observed proportions of *U* and *L* choices averaged over blocks of 10 trials, separately for type A and B games.

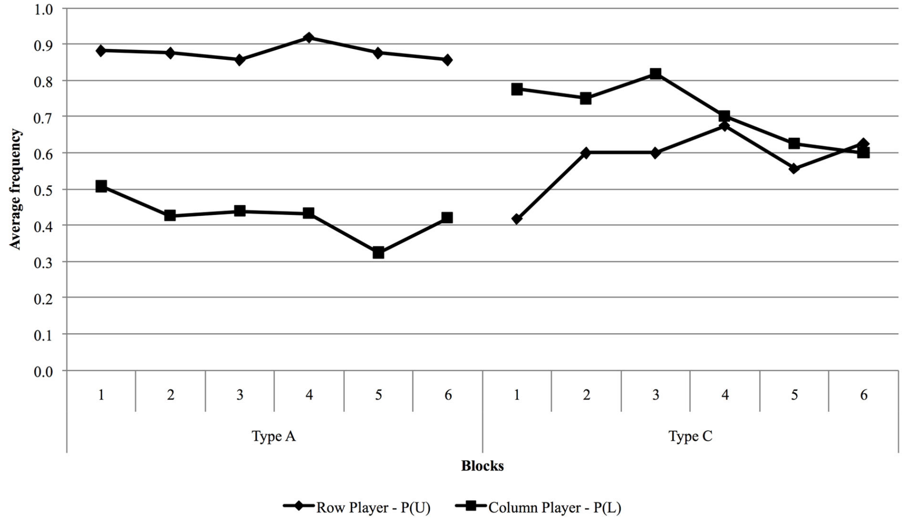

FIGURE 2 | Observed proportions of *U* and *L* choices averaged over blocks of 10 trials, separately for type A and C games.

EXPERIMENT 2

Experiment 2 was identical to the previous one, except for the fact that games A and C were used to build the four sequences (see **Table 1**). Game C was chosen in such a way that equilibrium probabilities were, for both players, close to equal chance; thus, no reversal of choice strategies was implied. Also in this case, in each cell of games A and B, payoffs sum up to the same constant.

Participants

Thirty-two students from the faculties of Economics, Law, and Sociology of the University of Trento (Italy) participated in Experiment 2. Subjects were paid based on their cumulated payoff in 12 randomly selected trials plus a show-up fee (see Experimental Instructions in Appendix).

Results

Figure 2 illustrates the results from Experiment 2. The relative frequency of U choices in type A games is systematically higher than that predicted by Nash's theory, similarly to what happened in Experiment 1. It is interesting to note that, in type C games, empirical behavior of both row and column players eventually converges to Nash play $[P(U) = P(L) = 0.6]$, confirming that Nash equilibrium is a good predictor (at least in the long run) when predicted choice probabilities are close to 0.5 (Erev and Roth, 1998; Erev and Haruvy, in preparation).

Cross-game learning

The question of how play in type A games is affected by the simultaneous play of games of a different kind can be easily answered by comparing choice frequencies in type A games in the two experiments. To this end, we ran a two-way, repeated measures analysis (results are summarized in A1 and A2 in Appendix), in which we tested the effects of the variables *Experiment* (i.e., the experimental condition) and *Time*, and of their interaction on choice frequencies for both row and column players. As a result, the variable Experiment has no significant effect, implying that no cross-game learning is taking place. We conclude that, when games of just two types are present, subjects are able to recognize the two strategic situations and act without confounding them.

THE MODEL

Since when McCulloch and Pitts (1943) introduced the first neuronal model in 1943, artificial neural networks have usually been intended as mathematical devices for solving problems of classification and statistical pattern recognition (see for example, Hertz et al., 1991; Bishop, 1995). For this reason, neural network-based learning models are the most natural candidates for predicting data from our multigame experiments, wherein a categorization task is implicit.

We present here a variant of the PB0 model proposed in Marchiori and Warglien (2008), which we call SOFTMAX-PB0. This model is a *simple perceptron*, i.e., a one-layer feed-forward neural network (Rosenblatt, 1958; Hopfield, 1987); its input units (labeled with in_i) are as many as the game payoffs, whereas its output units (labeled with out_j) are as many as the actions available to a player. Different from the PB0 model, according to SOFTMAX-PB0, the activation states of output units are determined via the *softmax* rule (1), and can thus be readily interpreted as choice probabilities.

$$\text{out}_j = \frac{e^{\sum_i \text{in}_i w_{ij}}}{\sum_k e^{\sum_n \text{in}_n w_{nk}}}, \tag{1}$$

The term w_{ij} in (1) is the weight of the connection from input unit in_i to output unit out_j.

Compared to the use of the *tanh* activation function, calculating activation states via the *softmax* rule avoids the premature saturation of output units, and in general results in a better fit of the data and has important theoretical implications[4].

Adaptive learning from time step $t-1$ to time step t occurs through modifications in the connection weights as follows:

$$w_{ij}^{t} = w_{ij}^{t-1} + \Delta w_{ij}, \tag{2}$$

with:

$$\Delta w_{ij} = -\lambda \cdot \left(\text{targ}_j - \text{out}_j\right) \cdot \text{regret} \cdot \text{in}_i. \tag{3}$$

In the current model, the parameter λ that appears in (3) is replaced by a deterministic function, whose value at time step t is defined as the ratio between the experienced cumulated regret and the maximum cumulated regret. It is worth noting that the SOFTMAX-PB0 is non-parametric, as also in the *softmax* activation function (1) no free parameters are introduced.

In (3), targ_j is the *ex-post* best response to the other players' actions, and it is equal to one if action j was the best response, and zero otherwise. Finally, the regret term is simply defined as the difference between the maximum obtainable payoff given other players' actions and the payoff actually received.

The SOFTMAX-PB0 and the PB0 models, behavior is the result of adjustments in the direction of the ex-post best response (*ex-post rationalizing* process), and these adjustments are proportional to a measure of regret, consistently with findings in the neuroscientific field (Coricelli et al., 2005; Daw et al., 2006).

The SOFTMAX-PB0 model, as well as the PB0 one, presents some architectural analogies with established models of learning in games, but it has also some peculiar features that differentiate it from its competitors, as illustrated in **Figure 3**. Established learning models have two main cyclic component processes: (1) behavior is generated by some *stochastic choice rule* that maps

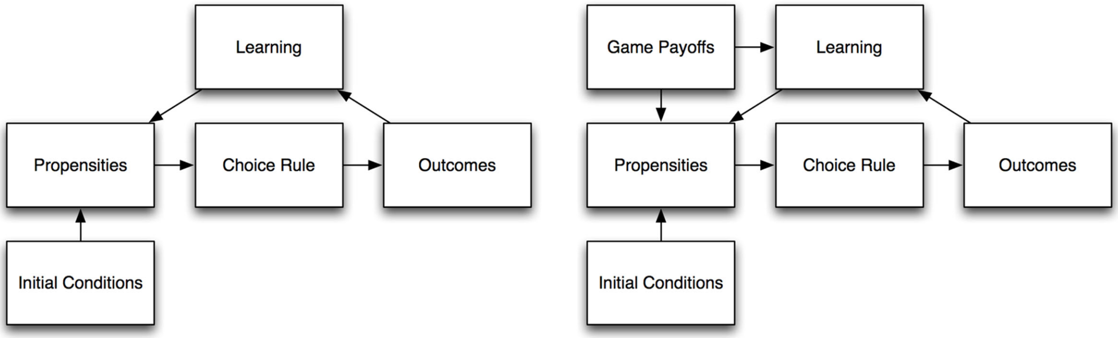

FIGURE 3 | Adapted from Marchiori and Warglien (2008): General architecture of a "propensities and stochastic choice rule" learning model (left), and general architecture of the (SOFTMAX-)PB0 model (right).

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[4] Moreover, when outputs are calculated via (1), the updating rule (3) leads to Cross-Entropy minimization or, in other terms, to the maximization of the likelihood of observing a given training set.

propensities into probabilities of play; (2) *Learning* employs feedback to modify propensities, which in turn affect subsequent choices.

The (SOFTMAX-)PB0 model's architecture is only partially similar to that of the other learning models. What distinguishes our models is the direct dependence of choice behavior upon game payoffs (represented in the "input layer"). Whereas in a typical economic learning model choice is a function of propensities only, here it is function of both propensities *and* the payoffs of the game.

This architecture provides the (SOFTMAX-)PB0 model with a peculiar capability to discriminate among different games. Conventional learning models in economics are designed for repeated games. There is learning, but no discrimination or generalization: the simulated agent is unable to discriminate between different games at a certain moment; if given abruptly a different game, it would respond in the same way, or just throw away what it had previously learned. On the other hand, discrimination is something perceptrons do very well, and since the output is also directly affected by perceived inputs (the activation states of input units), a network, besides learning, will respond differently to different games.

THE SAMPLING PARADIGM FOR MODELING LEARNING

Particularly relevant to the current analysis are the two contribution by Erev (2011) and by Gonzalez and Dutt (2011), in which the INERTIA SAMPLING AND WEIGHTING (I-SAW) and INSTANCE BASED LEARNING (IBL) models are proposed. According to these models, agents are supposed to make their decisions based on samples from their past experience. These models have been shown to capture important regularities of human behavior in decisions from experience (Erev et al., 2010; Gonzalez et al., 2011).

The most obvious way of modifying these models in order to perform conditional behavior is that of considering agents that draw from a subset of past experiences that are relevant to the current decision task. However, such an implementation would imply an exogenous intervention for the classification of the situation at hand, requiring an explicit theory of what is similar/relevant to what. On the other hand, the modeling approach based on sampling easily gives account for learning spillover effects (Marchiori et al., unpublished).

However, the classification operated by the (SOFTMAX-)PB0 model is endogenous; agents just observe inputs and respond to them without any external intervention and the entire process of classification is implicit in the structure of the model itself.

MATERIALS AND METHODS

Predicted choice frequencies were obtained by averaging results over 150 simulations, and, for parametric models, this procedure was repeated for each parameter configuration. **Table 2** collects the description of the portions of the parameter spaces investigated.

We tested models' predictive power by considering estimated choice frequencies corresponding to the parameter configurations that minimized the mean square deviation (henceforth MSD; Friedman, 1983; Selten, 1998) in our two experiments. Considering average MSD scores in the two experiments does not penalize directly the number of free parameters of a model; therefore, in this analysis, parametric models are advantaged over the non-parametric PB0 and SOFTMAX-PB0 ones.

In our comparative analysis, we considered the following learning models: normalized fictitious play (NFP; Erev et al., 2007); normalized reinforcement learning (NRL; Erev et al., 2007); Erev and Roth's reinforcement learning (REL; Erev and Roth, 1998); reinforcement learning (RL; Erev et al., 2007); stochastic fictitious play (Erev et al., 2007); and self-tuning experience weighted attraction (stEWA; Ho et al., 2007). Section "Competitor Models and Investigated Portions of Parameter Spaces" in Appendix briefly reviews these models.

SIMULATION RESULTS AND DISCUSSION

Although simple perceptrons suffer severe theoretical limitations in the discrimination tasks they can carry out (Minsky and Papert, 1969; Hertz et al., 1991), our simulation results show that they are nonetheless able to discriminate between two different strategic situations and predict well choice behavior observed in our multigame experiments. Simulation results are collected in **Figure 4** and, more in detail, in **Tables 3** and **4**.

Established learning models are not able to discriminate between the two different game structures, providing the same "average" behavior for both types of games (see **Tables 3** and **4**), and are always outperformed by Nash equilibrium. On the contrary, the SOFTMAX-PB0 and PB0 models are able to replicate subjects' conditional behavior, due to the direct dependence of their response on game payoffs, remarkably outperforming Nash equilibrium and all the other models of learning considered in this analysis.

Comparison of the performance of the PB0 and SOFTMAX-PB0 models shows how the introduction of the *softmax* rule for calculating output units' activations improves the fit of the data.

Table 2 | Explored portions of parameter spaces and the parameter configurations yielding the lowest average MSD in the two experiments.

Model	Portions of parameter spaces considered		Best fit parameters
NFP	λ in [1.5, 4.0] by = 0.25	w in [0.1, 0.9] by = 0.1	$\lambda = 4.0$, $w = 0.7$
NRL	λ in [3.0, 7.0] by = 0.5	w in [0.10, 0.90] by = 0.05	$\lambda = 5.5$, $w = 0.50$
RE	λ in [2.2, 3.4] by = 0.1	$N(1)$ in [27, 34] by = 1	$\lambda = 2.7$, $N(1) = 31$
RL	λ in [6.0, 10.0] by = 0.5	w in [0.10, 0.90] by = 0.05	$\lambda = 10.0$, $w = 0.50$
SFP	λ in [10.0, 14.0] by = 0.5	w in [0.05, 0.90] by = 0.05	$\lambda = 13.0$, $w = 0.75$
stEWA	λ in [1, 9] by = 0.1		$\lambda = 5.8$

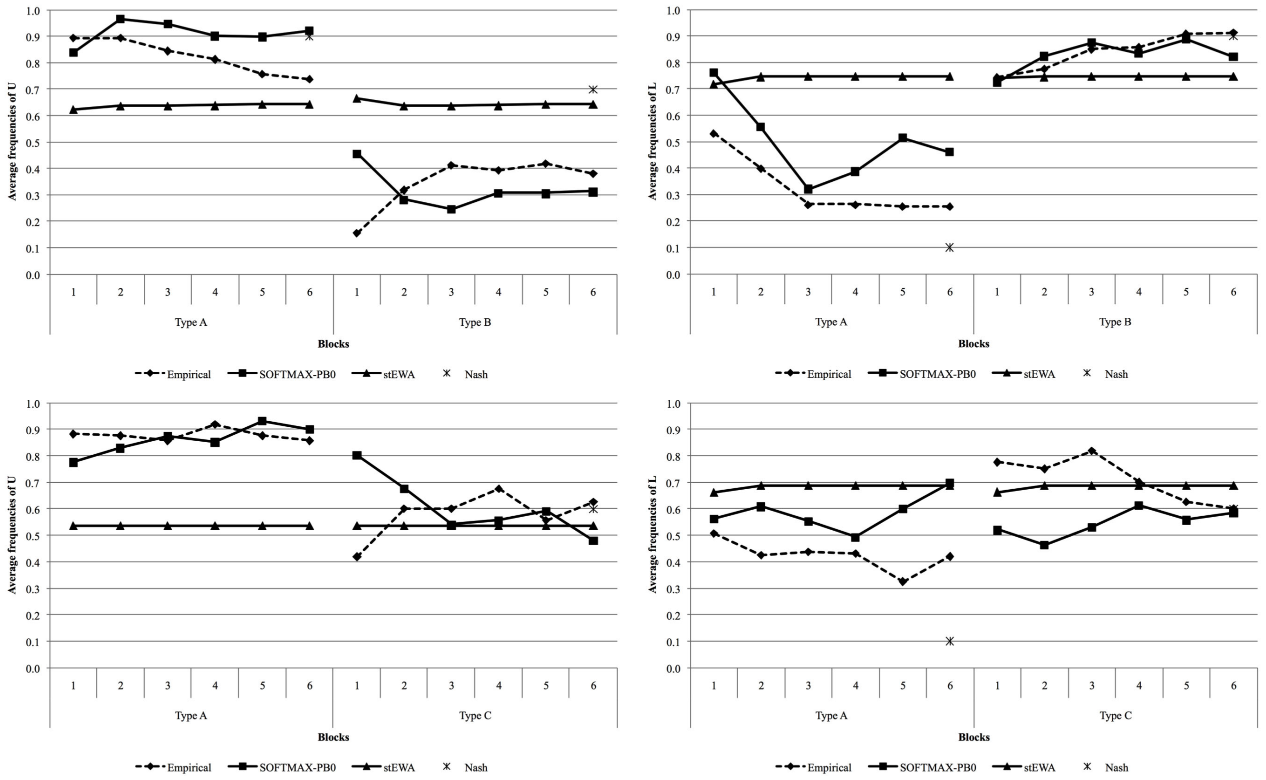

FIGURE 4 | Predicted and observed choice frequencies in Experiment 1 (top panels) and 2 (lower panels).

Table 3 | Predicted and observed choice frequencies in Experiment 1.

	MSD		Type A games						Type B games					
		Blocks	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**
Empirical		*P*(*U*)	0.89	0.89	0.84	0.81	0.76	0.74	0.16	0.32	0.41	0.39	0.42	0.38
		P(*L*)	0.53	0.40	0.26	0.26	0.26	0.26	0.74	0.78	0.85	0.86	0.91	0.91
Nash	0.053	*P*(*U*)	0.90	0.90	0.90	0.90	0.90	0.90	0.70	0.70	0.70	0.70	0.70	0.70
		P(*L*)	0.10	0.10	0.10	0.10	0.10	0.10	0.90	0.90	0.90	0.90	0.90	0.90
NFP	0.081	*P*(*U*)	0.55	0.65	0.57	0.56	0.58	0.51	0.62	0.51	0.63	0.60	0.56	0.67
		P(*L*)	0.59	0.50	0.60	0.54	0.64	0.55	0.64	0.65	0.60	0.70	0.57	0.62
NRL	0.094	*P*(*U*)	0.59	0.40	0.68	0.65	0.64	0.64	0.58	0.43	0.68	0.66	0.64	0.64
		P(*L*)	0.65	0.73	0.54	0.53	0.54	0.57	0.67	0.70	0.53	0.53	0.54	0.55
PB0	0.024	*P*(*U*)	0.78	0.96	0.97	0.96	0.95	0.95	0.49	0.35	0.26	0.28	0.16	0.25
		P(*L*)	0.77	0.68	0.47	0.38	0.35	0.33	0.71	0.80	0.85	0.86	0.93	0.87
REL	0.076	*P*(*U*)	0.50	0.49	0.51	0.51	0.51	0.49	0.51	0.48	0.51	0.50	0.49	0.49
		P(*L*)	0.50	0.50	0.50	0.49	0.50	0.49	0.50	0.50	0.51	0.50	0.49	0.49
RL	0.097	*P*(*U*)	0.60	0.37	0.64	0.63	0.63	0.64	0.57	0.40	0.64	0.63	0.63	0.64
		P(*L*)	0.60	0.70	0.47	0.49	0.51	0.57	0.62	0.67	0.47	0.49	0.51	0.55
SFP	0.094	*P*(*U*)	0.57	0.53	0.67	0.59	0.51	0.50	0.63	0.50	0.48	0.42	0.60	0.60
		P(*L*)	0.54	0.50	0.51	0.32	0.52	0.41	0.58	0.69	0.65	0.79	0.68	0.69
SOFTMAX-PB0	0.018	*P*(*U*)	0.84	0.97	0.95	0.90	0.90	0.92	0.46	0.28	0.25	0.31	0.31	0.31
		P(*L*)	0.76	0.56	0.32	0.39	0.51	0.46	0.72	0.82	0.87	0.83	0.89	0.82
stEWA	0.086	*P*(*U*)	0.62	0.64	0.64	0.64	0.64	0.64	0.67	0.64	0.64	0.64	0.64	0.64
		P(*L*)	0.72	0.75	0.75	0.75	0.75	0.75	0.74	0.75	0.75	0.75	0.75	0.75

The second column from the left reports the MSD scores associated to each model. For parametric models, predicted frequencies have been obtained with the parameter configuration reported in the fourth column of ***Table 2****.*

Table 4 | Predicted and observed choice frequencies in Experiment 2.

	MSD		**Type A games**						**Type C games**					
		Blocks	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**	**4**	**5**	**6**
Empirical		*P*(*U*)	0.88	0.88	0.86	0.92	0.88	0.86	0.42	0.60	0.60	0.68	0.56	0.63
		P(*L*)	0.51	0.43	0.44	0.43	0.33	0.42	0.78	0.75	0.82	0.70	0.63	0.60
Nash	0.034	*P*(*U*)	0.90	0.90	0.90	0.90	0.90	0.90	0.60	0.60	0.60	0.60	0.60	0.60
		P(*L*)	0.10	0.10	0.10	0.10	0.10	0.10	0.60	0.60	0.60	0.60	0.60	0.60
NFP	0.036	*P*(*U*)	0.62	0.69	0.59	0.66	0.61	0.65	0.62	0.55	0.64	0.64	0.64	0.57
		P(*L*)	0.50	0.50	0.57	0.50	0.56	0.51	0.57	0.51	0.46	0.54	0.50	0.52
NRL	0.047	*P*(*U*)	0.72	0.92	0.87	0.58	0.56	0.70	0.76	0.85	0.86	0.61	0.55	0.70
		P(*L*)	0.52	0.49	0.45	0.43	0.49	0.49	0.56	0.57	0.60	0.46	0.49	0.49
PB0	0.029	*P*(*U*)	0.75	0.85	0.89	0.88	0.95	0.93	0.78	0.73	0.56	0.50	0.53	0.46
		P(*L*)	0.57	0.55	0.55	0.51	0.61	0.70	0.54	0.45	0.52	0.56	0.57	0.57
REL	0.055	*P*(*U*)	0.51	0.49	0.51	0.51	0.50	0.51	0.50	0.51	0.52	0.50	0.51	0.51
		P(*L*)	0.50	0.50	0.49	0.50	0.51	0.49	0.50	0.51	0.50	0.50	0.49	0.49
RL	0.053	*P*(*U*)	0.71	0.93	0.88	0.56	0.52	0.68	0.75	0.87	0.87	0.59	0.50	0.68
		P(*L*)	0.53	0.49	0.47	0.41	0.52	0.52	0.55	0.59	0.59	0.44	0.52	0.52
SFP	0.036	*P*(*U*)	0.62	0.71	0.59	0.61	0.60	0.70	0.59	0.50	0.59	0.60	0.63	0.40
		P(*L*)	0.51	0.48	0.55	0.41	0.46	0.50	0.58	0.51	0.47	0.56	0.56	0.60
SOFTMAX-PB0	0.028	*P*(*U*)	0.77	0.83	0.87	0.85	0.93	0.90	0.80	0.68	0.54	0.56	0.59	0.48
		P(*L*)	0.56	0.61	0.55	0.49	0.60	0.70	0.52	0.46	0.53	0.61	0.56	0.58
stEWA	0.058	*P*(*U*)	0.54	0.54	0.54	0.54	0.54	0.54	0.54	0.54	0.54	0.54	0.54	0.54
		P(*L*)	0.61	0.63	0.64	0.64	0.64	0.64	0.61	0.63	0.64	0.64	0.64	0.64

The second column from the left reports the MSD scores associated to each model. For parametric models, predicted frequencies have been obtained with the parameter configuration reported in the fourth column of ***Table 2****.*

CROSS-GAME LEARNING

As reported at the end of Section "The Multigame Experiments," our experimental data do not provide evidence of cross-game learning. In regard to this, simulation results show that there is a partial qualitative parallelism between the (SOFTMAX-)PB0 model's predictions and observed behavior. For example, for the row player, the (SOFTMAX-)PB0 model provides very similar trajectories in the two experiments. However, if we consider column player's predicted behavior, the (SOFTMAX-)PB0 model produces very different trajectories in the two experiments. This might imply that the (SOFTMAX-)PB0's structure is not complex enough to completely avoid spillover effects across games, although this aspect would deserve a more systematic investigation. However, it is not difficult to imagine situations in which learning spillovers do take place and this feature of the (SOFTMAX-)PB0 model would turn out to be advantageous.

CONCLUSION

The present paper presents an experimental design in which subjects faced a sequence of different interactive decision problems, making a step forward in the realism of the situations simulated in the lab. The problems in the sequences were different instances of two 2 × 2 completely mixed games. Thus, at each trial, subjects' task was twofold: recognize the type of the current decision problem, and then act according to this categorization. Our experimental results show that subjects are able to recognize the two different game structures in each sequence and play accordingly to this classification. Moreover, our experimental data do not provide evidence of cross-game learning, as there are no significant differences in the play of type A games in the two experiments.

Our experiments were designed with the precise goal of testing the discrimination capability of the PB0 and SOFTMAX-PB0 neural network models in comparison with that of other established models of learning proposed in the Psychology and Economics literature. Simulation results show that traditional "attraction and stochastic choice rule" learning models are not able to discriminate between the different strategic situations, providing a poor "average" behavior, and are always outperformed by Nash equilibrium. On the contrary, the (SOFTMAX-)PB0 model is able to replicate subjects' conditional behavior, due to the direct dependence of its response on game payoffs, and performs better than standard theory of equilibrium. This latter fact is particularly remarkable; in our experiments, the two classes of games were built based on their Nash equilibrium, so that the classification was induced by the different equilibrium predictions. On the contrary, our neural network models of adaptive learning were able to classify the different game structures without any external and predetermined partition of the game space.

We are well aware of the need for a more systematic and comprehensive analysis of categorization in games. Further experimental research could focus, for example, on sequences with more than two types of games, or on the effects of different degrees of payoff perturbations on learning spillovers.

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APPENDIX

EXPERIMENTAL INSTRUCTIONS

Instructions

You are participating in an experiment on interactive decision-making funded by the Italian Ministry of University and Research (MIUR). This experiment is not aimed at evaluating you neither academically nor personally, and the results will be published under strict anonymity.

You will be paid based on your performance, privately and in cash, according to the rules described below.

During the experiment, you will not be allowed to communicate with the other participants, neither verbally nor in any other way. If you have any problem or questions, raise your hand and a member of the staff will immediately contact you.

The experiment will consist of 120 rounds, and at each round you will face an interactive decision task. Specifically, at each round, you will be randomly matched with another participant and your payoff will depend on both your decision and that of the other participant. The structure of each decision task will be represented as shown in the following figure:

		The other player (column player)	
		Action 1	**Action 2**
YOU (row player)	Action 1	(6, 4)	(4, 7)
	Action 2	(3, 4)	(5, 6)

You have been assigned the role of "row player": therefore, the other player will *always* play the role of "column player."

For each player two actions are available (labeled "Action 1" and "Action 2"). For every possible combination of actions by row and column players, there corresponds a cell in the matrix. In every cell there are two numbers between parentheses: the first number corresponds to YOUR payoff (in experimental currency units), and the second corresponds to the payoff of the other player (again in experimental currency units).

As an example, referring to the matrix reported below, if YOU choose to play "Action 1" and the other player chooses to play "Action 2," then the payoffs will be four for YOU (row player) and seven for the other player (column player).

		The other player (column player)	
		Action 1	**Action 2**
YOU (row player)	Action 1	(6, 4)	(4, 7)
	Action 2	(3, 4)	(5, 6)

Please, remember that the experiment will consist of 120 rounds. At each round, you will be shown a sequence of two screenshots.

The first screenshot will show you the current payoff matrix, and you will be invited to make a decision. In order to make a decision, you must type either "1" or "2" in the box labeled "your decision," and then click on the button "confirm." Once you have clicked the confirmation button, you cannot change your decision. You will have a maximum of 30 s to choose: after those 30 s a blinking red message will appear on the right-up corner of the screen and spur you to make a decision. Delaying your decision will cause the other participants to wait for you.

Once all players have made their decision, the second screenshot will appear on your monitor. In this second screenshot there will be reported the action you chose, the action chosen by the other player, your respective payoffs, and the payoff matrix you saw in the first screenshot.

The second screenshot will be visible on your monitor for 10 s and then another round will start.

This process will be repeated for 120 times. After all rounds have been played, the experiment will be over and the procedure of payment will start. In order to determine your payment, 12 integers between 1 and 120 will be randomly drawn without replacement. In this way, 12 out of the 120 rounds will be randomly selected and you will be paid based on their outcomes. One experimental currency unit is equivalent to 10 eurocents (10 experimental units = 1 euro). Moreover, independently from your performance, you will be paid an additional show-up fee of 5 euro.

Before the beginning of the experiment, you will be asked to fill a questionnaire to verify whether the instructions have been understood. Then the experiment will start.

At the end of the experiment, you will be asked to fill a questionnaire for your payment.

Thank you for your kind cooperation!

REPEATED MEASURES ANOVA

Table A1 | Two-way, repeated measures ANOVA (row players).

	df	Sum Sq	Mean Sq	*F* value	Pr(>*F*)
Experiment	1	0.03	0.03	0.90	0.38
Residuals	6	0.23	0.04		

We tested the model Proportion (U)∼ Experiment ∗Time + Error (between groups). The effect of the experimental condition is not significant.

Table A2 | Two-way, repeated measures ANOVA (Column players).

	df	Sum Sq	Mean Sq	*F* value	Pr(>*F*)
Experiment	1	0.11	0.11	1.07	0.34
Residuals	6	0.61	0.10		

We tested the model Proportion (L)∼ Experiment ∗Time + Error (between groups). The effect of the experimental condition is not significant.

COMPETITOR MODELS AND INVESTIGATED PORTIONS OF PARAMETER SPACES

The REL model (Erev et al., 1999, 2002)

Attractions updating. The propensity of player i to play her k-th pure strategy at period $t+1$ is given by:

$$a_{ij}\left(t+1\right)=\begin{cases}\frac{a_{ij}(t)\cdot\left[N(1)+C_{ij}(t)-1\right]+x}{N(1)+C_{ij}(t)} & \text{if } k=j\\ a_{ij}\left(t\right) & \text{otherwise}\end{cases},$$

Table A3 | Two of the game sequences played in Experiment 1 and 2.

Profile:	Sequence 1 – Experiment 1								Sequence 1 – Experiment 2							
	U, L		***U, R***		***D, L***		***D, R***		***U, L***		***U, R***		***D, L***		***D, R***	
Game 1	190	56	179	67	89	156	190	56	93	27	87	32	43	76	93	27
Game 2	58	199	23	235	47	211	129	129	120	35	113	42	56	99	120	35
Game 3	152	44	143	53	71	125	152	44	166	49	156	58	78	137	166	49
Game 4	74	21	70	26	35	61	74	21	125	37	111	51	111	51	133	29
Game 5	235	69	221	83	110	194	235	69	156	46	147	55	73	128	156	46
Game 6	33	115	13	135	27	121	74	74	186	54	175	65	87	153	186	54
Game 7	135	39	127	47	63	111	135	39	91	26	80	37	80	37	96	21
Game 8	72	244	28	288	57	259	158	158	106	31	93	43	93	43	112	25
Game 9	34	118	13	139	27	125	76	76	163	48	144	67	144	67	173	38
Game 10	42	142	16	168	33	151	92	92	148	43	131	61	131	61	157	34
Game 11	52	180	21	211	42	190	116	116	162	47	142	66	142	66	171	38
Game 12	170	50	160	60	80	140	170	50	170	50	160	60	80	140	170	50
Game 13	51	174	20	205	41	185	113	113	105	30	92	43	92	43	111	24
Game 14	53	183	21	215	43	194	118	118	195	57	184	69	92	161	195	57
Game 15	124	36	117	44	58	102	124	36	212	62	199	74	99	174	212	62
Game 16	62	213	25	250	50	225	137	137	188	55	177	66	88	155	188	55
Game 17	232	68	218	81	109	191	232	68	141	41	124	58	124	58	149	33
Game 18	64	219	25	258	51	232	141	141	74	21	65	30	65	30	78	17
Game 19	218	64	205	77	102	180	218	64	298	87	263	122	263	122	315	70
Game 20	192	56	181	68	90	158	192	56	183	54	172	64	86	151	183	54
Game 21	60	205	24	242	48	217	133	133	173	51	153	71	153	71	183	40
Game 22	100	29	94	35	47	82	100	29	95	27	83	39	83	39	100	22
Game 23	49	166	19	196	39	176	107	107	106	31	100	37	50	87	106	31
Game 24	148	43	139	52	69	122	148	43	97	28	91	34	45	80	97	28
Game 25	79	270	31	318	63	286	175	175	109	32	102	38	51	90	109	32
Game 26	246	72	232	87	116	203	246	72	189	55	178	66	89	155	189	55
Game 27	61	210	24	247	49	222	135	135	148	43	131	61	131	61	157	34
Game 28	142	42	134	50	67	117	142	42	158	46	140	65	140	65	168	37
Game 29	229	67	215	80	107	188	229	67	161	47	142	66	142	66	171	38
Game 30	48	166	19	195	39	175	107	107	153	45	144	54	72	126	153	45
Game 31	54	183	21	216	43	194	118	118	164	48	145	67	145	67	174	38
Game 32	203	59	191	71	95	167	203	59	182	53	171	64	85	150	182	53
Game 33	72	245	28	288	57	259	158	158	109	32	96	45	96	45	116	25
Game 34	52	179	21	210	42	189	116	116	170	50	150	70	150	70	180	40
Game 35	170	50	160	60	80	140	170	50	128	37	120	45	60	105	128	37
Game 36	151	44	142	53	71	124	151	44	166	48	156	58	78	136	166	48
Game 37	171	50	161	60	80	141	171	50	220	64	207	77	103	181	220	64
Game 38	61	209	24	246	49	222	135	135	164	48	145	67	145	67	174	38
Game 39	44	150	17	176	35	158	97	97	72	21	64	29	64	29	77	17
Game 40	146	43	137	51	68	120	146	43	92	27	86	32	43	75	92	27
Game 41	240	70	225	84	112	197	240	70	144	42	135	50	67	118	144	42
Game 42	74	252	29	296	59	267	163	163	240	70	212	99	212	99	255	56
Game 43	240	70	226	85	113	198	240	70	38	11	33	15	33	15	40	8
Game 44	122	35	114	43	57	100	122	35	189	55	167	78	167	78	201	44
Game 45	47	161	18	189	37	170	104	104	145	42	137	51	68	119	145	42

(Continued)

Table A3 | Continued

Profile:	Sequence 1 – Experiment 1								Sequence 1 – Experiment 2							
	U, L		***U, R***		***D, L***		***D, R***		***U, L***		***U, R***		***D, L***		***D, R***	
Game 46	41	140	16	165	33	149	91	91	151	44	133	62	133	62	160	35
Game 47	203	59	191	71	95	167	203	59	190	56	179	67	89	156	190	56
Game 48	52	180	21	211	42	190	116	116	146	43	137	51	68	120	146	43
Game 49	61	209	24	246	49	221	135	135	182	53	160	75	160	75	193	42
Game 50	180	53	169	63	84	148	180	53	216	63	203	76	101	178	216	63
Game 51	198	58	187	70	93	163	198	58	239	70	211	98	211	98	253	56
Game 52	196	57	185	69	92	162	196	57	115	34	109	40	54	95	115	34
Game 53	284	83	268	100	134	234	284	83	142	41	134	50	67	117	142	41
Game 54	44	152	17	179	35	161	98	98	90	26	84	31	42	74	90	26
Game 55	34	117	13	138	27	124	75	75	152	44	134	62	134	62	161	35
Game 56	26	91	10	107	21	97	59	59	156	46	138	64	138	64	165	36
Game 57	57	196	23	231	46	208	127	127	210	61	185	86	185	86	222	49
Game 58	121	35	113	42	56	99	121	35	238	70	210	98	210	98	252	56
Game 59	187	55	176	66	88	154	187	55	180	53	170	63	85	148	180	53
Game 60	54	184	21	217	43	195	119	119	82	24	77	29	38	67	82	24
Game 61	61	209	24	245	49	221	135	135	177	52	156	73	156	73	188	41
Game 62	35	121	14	142	28	128	78	78	141	41	133	49	66	116	141	41
Game 63	21	73	8	87	17	78	47	47	235	69	221	83	110	194	235	69
Game 64	208	61	196	73	98	171	208	61	278	82	246	114	246	114	295	65
Game 65	163	47	153	57	76	134	163	47	235	69	221	83	110	193	235	69
Game 66	42	143	16	168	33	151	92	92	204	60	180	84	180	84	216	48
Game 67	31	107	12	126	25	114	69	69	201	59	178	83	178	83	213	47
Game 68	258	75	243	91	121	212	258	75	159	46	150	56	75	131	159	46
Game 69	163	48	153	57	76	134	163	48	163	48	153	57	76	134	163	48
Game 70	125	37	118	44	59	103	125	37	161	47	142	66	142	66	170	37
Game 71	47	162	19	191	38	171	105	105	177	52	167	62	83	146	177	52
Game 72	147	43	138	52	69	121	147	43	169	49	159	59	79	139	169	49
Game 73	18	64	7	75	15	67	41	41	59	17	52	24	52	24	63	14
Game 74	145	42	136	51	68	119	145	42	185	54	163	76	163	76	196	43
Game 75	38	130	15	153	30	138	84	84	108	31	102	38	51	89	108	31
Game 76	132	39	124	46	62	109	132	39	218	64	205	77	102	180	218	64
Game 77	79	271	31	319	63	287	175	175	168	49	148	69	148	69	178	39
Game 78	118	34	111	41	55	97	118	34	128	37	112	52	112	52	135	30
Game 79	123	36	116	43	58	101	123	36	187	55	165	77	165	77	198	44
Game 80	44	152	17	178	35	161	98	98	225	66	212	79	106	186	225	66
Game 81	54	186	21	219	43	197	120	120	121	35	107	50	107	50	128	28
Game 82	125	36	117	44	58	103	125	36	269	79	237	110	237	110	284	63
Game 83	232	68	218	82	109	191	232	68	237	69	209	97	209	97	251	55
Game 84	61	210	24	247	49	223	136	136	196	57	185	69	92	162	196	57
Game 85	41	140	16	165	33	148	90	90	55	16	52	19	26	45	55	16
Game 86	29	100	11	118	23	106	65	65	202	59	190	71	95	166	202	59
Game 87	155	45	146	54	73	128	155	45	125	36	118	44	59	103	125	36
Game 88	131	38	123	46	61	107	131	38	121	35	114	42	57	100	121	35
Game 89	58	198	23	233	46	210	128	128	187	55	165	77	165	77	198	44
Game 90	315	92	296	111	148	259	315	92	256	75	226	105	226	105	271	60

(Continued)

Table A3 | Continued

Profile:	Sequence 1 – Experiment 1								Sequence 1 – Experiment 2							
	U, L		*U, R*		*D, L*		*D, R*		*U, L*		*U, R*		*D, L*		*D, R*	
Game 91	200	58	188	70	94	165	200	58	228	67	215	80	107	188	228	67
Game 92	220	64	207	77	103	181	220	64	135	39	119	55	119	55	143	31
Game 93	43	146	17	172	34	155	95	95	155	45	146	54	73	128	155	45
Game 94	161	47	152	57	76	133	161	47	116	34	109	40	54	95	116	34
Game 95	186	54	175	65	87	153	186	54	270	79	238	111	238	111	286	63
Game 96	30	104	12	123	24	111	67	67	151	44	142	53	71	125	151	44
Game 97	55	189	22	222	44	200	122	122	148	43	140	52	70	122	148	43
Game 98	218	64	205	77	102	179	218	64	195	57	172	80	172	80	206	45
Game 99	51	174	20	205	41	184	113	113	193	56	170	79	170	79	204	45
Game 100	62	211	24	249	49	224	137	137	196	57	173	80	173	80	208	46
Game 101	202	59	190	71	95	166	202	59	145	42	136	51	68	119	145	42
Game 102	67	230	27	271	54	244	149	149	156	45	137	64	137	64	165	36
Game 103	62	212	25	250	50	225	137	137	169	49	149	69	149	69	179	39
Game 104	195	57	183	68	91	160	195	57	123	36	108	50	108	50	130	28
Game 105	266	78	250	94	125	219	266	78	129	38	121	45	60	106	129	38
Game 106	64	218	25	257	51	231	141	141	123	36	116	43	58	101	123	36
Game 107	103	30	97	36	48	85	103	30	218	64	192	89	192	89	230	51
Game 108	45	154	18	181	36	163	100	100	152	44	134	62	134	62	161	35
Game 109	40	137	16	162	32	145	89	89	228	67	215	80	107	188	228	67
Game 110	111	32	104	39	52	91	111	32	227	66	214	80	107	187	227	66
Game 111	44	150	17	177	35	159	97	97	159	46	150	56	75	131	159	46
Game 112	47	159	18	188	37	169	103	103	189	55	167	78	167	78	201	44
Game 113	29	101	11	119	23	107	65	65	183	54	172	64	86	151	183	54
Game 114	135	39	127	47	63	111	135	39	59	17	56	21	28	49	59	17
Game 115	143	42	135	50	67	118	143	42	208	61	184	85	184	85	221	49
Game 116	44	151	17	178	35	160	98	98	160	47	141	66	141	66	170	37
Game 117	207	61	195	73	97	171	207	61	146	43	129	60	129	60	155	34
Game 118	32	109	12	129	25	116	70	70	204	60	180	84	180	84	216	48
Game 119	195	57	183	68	91	160	195	57	138	40	130	48	65	113	138	40
Game 120	110	32	104	39	52	91	110	32	199	58	188	70	94	164	199	58

where $C_{ij}(t)$ indicates the number of times that strategy j has been chosen in the first t rounds, x is the obtained payoff, and $N(1)$ a parameter of the model determining the weight of the initial attractions.

Stochastic choice rule. Player i's choice probabilities are calculated as follows:

$$p_{ik}(t) = \frac{\exp\left[\frac{\lambda \cdot a_{ik}(t)}{S(t)}\right]}{\sum_j \exp\left[\frac{\lambda \cdot a_{ij}(t)}{S(t)}\right]},$$

where λ is a sensitivity parameter, whereas $S(t)$ gives a measure of payoff variability.

Initial attractions. $S(1)$ is defined as the expected absolute distance between the payoff from random choices and the expected payoff given random choices, denoted as $A(1)$. At period $t > 1$:

$$S(t+1) = \frac{S(t) \cdot [t + m \cdot N(1)] + |A(t) - x|}{t + m \cdot N(1) + 1},$$

where x is the received payoff, m the number of player i's pure strategies, and $A(t + 1)$ is:

$$S(t+1) = \frac{A(t) \cdot [t + m \cdot N(1)] + x}{t + m \cdot N(1) + 1}.$$

Initial attractions are such that $a_{ij}(1) = A(1)$, for all i and j. This model has two free parameters, namely λ and $N(1)$.

The RL model (Erev and Roth, 1998; Erev et al., 2007)

Initial propensities. Initial propensities are set equal to the expected payoff from random choice [denoted by $A(1)$], so that $a_{ij}(1) = A(1)$, for all i and j.

Attractions updating. Propensities are updated as follows:

$$a_{ij}(t+1) = \begin{cases} (1-w)\cdot a_{ij}(t) + w\cdot v_{ik}(x) & \text{if } j=k \\ a_{ij}(t) & \text{otherwise} \end{cases},$$

where $v_{ij}(t)$ is the realized payoff, and w parameter expressing the weight of past experience. The updating rule above implies agents' insensitivity to foregone payoffs.

Stochastic choice rule. Choice probabilities are calculated as follows:

$$p_{ik}(t) = \frac{\exp\left[\lambda\cdot a_{ik}(t)\right]}{\sum_j \exp\left[\lambda\cdot a_{ij}(t)\right]},$$

where λ is a payoff sensitivity parameter.

The NRL model (Erev et al., 2007)

Initial propensities. Initial propensities are set equal to the expected payoff from random choice [denoted by $A(1)$], so that $a_{ij}(1) = A(1)$, for all i and j.

Attractions updating. Propensities are updated according to the following:

$$a_{ij}(t+1) = \begin{cases} (1-w)\cdot a_{ij}(t) + w\cdot v_{ik}(x) & \text{if } j=k \\ a_{ij}(t) & \text{otherwise} \end{cases},$$

where $v_{ij}(t)$ is the realized payoff and w a weight parameter. The updating rule implies agents' insensitivity to foregone payoffs.

Stochastic choice rule. Choice probabilities are defined as:

$$p_{ik}(t) = \frac{\exp\left[\frac{\lambda\cdot a_{ik}(t)}{S(t)}\right]}{\sum_j \exp\left[\frac{\lambda\cdot a_{ij}(t)}{S(t)}\right]},$$

where $S(t)$ gives a measure of payoff variability and λ is payoff sensitivity parameter.

$$S(t+1) = (1-w)\cdot S(t) + w\left|\max\{\text{recent}_1, \text{recent}_2\} - v_{ij}(t)\right|,$$

where recent_i is the most recent experienced payoff from action $i = 1, 2$. At the first period, $\text{recent}_i = A(1)$, and $S(1)$ is set equal to λ. Similarly to the NFP model, payoff sensitivity [the ratio $\lambda/S(t)$] is assumed to decrease with payoff variability.

The NFP model (Erev et al., 2007; Ert and Erev, 2007)

Initial propensities. Initial propensities are set equal to the expected payoff from random choice [denoted by $A(1)$], so that $a_{ij}(1) = A(1)$, for all i and j.

Attractions updating. Propensities are updated according to the following:

$$\mathrm{a}_{ij}(t+1) = (1-w)\cdot a_{ij}(t) + w\cdot v_{ij}(t), \text{ for all } i \text{ and } j,$$

where $v_{ij}(t)$ is the expected payoff in the selected cell and w is a parameter that measures sensitivity to foregone payoffs.

Stochastic choice rule. Choice probabilities are obtained as follows:

$$p_{ik}(t) = \frac{\exp\left[\frac{\lambda\cdot a_{ik}(t)}{S(t)}\right]}{\sum_j \exp\left[\frac{\lambda\cdot a_{ij}(t)}{S(t)}\right]},$$

where $S(t)$ gives a measure of payoff variability, and λ is payoff sensitivity parameter.

$$S(t+1) = (1-w)\cdot S(t) + w\left|\max\{\text{recent}_1, \text{recent}_2\} - v_{ij}(t)\right|,$$

where *recent*$_i$ is the last experienced payoff from action $i = 1, 2$. At the first period, $\text{recent}_i = A(1)$, and $S(1)$ is set equal to λ.

The SFP model (Erev et al., 2007)

Initial propensities. Initial propensities are set equal to the expected payoff from random choice [denoted by $A(1)$], so that $a_{ij}(1) = A(1)$, for all i and j.

Attractions updating. Propensities are updated according to the following:

$$a_{ij}(t+1) = (1-w)\cdot a_{ij}(t) + w\cdot v_{ij}(t), \text{ for all } i \text{ and } j,$$

where $v_{ij}(t)$ is the expected payoff in the selected cell and, w is a parameter that measures sensitivity to foregone payoffs.

Stochastic choice rule. Choice probabilities are calculated as follows:

$$p_{ik}(t) = \frac{\exp\left[\lambda\cdot a_{ik}(t)\right]}{\sum_j \exp\left[\lambda\cdot a_{ij}(t)\right]},$$

where λ is a payoff sensitivity parameter.

The stEWA model (Camerer and Ho, 1999; Ho et al., 2007)

Attractions updating. At time t, player i associates to his j-th pure strategy the attraction $a_{ij}(t)$, given by:

$$a_{ij}(t) = \frac{\phi_i(t)\cdot N(t-1)\cdot a_{ij}(t-1) + \left[\delta_{ij}(t) + \left(1-\delta_{ij}(t)\right)\cdot I\left(s_{ij}, s_i(t)\right)\right]\cdot \pi_i\left(s_{ij}, s_{-i}(t)\right)}{N(t-1)\cdot\phi_i(t) + 1},$$

where $s_i(t)$ and $s_{-i}(t)$ are the strategies played by player i and his opponents, respectively, and $\pi_i(s_{ij}, s_{-i}(t))$ is the ex-post payoff deriving from playing strategy j, and $I(\cdot)$ is the Kronecker function. Functions $\delta_{ij}(t)$ and $\phi_i(t)$ are called, respectively, *attention function* and *change detector function*. The latter depends primarily on the difference between the relative frequencies of chosen strategies in the most recent periods and the relative frequencies calculated on the entire series of actions. The attention function essentially determines the importance that players give to past experience.

Stochastic choice rule. Choice probabilities are calculated as follows:

$$p_{ij}(t+1) = \frac{\exp\left(\lambda\cdot a_{ij}(t)\right)}{\sum_j \exp\left(\lambda\cdot a_{ij}(t)\right)},$$

where λ is the unique free parameter of the model.

Initial attractions. Authors suggest at least four ways of setting initial attractions $a_{ij}(0)$. In our implementation, initial attractions are set equal to the average payoff from random choice, leading to first period uniformly distributed choices.

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Ubiquitous log odds: a common representation of probability and frequency distortion in perception, action, and cognition

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In decision from experience, the source of probability information affects how probability is distorted in the decision task. Understanding how and why probability is distorted is a key issue in understanding the peculiar character of experience-based decision. We consider how probability information is used not just in decision-making but also in a wide variety of cognitive, perceptual, and motor tasks. Very similar patterns of distortion of probability/frequency information have been found in visual frequency estimation, frequency estimation based on memory, signal detection theory, and in the use of probability information in decision-making under risk and uncertainty. We show that distortion of probability in all cases is well captured as linear transformations of the log odds of frequency and/or probability, a model with a slope parameter, and an intercept parameter. We then consider how *task* and *experience* influence these two parameters and the resulting distortion of probability. We review how the probability distortions change in systematic ways with task and report three experiments on frequency distortion where the distortions change systematically in the same task. We found that the slope of frequency distortions decreases with the sample size, which is echoed by findings in decision from experience. We review previous models of the representation of uncertainty and find that none can account for the empirical findings.

Keywords: log odds, subjective probability, probability distortion, frequency estimation, decision-making, uncertainty

Estimates of the frequency of events by human observers are typically distorted. In **Figure 1A** we re-plot data from one of the earliest reports of this phenomenon (Attneave, 1953). Attneave asked participants to estimate the relative frequency of English letters in text and **Figure 1A** is a plot of their frequency estimates versus actual frequency. Although participants had considerable experience with English text, the estimates were markedly distorted, with the relative frequency of rare letters overestimated, that of common letters, underestimated.

Such S-shaped distortions[1] of relative frequency and probability are found in many research areas including decision under risk (for reviews see Gonzalez and Wu, 1999; Luce, 2000), visual perception (Pitz, 1966; Brooke and MacRae, 1977; Varey et al., 1990), memory (Attneave, 1953; Lichtenstein et al., 1978), and movement planning under risk (Wu et al., 2009, 2011).

Figure 1B shows an example from decision under risk (Tversky and Kahneman, 1992). Different participants in the same experiment can have different distortions (Gonzalez and Wu, 1999; Luce, 2000) and a single participant can exhibit different distortion patterns in different tasks (Brooke and MacRae, 1977; Wu et al., 2009) or in different conditions of a single task (Tversky and Kahneman, 1992). We currently do not know what controls probability distortion or why it varies as it does. Gonzalez and Wu (1999) identified this issue as central to research on decision under risk.

We use a two-parameter family of transformations to characterize the distortions of frequency/probability. This family of distortion functions is defined by the implicit equation,

$$\mathrm{Lo}\left(\pi\left(p\right)\right) = \gamma\,\mathrm{Lo}\left(p\right) + (1-\gamma)\,\mathrm{Lo}\left(p_0\right) \tag{1}$$

where p denotes true frequency/probability, $\pi(p)$ denotes the corresponding distorted frequency/probability estimate and,

$$\mathrm{Lo}(p) = \log\frac{p}{1-p} \tag{2}$$

is the log odds (Barnard, 1949) or logit function (Berkson, 1944). The transformation is an S-shaped curve (examples shown in both panels of **Figure 2**).

The two parameters of the family are readily interpretable. The parameter γ in Eq. 1 is the slope of the linear transformation and the remaining parameter p_0 is the "fixed point" of the linear transformation, the value of p which is mapped to itself. To show this, we need only set $p = p_0$ and simplify to get,

$$\mathrm{Lo}\left(\pi\left(p_0\right)\right) = \gamma\,\mathrm{Lo}\left(p_0\right) + (1-\gamma)\,\mathrm{Lo}\left(p_0\right) = \mathrm{Lo}\left(p_0\right). \tag{3}$$

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[1] We use the term "distortion" to cover transformations in probability or relative frequency implicit in tasks involving probability or relative frequency. We use "S-shaped" to refer to both S-shaped and inverted-S-shaped. Precisely, Attneave's (1953) case is an inverted-S-shaped distortion.

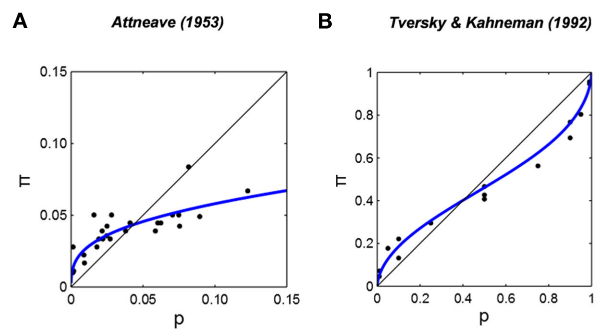

FIGURE 1 | S-shaped distortions of frequency estimates. (A) Estimated relative frequencies of occurrence of English letters in text plotted versus actual relative frequency from Attneave (1953). **(B)** Subjective probability of winning a gamble (decision weight) plotted versus objective probability from Tversky and Kahneman (1992). R^2 denotes the proportion of variance accounted by the fit.

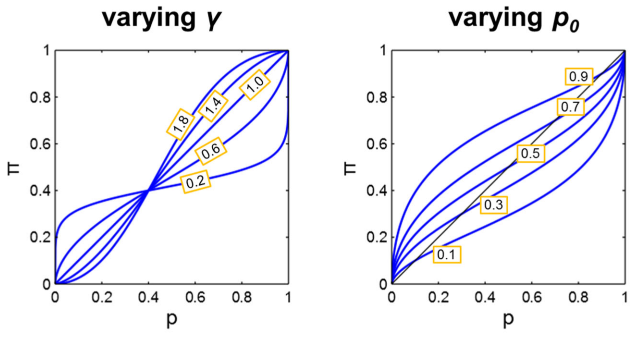

FIGURE 2 | Demonstration of the effects of varying the parameters γ and p_0. The parameter p_0 in the LLO function is the "fixed point" of the transformation, the value of p which is mapped to itself. The parameter γ, is the slope of the linear transformation on log odds scales, and on linear scales, is the slope of the curve at the crossover point p_0. Left: p_0 fixed at 0.4 and γ varied between 0.2 and 1.8. Note that the line at $\gamma = 1$ overlaps with the diagonal line, i.e., no distortion of probability. Right: γ fixed at 0.6 and p_0 varied between 0.1 and 0.9.

Since Lo() is invertible, $\pi(p_0) = p_0$. We refer to p_0 as the *crossover point.*

In **Figure 2** we illustrate more generally how the two parameters affect the shape of the distortion function, plotting π against p on linear scales. The transformation maps 0–0, 1–1, and p_0 to p_0. At point (p_0, p_0), the slope of the curve equals γ. When $\gamma = 1$, $\pi(p) = p$, the curve overlaps with the diagonal line, that is, there is no distortion at all. When $\gamma > 1$ and $0 < p_0 < 1$ we see an S-shaped curve. When $0 < \gamma < 1$ and $0 < p_0 < 1$ we see an inverted-S-shaped curve. When the crossover point p_0 is set to either 0 or 1, the curve is no longer S-shaped but simply concave or convex.

This family of functions, with a slightly different parameterization, has been previously used to model frequency distortion (Pitz, 1966). In decision under risk or uncertainty, it has been used to model probability distortion (Goldstein and Einhorn, 1987; Tversky and Fox, 1995; Gonzalez and Wu, 1999). A one-parameter form without the intercept term was first used by Karmarkar (1979) to explain the Allais paradox (Allais, 1953). Following Gonzalez and Wu (1999) we refer to this family of functions as "LLO."

The LLO function we use is just one family of the functions that can capture the S-shaped transformations. Prelec (1998) proposed another family of functions, which, in most cases, are empirically indistinguishable from the LLO function (Luce, 2000). We return to this point below.

The present paper is organized into four sections. In Section "Ubiquitous Log Odds in Human Judgment and Decision," we demonstrate good fits of the LLO function to frequency/probability data in a wide variety of experimental tasks. We retrieved data for p and π from tables or figures of published papers and re-plotted them on the log odds scales. The parameters (γ and p_0) and goodness-of-fit (R^2) of the LLO fit are shown on each plot. We see dramatic differences in γ and p_0 across tasks and individuals. We are concerned with two questions: how can we explain the LLO transformation? What determines the slope γ and crossover point p_0? We address these two questions in the following sections.

We conducted three experiments to investigate the factors that influence γ and p_0. We report them in Section "What Controls the Slope and the Crossover Point?" The task we used was to estimate the relative frequency of a category of symbols in a visual display. We observed systematic distortions of relative frequency consistent with the LLO function and identified several factors that influence γ and p_0. We discuss the results in the light of recent findings in decision under risk, especially those in the name of "decision from experience" (Hertwig et al., 2004; Hau et al., 2010).

Although no attempts have been made to explain the various S-shaped distortions of frequency/probability in one theory, there are quite a few accounts for the distortion in one specific task or area. In Section "Previous Accounts of Probability Distortion," we review these theories or models and contrast them with the empirical findings summarized in Sections "Ubiquitous Log Odds in Human Judgment and Decision" and "What Controls the Slope and the Crossover Point?"

In Section "LLO as the Human Representation of Uncertainty," we argue that log odds is a fundamental representation of frequency/probability used by the human brain. The LLO transformation in various areas is not coincidence but reflects a common mechanism to deal with uncertainty.

UBIQUITOUS LOG ODDS IN HUMAN JUDGMENT AND DECISION

We now demonstrate that the subjective frequency/probability in a wide variety of tasks can be fitted by the LLO function with two parameters γ and p_0. In the accompanying figures, we plot subjective frequency/probability versus true frequency/probability on log odds scales. On these scales the LLO function is a straight line with slope γ and crossover point p_0. Black dots denote data points. The blue line denotes the LLO fit. When you read the plot, note how different γ and p_0 can be for different tasks or individuals. These plots pose quantitative tests for any theory that is aimed at accounting for probability distortions.

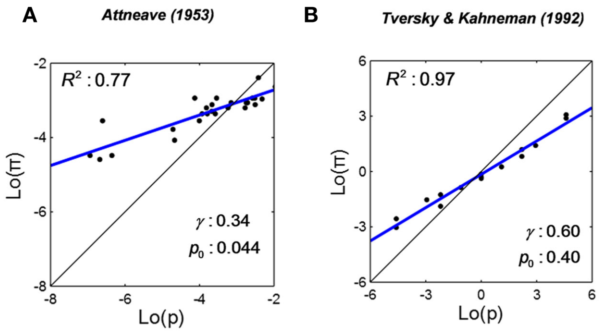

FIGURE 3 | Linear in log odds fits: frequency estimates. The two data sets in **Figures 1A,B** are re-plotted on log odds scales as **(A,B)**, respectively. The blue line is the best-fitting LLO fit. R^2 denotes the proportion of variance accounted by the fit. The S-shaped distortions of frequency/probability on linear scales in **Figures 1A,B** are well captured by the LLO fits.

FREQUENCY ESTIMATION

We introduced Attneave (1953) earlier as an example of overestimation of small relative frequency and underestimation of large relative frequencies. In his experiment, participants estimated the relative frequency of each letter in written English (**Figure 1A**). While a linear fit could only account for 63% of the variance, the LLO function fitted to the same data transformed in **Figure 3A** accounts for 77% of the variance.

Note that the relative frequency of even the most common letter ("e") is less than 0.15. Intriguingly, the estimated crossover point $\hat{p}_0$, 0.044, for Attneave's (1953) data is not far from 1/26 (=0.039), the reciprocal of the number of letters in the alphabet. We return to this point later.

Another impressive example is Lichtenstein et al. (1978). Participants were given a list of 41 possible causes of death in the US, such as flood, homicide, and motor vehicle accidents (MVA). Participants were asked to estimate the frequencies of the causes. The true frequency of one cause was provided to participants as a reference. One group of participants was provided with the frequency of Electrocution (1000) as the reference and a second group, the frequency of MVA (50000). We divided the true frequencies and estimated frequencies (averaged across participants) by the US population (2.05×10^8) to obtain the relative frequencies, p and π. We noticed that although some specific causes were unreasonably overestimated relative to others (e.g., floods were estimated to take more lives than asthma although the latter is nine times more likely), the overestimation or underestimation of relative frequency of all causes as a whole can be satisfactorily accounted by the LLO function. **Figure 4A** shows the LLO fits for the two groups.

In the above two examples, participants' estimation of frequency was based on their memory of events (e.g., reading of a case of lethal events on the newspaper). To show the LLO transformation is not unique to memory nor to sequential presentation of events, our third example is Varey et al. (1990), which demonstrates an LLO transformation in frequency estimation from one visual stimulus. The task was to estimate the relative frequency of either black or white dots among an array of black and white dots. White dots were always less than half of the total number of dots. Eleven levels of relative frequency were used. Participants reported the relative frequency immediately after they saw the visual display. Varey et al. (1990) found considerable distortion of relative frequency. **Figure 4B** shows the LLO fits separately for participants who estimated the relative frequency of white dots and those who estimated black dots.

CONFIDENCE RATING

Confidence rating refers to the task where participants estimate the probability of correctness or success of their own action. For example, in Gigerenzer et al. (1991), participants answered forced-choice questions like "Who was born first? (a) Buddha or (b) Aristotle" and then chose for each question how confident they were to be correct: 50, 51–60, 61–70, 71–80, 81–90, 91–99, or 100% confident. Participants choosing 51–60% were counted to be 55% confident about the answer, and so on. Converted to proportion, the rated confidence is a counterpart of estimated probability, π. The true probability, p, in the confidence rating task is defined as the relative frequency to be correct for a specific choice of confidence level. We re-plot the representative set condition of Gigerenzer et al. (1991) **Figure 6** in **Figure 5A**. The slope γ of the LLO fit is greater than one. That is, an underestimation of small probability (the probability of the harder task) and overestimation of large probability (the probability of the easier task). A qualitative description of this phenomenon is usually referred as a hard–easy effect. This pattern is the reverse of that of the above examples of frequency estimation tasks. We discuss this difference later.

Gigerenzer et al. (1991) is an example of human confidence on a cognitive task. Similar LLO transformations are found in confidence ratings in motor tasks. McGraw et al. (2004) required participants to attempt basketball shots and give a confidence rating before each attempt. Their results are re-plotted as **Figure 5B**.

DECISION UNDER RISK OR UNCERTAINTY

A classical task of decision under risk is to choose between two gambles or between one gamble and one sure payoff. Kahneman and Tversky (1979) proposed that the subjective probability used in decision-making, a.k.a. the decision weight function[2], is a non-linear function of the probability stated in the gamble.

Based on their choices between different gambles and different sure payoffs, participants' decision weight (a counterpart of π) for any specific stated probability (p) can be estimated. In **Figures 1B** and **3B**, we re-plot the decision weight for gains of Tversky and Kahneman (1992) against stated probability on linear scales and log odds scales. The LLO fit explains 97% of the variance, with $\gamma = 0.60$ and $p_0 = 0.40$.

The data presented in most decision-making studies are averaged across participants. As an exception, Gonzalez and Wu (1999) elicited decision weights for each individual participants. We

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[2] We use the generic term "probability distortion" to refer to non-linear transformations of probability in different kinds of task. In decision under risk, the term "probability weight function" or "decision weight function" would coincide with what we refer to as probability distortion.

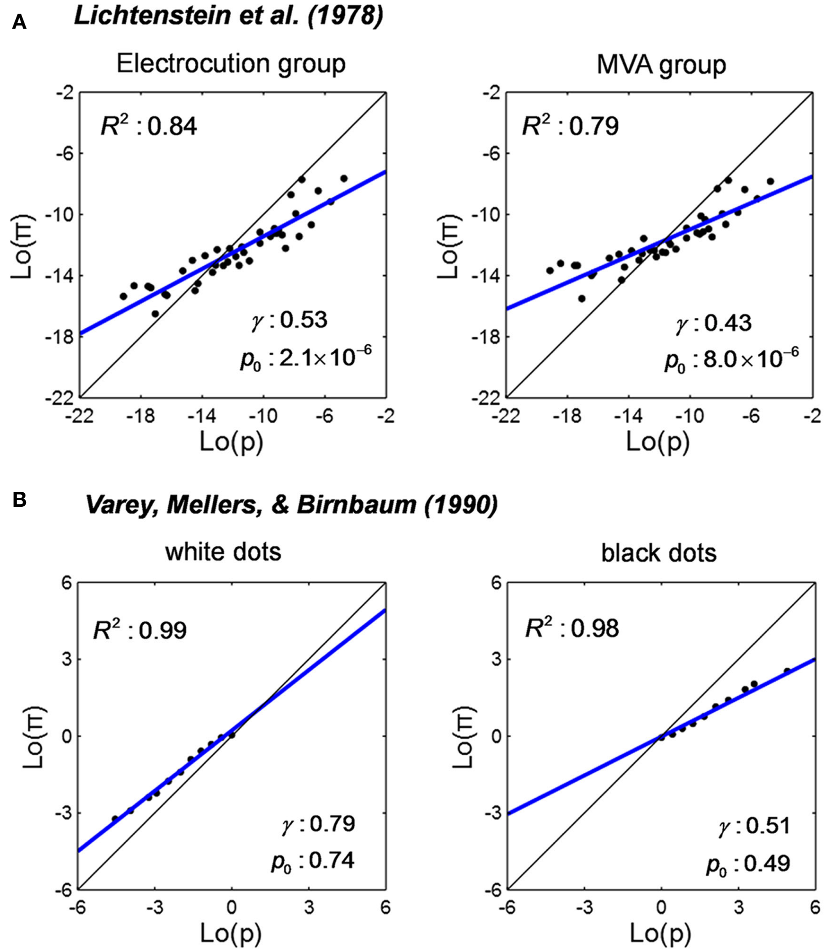

FIGURE 4 | Linear in log odds fits: frequency estimates from memory or perception. Estimated relative frequency is plotted against true relative frequency on log odds scales and fitted by the LLO function. Black dots denote data. The blue line denotes the LLO fit. R^2 denotes the proportion of variance accounted by the fit. **(A)** Estimated frequency of lethal events from Lichtenstein et al. (1978). Participants were asked to estimate the number of occurrences of different causes of death per year in the US. The actual frequency of one cause was provided as a reference for participants to estimate the frequencies of the other causes. The relative estimated and actual frequencies in the plot were the frequencies divided by the then US population. Left: when the frequency of Electrocution (1000) was given as reference. Right: when the frequency of MVA (motor vehicle accident, 50000) was given as reference. **(B)** Estimated frequency of visual stimuli from Varey et al. (1990). The task was to estimate the relative frequency of black or white dots among a visual array of black and white dots. The proportion of black dots was larger than the proportion of white dots. Two groups of participants respectively estimated the relative frequency of white dots (small p) and black dots (large p). Left: the white dots group ($p \le 0.5$) was estimated. Right: the black dots group ($p \ge 0.5$) was estimated.

re-plot their results on log odds scales in **Figure 6A**. Each panel is for one participant. The large individual differences are impressive. The slope γ ranges from 0.17 to 0.82, with a median of 0.30. The crossover point p_0 ranges from 0.26 to 0.98, with a median of 0.46. The only common point across participants seems to be that all the slopes are lesser than one.

When the probabilities of possible consequences of a decision are known, it is decision under risk. When the probabilities are unknown, it is decision under uncertainty. Tversky and Fox (1995) compared probability distortions in decision under risk versus uncertainty. We re-plot their **Figures 7–9** on log odds scales in **Figure 6B**. In the left panel (decision under risk), the probability associated with a gamble, p, was explicitly stated. In the middle and right panels (decision under uncertainty), the probability p was the probability of a specific event in Super Bowl or Dow-Jones and came from participants' own judgments. Similar probability distortions are revealed in the three panels.

SIGNAL DETECTION THEORY

Signal detection theory (Green and Swets, 1966/1974) is an application of statistical decision theory (Blackwell and Girshick, 1954) to deciding whether a signal is present. In each trial, the observer makes the decision based on her perception of the stimulus. There are four possible outcomes: hit (correctly say "yes" at signal presence), miss (incorrectly say "no" at signal presence), false alarm (FA, incorrectly say "yes" at signal absence), and correct rejection (CR, correctly say "no" at signal absence). If each outcome is associated with a specific payoff and the prior probability of a signal

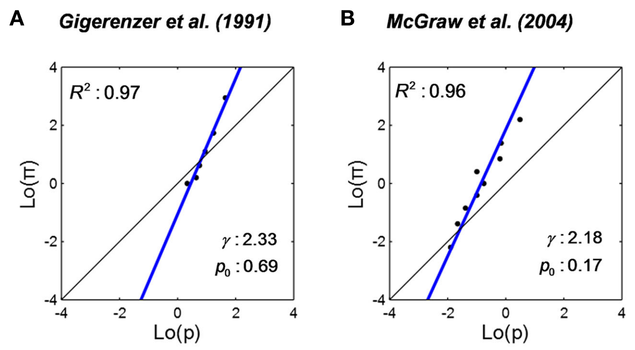

FIGURE 5 | Linear in log odds fits: confidence rating for cognitive and motor responses. Estimated probability of being correct or successful is plotted versus the actual probability on log odds scales and fitted by the LLO function. Black dots denote data. The blue line denotes the LLO fit. R^2 denotes the proportion of variance accounted by the fit. **(A)** Estimated probability of being correct in general-knowledge questions from Gigerenzer et al. (1991). Participants first chose an answer for two alternative general-knowledge questions and then indicated the probability that the answer was correct. **(B)** Estimated probability of success in basketball shooting from McGraw et al. (2004). Participants rated their probability of success before each basketball shot.

is known, there exists an optimal decision criterion, maximizing expected gain. This decision criterion is determined by the prior probability of signal and the specified rewards.

Based on the relative frequencies of hit, miss, FA, and CR, the actual decision criterion used by the observer can be measured and the experiment can compare the subject's decision criterion with the optimal criterion. Systematic deviations from the optimal decision criterion have been found in many studies (Green and Swets, 1966/1974; Healy and Kubovy, 1981). It is as if participants overestimate the prior probability when it is small and underestimate the prior probability when it is large.

In **Figure 7**, we plot Tanner et al.'s (Green and Swets, 1966/1974) data from an auditory signal detection task for one participant on log odds scales. Each data point is obtained from a block of 600 trials with a specific probability of signal present. The straight line is the LLO fit. The slope γ of the probability distortion is 0.36.

In a cognitive signal detection task where participants were asked to classify a number into two categories with different means (Healy and Kubovy, 1981), a similar slope, 0.30, was found.

SUMMARY

At this moment, you are probably intrigued by the same two questions as the authors are: why does probability distortion in so many tasks conform to an LLO transformation? What determines the slope γ and crossover point p_0?

The plots we present here reflect only part of the empirical results we have reviewed. To provide a more complete picture, we clarify the following two points.

First, the slope $\gamma$of the LLO transformation is not determined by the type of task. The slope γ of the same task can be less than one under some conditions and greater than one under others, not to mention the quantitative differences. For example, the typical distortion in relative frequency estimation is an overestimation of small relative frequency and underestimation of large relative frequency, corresponding to $\gamma < 1$. But in a visual task that resembles Varey et al. (1990), Brooke and MacRae (1977) found the reverse distortion pattern: an underestimation of small relative frequencies and overestimation of large relative frequencies.

In decision-making under uncertainty, a reversal is reported in Wu et al. (2009), where the probability of a specific outcome is determined by the variance of participants' own motor errors. The reverse distortion pattern is also implied in a variant of the classical task of decision under risk called "decision from experience" (Hertwig et al., 2004; Ungemach et al., 2009), in which participants acquire the probability of specific outcomes by sampling the environment themselves. We will go into more details in the next section.

Second, the crossover point of the LLO transformation is not determined by the type of task, either. See the difference between Attneave (1953) and Lichtenstein et al. (1978).

Luce (2000, Section 3.4.1–3.4.2) discusses the form of the probability weighting function noting that it is not always S-shaped but can be a simple convex or concave curve. As we noted above, LLO with the crossover point set to 0 or 1 can generate such shapes.

While the LLO family provides good fits to all of the data we have obtained, a two-parameter form of Prelec's model of the probability weighting function (Prelec, 1998; Luce, 2000, Section 3.4) also provides good fits (not reported here). We concentrate on LLO primarily because of the ready interpretability of its parameters and its links to current work on the neural representation of uncertainty discussed below. As Luce (2000) notes, it is difficult to discriminate competing models of the probability weighting function in decision under risk by their fits to data.

WHAT CONTROLS THE SLOPE AND THE CROSSOVER POINT?

What controls the slope γ and crossover point of the LLO transformation in a specific task? In this section we report three new experiments on frequency/probability distortions.

Gonzalez and Wu (1999) identified some of the factors that make decision under risk a less than ideal paradigm for studying distortions in probability. The most evident is that analysis of data requires simultaneous consideration of probability distortion and valuation of outcomes.

The task we consider here is estimation of the relative frequency of one color of dot among a crowd of two or more colors of dots, a task used by Varey et al. (1990) and other earlier researchers (Stevens and Galanter, 1957). The task is illustrated in the two displays on **Figure 8A** which consists of 200 (left) or 600 (right) dots placed at random. In both cases, 20% of the dots are black. The observer viewed briefly presented arrays like these and judged the relative frequency of black dots (alternatively, white dots). We varied the true relative frequencies from trial to trial and fit the estimated relative frequencies against the true relative frequencies with the LLO function to obtain γ and p_0. We compared γ and p_0 across conditions.

EXPERIMENT 1: SLOPE

In earlier studies on frequency estimation, some researchers found that small relative frequencies are overestimated and large relative frequencies underestimated (Stevens and Galanter, 1957; Erlick,

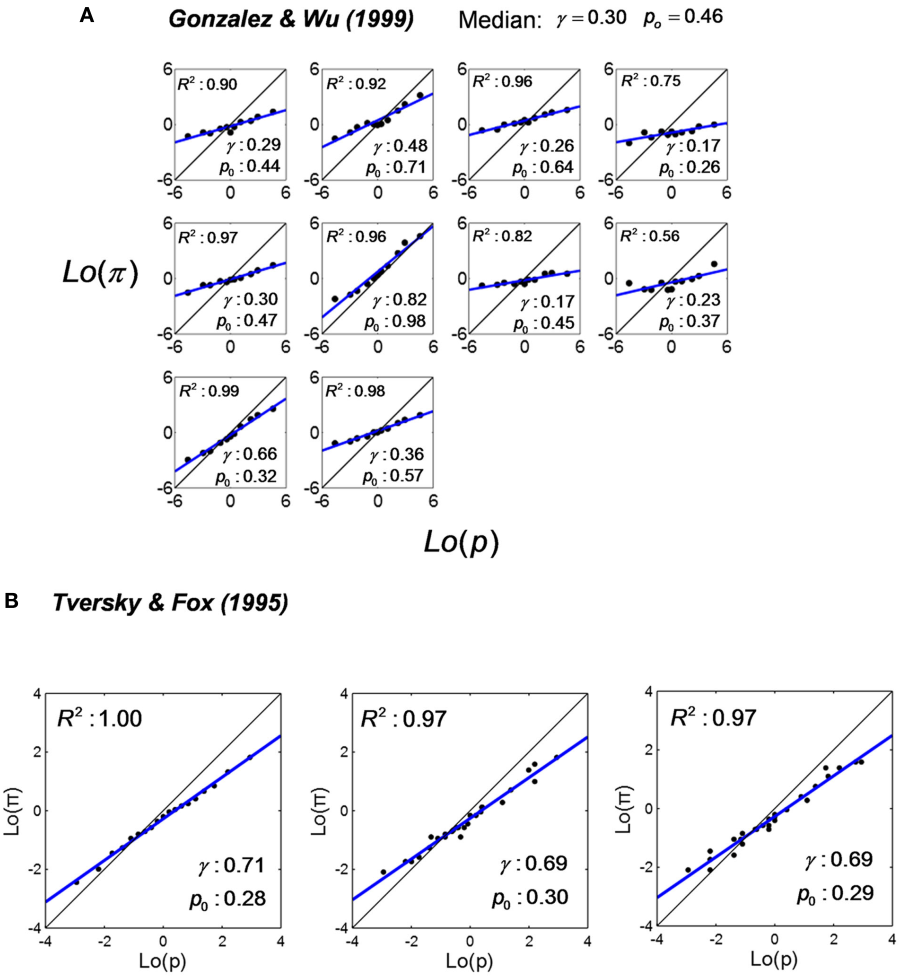

FIGURE 6 | Linear in log odds fits: decision under risk or uncertainty. Decision weight is plotted versus experimenter-stated probability (in decision under risk) or self-judged probability (in decision under uncertainty) and fitted by the LLO function. Black dots denote data. The blue line denotes the LLO fit. R^2 denotes the proportion of variance accounted by the fit. **(A)** Decision weights of individual participants from Gonzalez and Wu (1999). Each panel is for one participant. Participants chose between a two-outcome lottery and a sure reward. The probability of winning the larger reward of the lottery was stated as *p*. Decision weight, the counterpart of subjective probability π, was inferred from each participant's choices based on the Cumulative Prospect Theory. Re-plotted from Figure 6 of Gonzalez and Wu (1999). **(B)** Decision weights from Tversky and Fox (1995). Participants chose between a lottery offering a probability of a reward or otherwise zero and a sure reward. The probability of winning the larger reward of the lottery *p* was stated (left panel), or estimated by participants themselves as the probability of a specific Super Bowl prospect (middle panel), or as the probability of a specific Dow-Jones prospect (right panel). Decision weight, the counterpart of subjective probability π, was inferred from participants' choices based on the Cumulative Prospect Theory Re-plotted respectively from Figures 7–9 of Tversky and Fox (1995).

1964; Varey et al., 1990) while others found no distortion or even the reverse distortion (Shuford, 1961; Pitz, 1966; Brooke and MacRae, 1977). Different researchers obtained contradictory results even when the task they used was almost the same (e.g., Erlick, 1964; Pitz, 1966). Expressed in the language of LLO, it is a controversy about the slope γ. There is clue in the literature that the numerosity of samples might play a role.

In Experiment 1, participants estimated the relative frequency of either black or white dots among black and white dots. Each participant completed eight blocks. We examined the effects of two factors on γ and p_0: *experience* (block number) and *sample numerosity*, *N*, the total number of dots in a trial, which could be 200, 300, 400, 500, or 600.

Methods

Participants. Eleven participants, seven female and four male, participated. Six of them estimated the relative frequency of black dots, the remaining five, white. One additional participant was excluded from the analysis because of marked inaccuracy. All participants gave informed consent and were paid $12/h for their time. The University Committee on activities involving human subjects (UCAIHS) at New York University approved the experiment.

Apparatus and Stimuli. Stimuli were black and white dots displayed on a gray background. They were presented on a SONY GDM-FW900 Trinitron 24″ CRT monitor controlled by a Dell

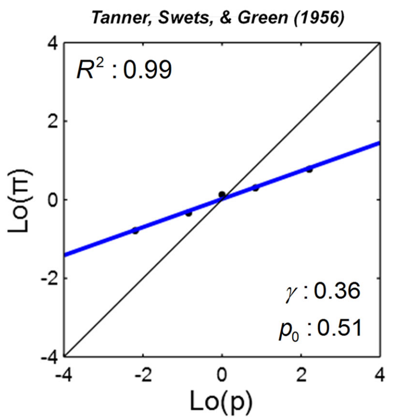

FIGURE 7 | Linear in log odds fit: signal detection theory. Estimated probability of signal present is plotted against the true probability on log odds scales for one participant. Black dots denote data. The blue line denotes the LLO fit. R^2 denotes the proportion of variance accounted by the fit. In Tanner et al. (1956), c.f. Green and Swets (1966/1974), participants were asked to report whether a sound signal was present or absent. Estimated probability was inferred from the participant's decision criterion based on signal detection theory. Data are from Table 4-1 of Green and Swets (1966/1974).

Pentium D Optiplex 745 computer using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). A chinrest was used to help maintain a viewing distance of 40 cm. The dots were randomly scattered uniformly within a 17° × 17° area at the center of screen. Each dot had a nominal diameter of 0.26°.

Procedure. On each trial the display of black and white dots was presented for 1.5 s. Participants were asked to estimate the relative frequency of black or white dots. Their estimates were numbers between 1 and 999 interpreted as their estimate of relative frequency out of as 1000. Each participant made estimates for only one color of dots (black or white) and the color assigned to each participant was randomized. Participants were encouraged to be as accurate as possible. No feedback was given.

Trials were organized into blocks of 100 trials. In each block all of the relative frequencies 0.01, 0.02, . . ., 0.99 except 0.50 occurred once and 0.50 occurred twice. The total number of dots (*numerosity, N*) in a display could be 200, 300, 400, 500, or 600, with each numerosity occurring in 20 trials of each block. Their order within a block was randomized. Each participant completed two sessions of four blocks on two different days, completing a total of two sessions × four blocks × 100 trials = 800 trials. Before the first block of each session there were five trials of practice.

Results

Effect of experience. The experimental blocks were numbered from 1 to 8 in order. We refer to block index as *experience.* We fitted the estimated relative frequency to Eq. 1 separately for each participant and each block and then averaged the coefficients γ and p_0 across the 11 participants.

Starting from slightly less than one, the slope γ became shallower with experience (**Figure 8B**), dropping by 16% from Block 1 (0.91) to Block 8 (0.76). A repeated-measures ANOVA showed a significant effect of experience on γ, $F(7,70) = 5.59$, $p < 0.0001$, $\eta_p^2 = 0.36$. *Post hoc* analyses using Tukey's honestly significant difference criterion at 0.05 significance level indicated that Block 1 had a significantly larger γ than all the other blocks except Block 2.

The crossover point p_0 fluctuated around 1/2 (0.5) in all the blocks, ranging from 0.42 to 0.55. According to a repeated-measures ANOVA, p_0 did not vary significantly across blocks, $F(7,70) = 0.69$, $p = 0.68$, $\eta_p^2 = 0.06$. We concluded that experience affected the slope parameter γ but not the crossover point p_0.

Effect of sample numerosity. We used a similar procedure to analyze the effect of sample numerosity as we used in the effect of experience above.

As sample numerosity increased, the slope γ declined (**Figure 8C**). The γ for displays of 600 dots (0.73) was 18% smaller than that of 200 dots (0.88). A repeated-measures ANOVA showed a significant effect of sample numerosity on γ, $F(4,40) = 17.71$, $p < 0.0001$, $\eta_p^2 = 0.64$. *Post hoc* analyses using Tukey's honestly significant difference criterion at 0.05 significance level indicated significant decline from 200 to all the larger numerosities, and from 300 to 500 and 600.

Moreover, the relationship of γ to N can be best fitted with a function with one-parameter C:

$$\gamma = \log C \big/ \log N \tag{4}$$

A least-squares fit of Eq. 4 captured 99% of the variance of γ (**Figure 8D**). The estimate for the parameter C was 104.

The crossover point p_0 was 0.50, 0.54, 0.51, 0.68, 0.68, respectively for the numerosity of 200, 300, 400, 500, 600. Similar to experience, the effect of sample numerosity failed to reach significance, $F(4,40) = 2.17$, $p = 0.08$, $\eta_p^2 = 0.18$. To conclude, we found that sample numerosity affected the γ but found only a marginally significant effect of sample numerosity on p_0.

EXPERIMENT 2: CROSSOVER POINT

What determines the crossover point p_0? In Experiment 1, p_0 was around 0.5 and little affected by experience or sample numerosity. But recall that the estimation of the relative frequency of the 26 English letters (Attneave, 1953) ends up with $p_0 = 0.044$, very different from 0.5 and coincidently not far from 1/26. Fox and Rottenstreich, 2003; See et al., 2006) suggested that when there are m categories, the crossover point should be $p_0 = 1/\mathrm{m}$.

Experiment 2 was focused on testing the prediction of $p_0 = 1/\mathrm{m}$. The results of Experiment 1 were consistent with the prediction where there were two categories of dots, black and white. In Experiment 2, we set $m = 4$ (participants were asked to estimate the relative frequency of a specific color among four colors of dots).

Methods

Participants. Ten participants, nine female and one male, participated. None had participated in Experiment 1. All reported normal color vision and passed a color counting test. All subjects

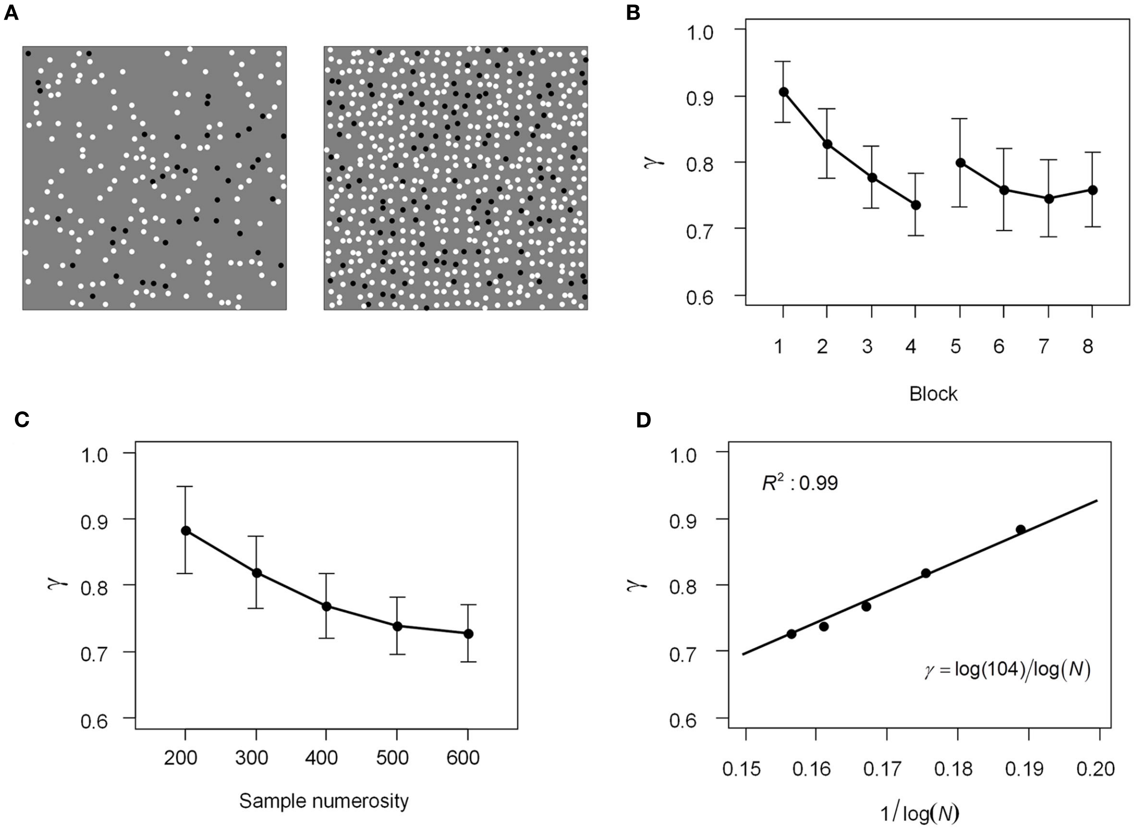

FIGURE 8 | Slope of distortion in relative frequency estimation. The methods and results of Experiment 1. **(A)** Examples of the relative frequency task: what proportion of the dots are black? The left display contains 200 dots in total, the right, 600. In both displays, 20% of the dots are black. **(B)** Effect of experience. The mean slope γ across 11 participants is plotted against block index, one to four for the first session, five to eight for the second session. Later blocks are supposed to be associated with more experience. More experience led to greater distortion (γ further from 1). Error bars denote SEs of the mean. **(C)** Effect of sample numerosity. The slope γ across 11 participants is plotted as a function of sample numerosity *N* (the total number of dots displayed in a trial). Larger sample numerosity resulted in greater distortion (γ further from 1). Error bars denote SEs of the mean. **(D)** The function of the mean γ to sample numerosity, *N*. Dots denote data. Solid line denotes the fit of γ as proportional to the reciprocal of log *N*.

gave informed consent and were paid $12/h for their time. The UCAIHS at New York University approved the experiment.

Apparatus and stimuli. The same as Experiment 1, except that dots could any of four colors, red, green, white, or black.

Procedure. In each trial a display of black, white, red, and green dots were presented for 3 s. Afterward one of the four colors was randomly chosen and participants were asked to estimate the relative frequency of dots of this specific color. As in Experiment 1, participants input a number between 1 and 999 as the numerator of 1000 and no feedback was given.

In any trial, the relative frequencies of the four colors were multinomial-like random distributions centered at (0.1, 0.2, 0.3, 0.4) and each relative frequency was constrained to be no less than 0.02. The order of relative frequencies for different colors was randomized. The total number of dots in a display could be 400, 500, or 600, each numerosity occurring in 32 trials of a block. Each participant completed one session of five blocks. That is, five blocks × 96 trials = 480 trials in total.

Results

Fox and Rottenstreich, 2003; See et al., 2006) suggested the crossover point of $1/m$ but reasoned that it is because people are using a "guessing $1/m$" when they are totally ignorant of the relative frequency. In our case, because the to-be-estimated color was indicated after the display of dots, there is a good chance participants might fail to encode the color in question.

In an attempt to further test the "guessing $1/m$" heuristic, we considered an additional measure. The preferred response of a participant was defined as the value (rounded to the second digit after the decimal point) that the participant used most often in estimation. The actual relative frequencies in all trials were close to uniformly distributed within the range of [0.06, 0.36] and had a much lower density outside. If on some proportion of trials observers defaulted to the fixed prior value 0.25, as suggested by the heuristic, we would expect to find a "spike" in observers' estimates of relative frequency at that value.

For each participant, we left out the trials whose estimated relative frequencies were within preferred response ± 0.04 and fit the remaining trials to Eq. 1 to get the crossover point.

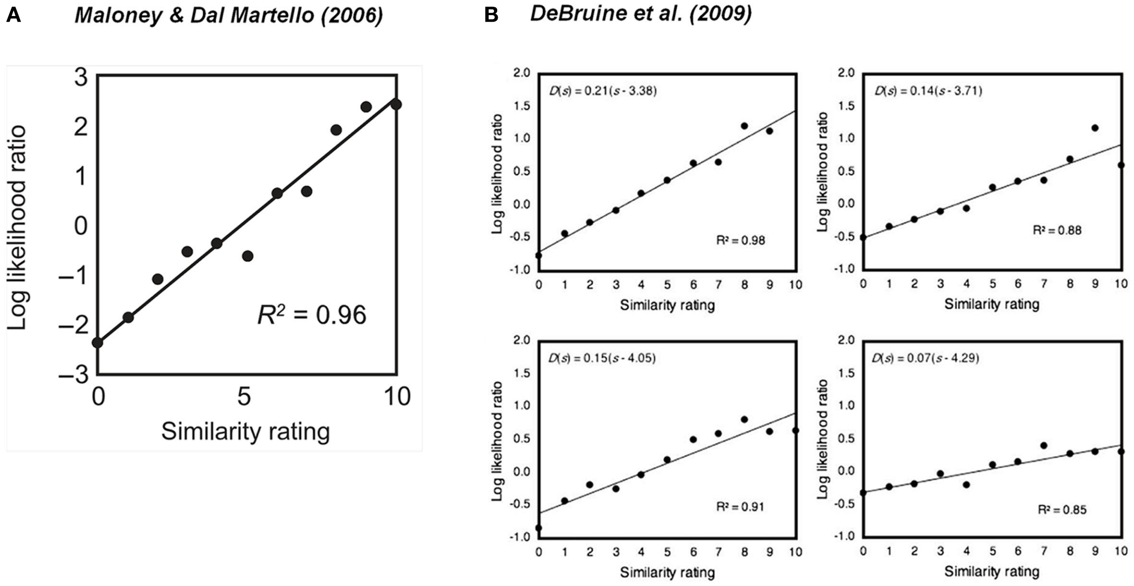

FIGURE 9 | Evidence for log odds as an inherent representation of uncertainty. Participants saw pairs of photos of faces. One group of participants rated the similarity between the two faces in each pair. A second group judged whether the two persons on each pair were related or not. **(A)** The similarity rating of two children faces is a linear transformation of the log odds of the two children being judged to be related. Reproduced from Maloney and Dal Martello (2006). **(B)** The similarity rating of two adult faces is a linear transformation of the log odds of the two adults being judged to be related. Reproduced from DeBruine et al. (2009). R^2 denotes the proportion of variance accounted by the linear fit. See text for implications.

For the 10 participants, we computed the mean and 95% confidence interval separately for crossover point and for preferred response. The crossover point was 0.22 ± 0.07, indistinguishable from 1/4 (0.25). Note that it was much lower than 0.5. If this were the result of the "guessing 1/4" heuristic, we would expect a positive correlation between crossover point and preferred response. However, no significant correlation was detected, Pearson's $r = 0.29$, $p = 0.42$. Moreover, the preferred response was 0.18 ± 0.06, *lower* than 1/4 (0.25).

We concluded that the prediction of $p_0 = 1/\mathrm{m}$, was supported, but it was unlikely to be the result of the heuristics discussed above.

EXPERIMENT 3: SLOPE AND DISCRIMINABILITY

Tversky and Kahneman (1992) and Gonzalez and Wu (1999) conjecture that the shape of the probability weighting function is controlled by the "discriminability" of probabilities. In Experiment 3, we tested the "discriminability hypothesis" for relative visual numerosity judgments. We measured the just noticeable difference (JND) of relative frequency at 0.5 for the five numerosities used in Experiment 1. If the shallower slope for a larger sample numerosity is caused by a lower discriminability (as consistent with the intuition that a larger numerosity makes the estimation task more difficult), we would expect that the JND increases with an increasing numerosity.

Methods

Participants. Ten participants, seven female and three male, participated. None had participated in Experiment 1 or 2. One additional participant was excluded for failing to converge in the adaptive staircase procedures we used to measure JND. All subjects gave informed consent and were paid $12/h for their time. The UCAIHS at New York University approved the experiment.

Apparatus and stimuli. Same as Experiment 1.

Procedure. On each trial two displays of black and white dots were presented, each for 1.5 s, separated by a blank screen of 1 s. Half of the participants judged which display had a higher proportion of black dots, and the other half, white dots.

As in Experiment 1, the total number of dots (*numerosity, N*) in a display could be 200, 300, 400, 500, or 600. The two displays in a trial always had the same numerosity. To avoid participants comparing the number of black or white dots of the two displays rather than judging the proportion, we jittered the actual numerosity of each display randomly within the range of ±4%.

The proportion of black or white dots of one display was fixed at 0.5. The proportion of the other was adjusted by adaptive staircase procedures. For each of the five numerosity conditions, there was one 1-up/2-down staircase of 100 trials, resulting in 500 trials in total Each staircase had multiplicative step sizes of 0.175, 0.1125, 0.0625, 0.05 log unit, respectively for the first, second, third, and the remaining reversals. The five staircases were interleaved. Five practice trials preceded the formal experiment.

Results

The 1-up/2-down staircase procedure converges to the 70.7% JND threshold. For each participant and numerosity condition, we averaged all the trials after the first two reversals to compute the threshold. The mean threshold across participants was 0.57, 0.57, 0.56, 0.56, 0.55, respectively for the numerosity of 200, 300, 400, 500,

600. According to a repeated-measures ANOVA, there was no significant difference in the JND threshold for different numerosities, $F(4,36) = 2.05$, $p = 0.11$, $\eta_p^2 = 0.18$. Differences in discriminability are not responsible for the differences in probability distortion observed in Experiment 1.

DISCUSSION

As demonstrated in Section "Ubiquitous Log Odds in Human Judgment and Decision," the distortions of relative frequency and/or probability in a variety of judgment and decision tasks are closely approximated by a linear transformation of the log odds with two parameters, the slope γ and crossover point p_0 (LLO, the Eq. 1). We investigated in three experiments what determines these two parameters of the distortion of relative visual frequency.

In Experiment 1 we found that slope γ decreased with increasing experience or larger sample numerosity. Intuitively, these trends are surprising, because an accumulation of experience or a larger sample size should reduce "noise" and thus lead to more accurate estimation. Interesting, the slope γ was proportional to the reciprocal of log N. We cannot find a satisfactory explanation for these effects in the literature. However, there is a parallel sample numerosity effect emerging in an area of decision under risk. We explore the implications under the subtitles below.

In both Experiment 1 and 2 we found that the crossover point p_0 agrees with a prediction of $p_0 = 1/\text{m}$. Our results are consistent with the category effect found in Fox and Rottenstreich, 2003; See et al., 2006), but we also showed that this is unlikely to be due to the "guessing $1/m$" heuristic they suggested.

Decisions from experience

Recently, research on decision-making has begun to focus on how the source of probability/frequency information affects probability distortion. This new research area contrasts "decision from experience" (Barron and Erev, 2003; Hertwig et al., 2004; Hadar and Fox, 2009; Ungemach et al., 2009; for review, see Rakow and Newell, 2010), to traditional "decision from description."

What are the implications of our results for decision from experience? A typical finding in decision from experience is an underweighting of small probabilities (e.g., Hertwig et al., 2004), as opposed to the overweighting of small probabilities in decision from description (Luce, 2000). Several authors (Hertwig et al., 2004; Hadar and Fox, 2009) conjectured that this reversal is due to probability estimates based on small samples. Consistent with their conjecture, Hau et al. (2010) found that the magnitude of underweighting of small probabilities decreased as sample size increased. With a very large sample size, Glaser et al. (in press) even obtained the classical pattern of an overweighting of small probabilities.

In the language of LLO, the larger the numerosity (sample size), the shallower the slope of the probability distortion (underweighting small probabilities corresponds to a slope of over one). Note that this effect of sampling size on the probability distortion in decision from experience qualitatively parallels to what is found in Experiment 1. And according to Eq. 4, the empirical fit we found for γ, when $N = C$, there would be no probability distortion. We conjecture that for decision from experience, there exists a specific sample size at which there is no distortion of probability.

There is another hint in the literature that the highly ordered changes in probability distortion that we observe in visual numerosity tasks would also show up in decision-making tasks where probability information is presented as visual numerosity. Denes-Raj and Epstein (1994) asked participants to choose between two bowls filled with jelly beans, one large (100 jelly beans) and one small (10 jelly beans). Participants were explicitly told the proportion of winning jellybeans in both bowls by the experimenters but they still showed a strong preference for the large bowl with 60% of participants choosing a large bowl with 9/100 winning jellybeans over a small bowl with 1/10 winning jellybeans. This outcome suggests an effect of numerosity qualitatively consistent with our results.

We have also shown that we can systematically manipulate the crossover point p_0 in a relative visual numerosity task. The crossover point is often assumed not to vary in decision-making under risk (Tversky and Kahneman, 1992; Tversky and Fox, 1995; Prelec, 1998). Our results lead to the conjecture that, in decisions with relative frequency signaled by displays with $m > 2$ categories, the crossover point will vary systematically.

Confidence ratings

Gigerenzer (Gigerenzer et al., 1991; Gigerenzer, 1994) distinguished between human reasoning about single-event probability and frequency. When asked to rate their confidence about one event, people's default response was to treat the event as a special one that never occurred before and will never occur after, rather than to group the event into a category of events whose frequency is observable.

Probability distortion in confidence rating typically has a slope of $\gamma > 1$ (see **Figure 5**), as reversed to the typical pattern in frequency estimation and decision-making. We conjecture this to be a special case of the sample numerosity effect. That is, $\gamma > 1$ when the sample numerosity is very small. It was as if people treat the to-be-rated action as a single-event and sampled very few previous events to making the confidence rating.

PREVIOUS ACCOUNTS OF PROBABILITY DISTORTION

Why do humans distort frequency/probability in the ways that they do? The subjective probability may deviate from the true probability for many reasons, but no simple reason can explain the S-shaped patterns we have observed.

For example, people might overestimate the frequencies of the events that attract more media exposure (Lichtenstein et al., 1978) or are just more accessible to memory retrieval (Tversky and Kahneman, 1974). But this would not cause a patterned distortion of all events. People might be risk-averse in order to maximize biological utility (Real, 1991), or just be irrationally risk-seeking, but neither risk-averse nor risk-seeking tendencies could explain the coexistence of overestimation and underestimation of probabilities.

The S-shaped distortion has received much attention in quite a few areas. Theories and models have been developed to account for the S-shaped distortion in a specific area, although little efforts have been made to build a unified theory for all the areas. In this section, we briefly describe the representative theories and models, organizing them by area. Their predictions, quantitative or qualitative, on slope, and crossover point of the distortion are compared with the empirical results we summarized in Sections "Ubiquitous Log Odds in Human Judgment and Decision" and "What Controls the Slope and the Crossover Point?"

FREQUENCY ESTIMATION

Power models

Spence's (1990) power model and Hollands and Dyre's (2000) extension of it, the cyclical power model, are intended to explain the S-shaped patterned distortion in proportion judgment. Proportion here refers to the ratio of the magnitude of a smaller stimulus to the magnitude of a larger one on a specific physical scale, such as length, weight, time, and numerosity. Relative frequency can be regarded as the proportion of numerosity.

The basic assumption is Stevens' power law: the perceived magnitude of a physical magnitude, such as the number of black dots in a visual array of different colors of dots, is a power function of the physical magnitude with a specific exponential. We apply the power assumption to the estimation of relative frequency as below. Suppose among N dots, there are n_1 black dots and n_2 other colors of dots. The perceived numerosity would be n_1^α and n_2^α, respectively. Accordingly, the estimated relative frequency of black dots is:

$$\pi = \frac{n_1^\alpha}{n_1^\alpha + n_2^\alpha} \tag{5}$$

Dividing both the numerator and denominator of the right side by N^α, we get the perceived relative frequency as a function of the true relative frequencies:

$$\pi\left(p\right) = \frac{p^\alpha}{p^\alpha + \left(1 - p\right)^\alpha} \tag{6}$$

It is easy to see this is a variant of LLO (substitute Eq. 6 into Eq. 1) which predicts $\gamma = \alpha$ and $p_0 = 0.5$. Thus an S-shaped distortion follows the assumption of Stevens' power law.

Hollands and Dyre (2000) assumed that the slope of the distortion of the proportion of a specific physical magnitude depends on the Stevens exponent of the physical magnitude. For instance, length, area, and volume have different Stevens exponential but the exponent of each of them is fixed. This prediction has some difficulties in applying to the estimation of relative frequency. The experiment we reported in Section "What Controls the Slope and the Crossover Point?" would imply that the exponent is not fixed and changes systematically with the total numerosity.

As to the crossover point, Hollands and Dyre (2000) treated it as an arbitrary value, depending on the reference point available to the observer at the time of judgment. This is not consistent with our observation that $p_0 = 1/m$, where m is the number of categories.

Support theory

Tversky et al.'s support theory (Tversky and Koehler, 1994; Rottenstreich and Tversky, 1997) concerns how humans estimate the probability of specific events. The term *degree of support* refers to the strength of evidence for a hypothesis. The estimated probability of an event is the degree of support for the presence of the event divided by the sum of the degrees of support for the presence and absence of the event.

To explain the inverted-S-shaped distortion of relative frequency, Fox and Rottenstreich, 2003; See et al., 2006) added two assumptions to support theory. First, they assumed that the original degree of support for both the presence and absence of an event are proportional to the corresponding frequencies. Second, before transforming the degree of support into probability, the log odds of degree of support is linearly combined with a prior log odds and the coefficients of the two add up to 1. Following these two assumptions, the resulting estimated probability has the same form as the LLO function.

The value of the prior probability was the crossover point. Fox and Rottenstreich, 2003; See et al., 2006) called this prior the *ignorance prior*, echoing the human tendency for equal division when in total ignorance of probability information. It follows that $p_0 = 1/m$.

However, the weighted addition of a true log odds and a prior log odds would lead to a γ never greater than 1, unless the prior log odds has a negative weight. Therefore, it cannot explain the $\gamma > 1$ cases (Shuford, 1961; Pitz, 1966; Brooke and MacRae, 1977).

The slope of the distortion equals the weight assigned to the true log odds in the combination. Fox and Rottenstreich, 2003; See et al., 2006) suggested that it is positively correlated with the confidence level of the individual who makes the estimation. We consider next model of the distortion of confidence ratings.

CONFIDENCE RATINGS

Calibration model

The calibration model of Smith and Ferrell (1983) attributes the probability distortion in confidence rating to a misperception of one's ability to discriminate between correct and incorrect answers, or between successful and unsuccessful actions.

The calibration model borrows the framework of signal detection theory. Correctness and wrongness of an answer, or success and failure of an action, are considered as two alternative states, i.e., signal present and absent. The observer's confidence, is assumed to be have a constant mapping to the perceived likelihood ratio of the two states. If the discriminability between the two states is perceived to be larger than the true value, small probabilities would be underestimated and large probabilities overestimated, amounting to $\gamma > 1$ (as in **Figure 5**). If the discriminability were underestimated, the reverse pattern would show up.

The calibration model does not necessarily lead to an LLO transformation and does not have any specific predictions for the selection of slope and crossover point.

Stochastic model

Erev et al., 1994; Wallsten et al., 1997) propose that the over- and under-confidence observed in confidence ratings are caused by stochastic error in response. They assume that at a specific time for a specific event, the participant experiences a degree of confidence and translates this experience into an overt report of confidence level by a response rule. The experienced degree of confidence is the log odds of the true judgment plus a random error drawn from a Gaussian distribution. The larger the variance of the random error, the greater the slope of probability distortion deviates from one.

With some specific response rules, the S-shaped distortion can be produced. The predictions of the stochastic model are not intuitive and are illustrated in their computational simulation. One of the predictions states that the underestimation of small probability and overestimation of large probability (i.e., the $\gamma > 1$ pattern) widely identified in confidence rating tasks, a seemingly reverse pattern of regression-to-the-mean, is actually a kind of regression-to-the-mean phenomenon disguised by the way how the true probability is defined. The true probability in the confidence rating task is usually defined as the actual success rate of a specific confidence level. That is, successful and unsuccessful actions are grouped by participants' confidence rating. Wallsten et al. (1997) re-analyzed previous empirical studies and show that if, instead, the true probability of success is computed for each action as an average across participants, the $\gamma > 1$ pattern would be obtained.

However, we doubt this effect of true probability definition can apply to the confidence rating data of McGraw et al. (2004), in which the $\gamma > 1$ pattern holds even when the success rate of basketball shot is grouped by the distance to the basket rather than by participants' confidence rating (not shown in **Figure 5B**).

DECISION UNDER RISK OR UNCERTAINTY

Adaptive probability theory

Martins (2006) proposed an adaptive probability theory model to explain the inverted-S-shaped distortion of probability in decision under risk. The observed distortions, under this account, reflect a misuse of Bayesian reference. In everyday life, people observe the frequency of a specific event in finite samples of events. The observed relative frequency of the event, even in the absence of observation errors, may deviate from the true probability of the event due to the random nature of sampling. To reduce the influence of sampling error, Martin assumes that people introduce a prior sample and combines it with the observed sample by Bayes' rule. The resulting estimated probability would be a linear combination of the observed frequency and the prior probability, determined by three parameters: the size of the imagined sample n, the frequency of the event in the prior sample a, the frequency of the other events in the prior sample b. But Martins (2006) did not characterize what controls these parameters or motivate the choice of prior. Martins (2006) further argued that, in the experimental condition, in front of a lottery, e.g., a probability of 0.1 to win $100, participants treat the probability stated by the experimenter not as a true probability, but as an observed frequency from an imagined sample. The decision weight was the result of the Bayesian inference for the true probability.

The involvement of a prior could explain why the estimated probabilities shrink toward a center. However, for any specific n, instead of a S-shaped transform, the estimated probability would be a linear function of the observed relative frequency, To overcome this difficulty, Martins (2006) assumes that sample size n changes with the observed relative frequency, greater for extreme probabilities and less for smaller probabilities. Thus, the parameter n is actually not one-parameter and is chosen arbitrarily to make theory conform to data.

Another difficulty that adaptive probability theory encounters is the underweighting of small probability observed in studies of decision from experience (e.g., Hertwig et al., 2004). Although Martins (2006) did not suggest the theory could be applied to decisions where the probability information comes from sampling, there is no obvious reason that people would not make the Bayesian inference with a real sample.

FUTURE DIRECTIONS

In this article we examined probability distortion in human judgment and the factors that affect it. An evident direction for future research is to develop process-based models of human use of probability and frequency information. The theories and models we reviewed above are among those that use specific cognitive processes to explain the emergency of the *S*-shaped distortion of probability (other examples include Stewart et al., 2006; Gayer, 2010, to name a few). While a full treatment of them is beyond the scope of the current paper, it would be interesting to see whether any existing process-based models can be modified to account for the changes in slope and crossover point we have summarized.

LLO AS THE HUMAN REPRESENTATION OF UNCERTAINTY

We conjecture that log odds to be a fundamental representation of frequency/probability used by the human brain. Here are a few pieces of evidence.

PEOPLE ARE LESS BIASED WHEN RESPONDING IN LOG ODDS

Phillips and Edwards (1966) asked participants to estimate the probability of one hypothesis to be correct among two alternative hypotheses. There were two types of bags of poker chips, differing in their proportions of red chips and blue chips. Participants were informed the proportions. They were given random draws from one bag and were asked to estimate the probability of each type of bag the sample came from. Participants responded with devices in the format of probability, log probability, or log odds. Phillips and Edwards found that when responding in log odds, participants had the least deviation from the correct answer.

SIMILARITY RATING AMOUNTS TO READING OUT LOG ODDS

Maloney and Dal Martello (2006) provided evidence of the involvement of log odds in kinship perception. Participants saw pairs of photos of children faces. The task of one group of participants was to judge for each pair whether the children were siblings or not. The task of the other group was to rate the similarity between the two faces shown in each pair. The similarity rating of a pair proved to be proportional to the log likelihood ratio of the pair to be and not to be sibling (**Figure 9A**). It is as if participants were reading out the log likelihood ratio when required to rate the similarity of two faces. DeBruine et al. (2009) replicated this result several times using young adult faces (**Figure 9B**).

A PLAUSIBLE NEURAL REPRESENTATION OF LOG ODDS

Gold and Shadlen (2001, 2002) propose a computational mechanism for neurons to represent the likelihood ratio of one hypothesis against another. Consider the binary decision whether hypothesis h_1 or hypothesis h_0 is true. Assume there is a pair of sensory neurons: "neuron" and "antineuron." The firing rate of "neuron," x, is a random variable whose distribution is conditional on whether h_1 or h_0 is true. So does the firing rate of "antineuron," y. The random distribution of y conditional on h_1 is the same as the random distribution of x conditional on h_0, and vice versa. For many families of random distributions, such as Gaussian, Poisson, and exponential distributions, Gold and Shadlen prove that the log likelihood ratio of h_1 to h_0, is a linear function of the firing rate differences between "neuron" and "antineuron," $x - y$. While Gold and Shadlen were concerned with making a decision between two alternatives, their proposed neural circuit can potentially be taken as a representation of uncertainty of frequency in log odds form. That is, the log odds can be encoded by two neurons as the difference between their firing rates.

CONCLUDING REMARKS

Log odds has been independently developed to fit psychophysical data in many areas of perception and cognition over the course of many years. As early as 1884, Peirce and Jastrow (1885) speculated that the degree of confidence participants gave to their sensation difference judgments was proportional to the log odds of their answers being right. Pitz (1966) used the linear log odds function as a convenient way to fit the data of estimated frequency to true frequency.

In the decision area, Karmarkar (1978, 1979) used a one-parameter linear log odds function to model decision weights. Goldstein and Einhorn (1987) modified Karmarkar's equation to include the intercept parameter, which was followed by later researchers (Tversky and Fox, 1995; Gonzalez and Wu, 1999; Kilka and Weber, 2001).

For signal detection theory, it is a common practice to plot the actual decision criterion against the optimal decision criterion in the log scale (Green and Swets, 1966/1974; Healy and Kubovy, 1981). It amounts to our log odds plot and the observed distortion of probability is referred to as "conservatism."

We are seeking for a general explanation for the linear transformation of log odds in these various areas. No matter how different these tasks look like, they are connected by the same evolutionary aim: using possibly imperfect probabilistic information to make decisions that lead to the greatest chance of survival. It is therefore surprising, at first glance, that organisms systematically distort probability. It is doubly surprising that the same pattern of distortion (LLO) is found across a wide variety of tasks.

A full explanation of the phenomena just described would require not only that we account for the form of the distortion but also for the large differences in the values of the two parameters across tasks and individuals and the factors that affect parameter settings. The key question that remains is, then, what determines the slope and crossover point of the linear log odds transformation? We found that in one task we could identify experimental factors that controlled both the slope and crossover point of the LLO transformation of perceived relative numerosity. We conjecture that there are factors in each of the domains we considered that are responsible for the particular choice of probability distortion observed. We need only find out what they are.

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To take risk is to face loss: a tonic pupillometry study

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The construct of risk taking is studied through the prism of the relation between tonic arousal and risk taking behavior. Several theories have proposed that high aroused individuals tend to exhibit risk aversion. We posit that this arousal–behavior association is activated much more strongly in risks with losses, as losses increase arousal and trigger relevant traits associated with the sensitivity to risk. In three studies we examined risk taking in experience-based decision tasks, with either token losses or relative-losses (in the gain domain). In Study 1 we found a negative correlation between pre-task pupil diameter and risk taking in the loss domain but not in the gain domain. In Study 2 we re-analyzed a previous pupillometry dataset involving symmetric mixed gains and losses. We found that the negative correlation in this mixed condition emerged even while the participants did not show loss aversion. This finding was replicated in Study 3. Thus, the effect of losses on arousal provides sufficient conditions for the moderation of the tonic arousal–behavior association. The findings suggest an important role for losses in the psychological and physiological experience of risk.

Keywords: risk, arousal, experience, decision, personality, individual differences, pupil

INTRODUCTION

In this study we examine the relation between losses and the psychophysiological experience of risk. Economic theory traditionally defines risk attitude as the sensitivity to payoff variance (Markowitz, 1952; Pratt, 1964; Sharpe, 1964; and see recent studies which relate brain activity to perceptions of risk as variance, e.g., Preuschoff et al., 2006, 2008). Yet several theories have proposed that losses are somehow implicated in the feeling of risk. For example, Coombs and Lehner (1981, 1984) examined a basic lottery where individuals have an equal chance of winning or losing $10. They found that adding $10 to the loss increased perceived risk more than adding the same amount to the gain, and therefore suggested that the constructs of risk and loss are not independent (see also Duxbury and Summers, 2004). A similar argument is made by attention-based theories of losses, though these theories posit a more general effect of losses on the sensitivity to incentives (Taylor, 1991; Yechiam and Hochman, 2011). Prospect theory (Kahneman and Tversky, 1979) likewise argues that loss aversion is an important component that steers people away from taking risk when it involves gains and losses, because the subjective weight of losses is larger than the subjective weight of equivalent gains. We examine whether losses are an inherent part of what make things risky through the prism of the relation between tonic arousal and risk taking behavior.

Several theories of personality have converged to predict a negative association between tonic arousal and risk taking. In their sensation seeking theory, Zuckerman et al. (1964) suggested that individuals differ in the level of stimulation required for maintaining optimal arousal, with those exhibiting lower levels of arousal requiring more stimulation in order to reach their optimal level of arousal. Since risk taking is one form by which stimulation is achieved, this account suggests that low tonic arousal is associated with a greater tendency to take risk (Farley and Farley, 1972; Ellis, 1987; McNamara and Ballard, 1999)[1]. Eysenck's (1967) personality theory similarly characterized extroverts as low-arousal individuals, who seek stimulating activities in order to heighten their arousal levels (see also Gray, 1987). A somewhat modified account appears in theories of trait anxiety (Zuckerman, 1960; Eysenck, 1992). The literature on trait anxiety suggests that anxious individuals are chronically more aroused on the one hand, and avoid risk and uncertainty on the other (Eysenck, 1992); thus, high arousal is naturally associated with risk aversion. In support of this prediction, studies have shown that high sensation seekers exhibit lower galvanic skin response (GSR) in response to various stimuli (Stelmack et al., 1983; Plouffe and Stelmack, 1986) and even at rest (Gatzke-Kopp et al., 2002).

We propose that the association between tonic arousal and risk taking is moderated by the presence of losses in the experience of risk. It is relatively well known that losses increase arousal and attention (Taylor, 1991; Rozin and Royzman, 2001). Recently, several studies have found that this attentional effect is exhibited independently from loss aversion (Hochman et al., 2010; Hochman and Yechiam, 2011; Yechiam and Telpaz, in press). Based on these findings, we have proposed that this attentional effect of losses provides sufficient conditions for many of the phenomena attributed to losses (Yechiam and Hochman, 2011). For example, it was found that the effect of losses on consistency in risk taking

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[1] In later writings Zuckerman (1990) maintained the idea of a negative association between arousal level and sensation seeking but focused on the complex interaction between the high reactivity of the dopaminergic system and the weakly reactive serotonergic system.

behavior emerges even in the absence of loss aversion (Yechiam and Telpaz, in press). Similarly, the effect of losses on decision performance was demonstrated even in tasks where usually participants exhibit no loss aversion (Bereby-Meyer and Erev, 1998; Erev et al., 1999). These effects are explained by a mere increase in on-task attention in response to losses.

Here, we extend this argument to suggest that because losses increase arousal and attention more than gains, risks with losses are more "rewarding" for individuals with low tonic arousal. Likewise, risks without losses are less intimidating for those having high arousal. Thus, without losses sensation seekers might not consistently relish and replenish on the risky experience, while anxious people might not be consistently intimidated by it. Therefore, the postulated negative correlation between tonic arousal and risk taking is observed more reliably for risky situations that involve losses. It is further predicted that this effect of losses is not contingent on the decision weight asymmetry induced by losses (i.e., loss aversion; Kahneman and Tversky, 1979). We suggest that the arousal and attention produced by losses are sufficient for producing this effect.

To examine these predictions, we used a pupillometric measure of tonic arousal. The pupil diameter (PD) is an immediate and direct index of autonomic activation (Granholm and Steinhauer, 2004). Changes in PD are controlled by two muscles, the dilator and the sphincter, which are differentially influenced by activity in the sympathetic and parasympathetic branches of the autonomic nervous system. The former channel is mediated primarily by norepinephrine and the latter by acetylcholine (Hutchins and Corbett, 1997). Thus, differently from the GSR, the PD is affected by both branches modulating autonomic arousal, and not only the sympathetic branch. Parasympathetic arousal may be relevant to risk taking behavior since this system is known to have a role in defensive reaction and anxiety (Lyonfields et al., 1995). Also, importantly, the tonic PD is unaffected by physical fitness factors (Filipe et al., 2003) and body mass (Piha et al., 1994; Filipe et al., 2003), which is not the case in other autonomic measures, such as heart rate and blood pressure (Gelber et al., 1997; Rennie et al., 2003). Accordingly, individual differences in physical capability affect tonic PD to a lesser extent than in other arousal measures.

There is very little data on whether PD is a reliable measure of tonic arousal. To clarify this issue, we conducted a pilot study where we measured the mean pupil size of 26 student participants for 1 min during rest, on two consecutive days. The test–retest correlation between the different measurements was high ($r = 0.83$, $p < 0.01$), supporting the reliability of the PD as a measure of tonic arousal.

STUDY 1: LOSS VERSUS GAIN DOMAIN RISKS

In this study we focused on two choice problems, one involving risks in the gain domain and the other involving risks in the loss domain. The two choice problems were as follows:

Problem 1. Gain Condition:

S	600 with certainty	
R	0 or 1200 with equal probability	$P(R) = 0.38$

Problem 2. Loss Condition:

S	−600 with certainty	
R	−1200 or 0 with equal probability	$P(R) = 0.52$

In each choice problem, the participants selected among two alternatives with equal expected value, a safe alternative (S) and a riskier alternative (R). These two problems are identical but for fact that in the Loss condition all outcomes are multiplied by -1. $P(R)$ denotes the average proportion of R selections in Study 1.

The two choice problems were administered in an experience-based task. The participants were not provided with a written description of the payoffs but rather had to learn to make choices by sampling the alternatives and receiving feedback. The task began with the participant facing two blank buttons. Upon selecting a button a payoff was sampled from the alternative's payoff distribution and the participant was presented with this payoff as feedback. The use of experience-based tasks is common in studies of physiological arousal and brain activity (e.g., Bechara et al., 1997). Risk taking in these experiential tasks is typically operationalized as the average proportion of selections from the alternative with the higher variance payoffs (see Yechiam and Ert, 2011). Our main prediction was that the association between tonic pupil size (as recorded prior to the task) and risk taking level would be more pronounced in the Loss condition.

METHOD

Participants

The participants were 20 undergraduates from the Technion (12 men and 8 women). Their average age was 23 (ranging from 20 to 27). Upon completing the experiment, they were given a fixed fee which was updated according to the accumulated amount of tokens won (or lost) in the experimental task. The conversion rate of experimental tokens to money was 1 Israeli Shekel per 1000 point earned (participants were informed of the conversion rate beforehand).

Behavioral task

All participants completed two experience-based decision tasks involving 100 trials. Half of them performed the Loss condition task followed by the Gain condition task and the others performed the tasks in reverse order. In both tasks, they were asked to operate a "money machine" with two choice alternatives presented as blank virtual buttons (see Hertwig et al., 2004; Newell and Rakow, 2007; Erev and Haruvy, in press). They were informed simply that their task would be to repeatedly select a button in the machine in order to maximize their total earning. They were further told that they would perform two tasks but their final payoffs would be set according to the accumulating amount from one of the tasks, selected at random. This was done to prevent diversification biases and income effects across different tasks (Cho and Luce, 1995).

Each button selection was followed by the presentation of the obtained payoff and the accumulated payoff, allowing participants to learn to select the choice alternatives from their experience. The outcomes from the two buttons were drawn from the payoff distributions for the Gain and Loss condition problems presented above. The allocation of the Safe and Risky alternative to the left and right buttons was randomized for each participant, but was kept constant throughout an experimental condition (e.g., in the Gain condition). The outcomes were randomly generated on each trial from the alternative's payoff distribution.

PD measure

Pupillometry data was collected using ViewPoint PC 60 EyeFrame system (Arrington Research, Scottsdale, Arizona). The system operates with a single tiny camera and an infrared illuminator mounted on a lightweight frame facing toward the participant's dominant eye, and supported by comfortable head straps. It records pupil data at approximately 30 frames per second (fps). Pre-task pupil size samples were taken just after the calibration and prior to the start of the decision-making task for a period of 30 s. During this time the participants looked at the center of the screen and were asked to wait for the experimenter's instructions. The eye tracking measures continued while the participants performed the decision task.

Like other autonomic measures (e.g., GSR) the tonic pupil size is affected by gender, with some studies demonstrating larger pupil sizes for women than men (Zinn, 1972; Alexandridis, 1985) though this is disputed (see Jones, 1990; Filipe et al., 2003). Accordingly, we examined the possible effect of gender on the pre-task PD, as well as on risk taking levels.

Design and analysis

Our main prediction pertained to the negative association between pre-task arousal and risk taking in the two within-subject task conditions. We therefore used a one-tailed test for this analysis (as explicitly noted in the results below). For all other analyses, we used two-tailed tests.

RESULTS AND DISCUSSION

Risk taking and pupil diameter during the task

The average proportion of risky selections in the Gain condition was 0.38 (SD = 0.23), while in the Loss condition it was 0.52 (SD = 0.24). Thus, the findings show greater risk seeking with losses. This pattern is similar to the reflection effect observed by Kahneman and Tversky's (1979). An examination of the median behavior showed more distinct changes in risk taking as a function of the payoff domain, with 0.4 selections of the risky alternative in the Gain condition and 0.63 in the Loss condition. This difference between conditions was statistically significant [$t(19) = 2.38$, $p = 0.03$]. The correlation between $P(R)$ in the two conditions was $r = 0.37$, $p = 0.10$; as found previously (Ert and Yechiam, 2010; Yechiam and Ert, 2011) participants had a somewhat consistent tendency to prefer certainty to risk or vise versa, though it was not statistically significant.

Although our main predictions pertained to pre-task PD, we also measured the PD during the task. The results are shown in **Figure 1**. Consistent with previous studies (e.g., Satterthwaite et al., 2007; Hochman and Yechiam, 2011) the participants' PD was higher following losses (of -1200 or -600) compared to equivalent gains. The difference between the PD following losses and gains was significant 0.375–0.875 s following the outcome presentation [$t(19) = 2.71$, $p = 0.04$]^2.

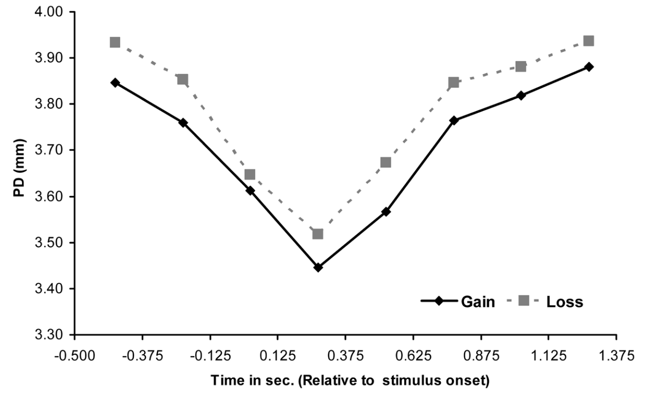

FIGURE 1 | Mean pupil diameter in the Loss and Gain conditions (in mm) across participants and events (of loss: − 600 or − 1200, or of gain: 600 or 1200). Time zero denotes the outcome presentation onset.

To examine the effect of losses on *extended* arousal we also compared the response time in the Gain and Loss conditions (see Porges, 1992). Previously, RTs were found to be longer in loss compared to gain domain tasks (e.g., Yechiam and Telpaz, in press). The average RT in the Loss condition was 0.61 s while in the Gain condition it was 0.46 s. The difference was significant [$t(19) = 2.52$, $p = 0.02$]. Thus, losses seemed to increase both immediate arousal and processing time beyond gains.

Pre-task pupil diameter

Scatter plots of risk taking proportions by pre-task PD appear in **Figure 2**. As clearly indicated in the figure, individuals with high pre-task PD tended to make fewer risky selections in the Loss condition, but this was much less evident in the Gain condition. In the Loss condition the correlation between pre-task PD and $P(R)$ was $r = -0.44$, $p = 0.026$ (one tailed). In the gain condition the correlation was only $r = -0.25$, $p = 0.15$ (one tailed).

To verify that this result is not due to women participants having larger PDs (as found previously; e.g., Alexandridis, 1985) and also taking less risk, we examined gender differences in the studied variables. The pre-task PD in women (Mean = 3.62 mm, SD = 0.40) was actually smaller than that of the men (Mean = 4.26 mm, SD = 0.40), but the difference did not reach significance $t(18) = 1.69$, $p = 0.11$. Additionally, there were no significant gender differences in the proportion of risky selections in the Loss and Gain conditions. We can thus rule out gender as leading to major differences in the studied variables.

The results are consistent with our prediction that tonic arousal – risk taking associations should be stronger in the Loss condition compared to the Gain condition. The direction of the effect is in turn consistent with the prediction of the

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[2] Note that as shown in **Figure 1** there was a (non-significant) difference in PD before obtaining losses and gains. This is to be expected given the fact that the participants knew they were about to face losses.

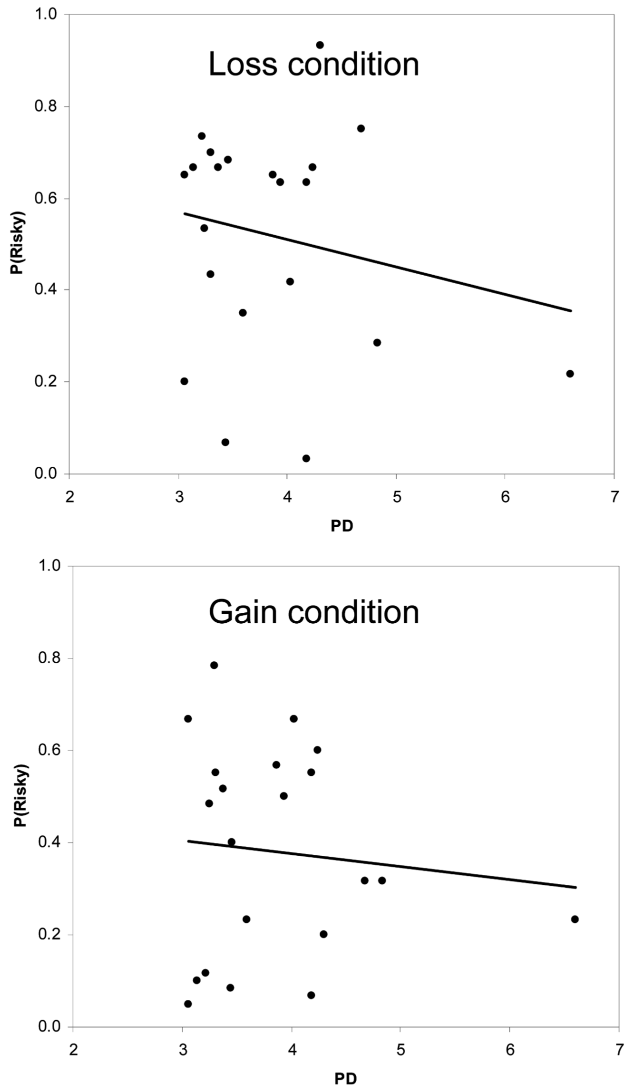

FIGURE 2 | Scatter plot and regression lines of the proportion of risky selections across 100 trials by pre-task PD in Study 1. Top: Loss condition. Bottom: Gain condition.

aforementioned personality theories: those showing low-arousal tended to take more risk. We have argued that this phenomenon is due to the attentional effects of losses. However, an alternative explanation is that it is due to loss aversion. If one assumes that (a) losses have greater subjective weight than gains, and (b) people behave more reliably in tasks that are of importance to them (Judd and Krosnick, 1989; Chaiken and Maheswaran, 1994; Kanfer et al., 1994), then it stands to reason that individuals would exhibit more reliable risk taking behavior in a loss-domain task. Loss aversion can therefore increase the association between tonic arousal and risk taking behavior. In our second study we therefore examined whether these effect of losses can be observed simultaneously with no loss aversion, namely with the participants showing no behavioral tendency to give greater weight to losses over gains.

STUDY 2: MIXED GAINS AND LOSSES RISK

In experience-based tasks it was previously found that people do not display loss aversion when the risk involves symmetric gains and losses (see Erev et al., 2008; Silberberg et al., 2008; Hochman and Yechiam, 2011; Yechiam and Telpaz, in press). While the generality of this finding into other situations is a matter or controversy (Rick, 2011), the fact that in the experiential setting there is no loss aversion provides a testing ground for whether different effects of losses may emerge even in the absence of a decision weight asymmetry of the sort proposed by Kahneman and Tversky (1979).

The study focused on the following two choice problems:

Problem 3. Gain Condition:

S	2 or 4 with equal probability	
R	1 or 5 with equal probability	$P(R) = 0.49$

Problem 4. Mixed Condition:

S	-1 or 1 with equal probability	
R	-2 or 2 with equal probability	$P(R) = 0.54$

The term Mixed refers to a choice problem producing both gains and losses. In the studied Mixed condition the risky alternative produced gains and losses of the same probability and magnitude. Under loss aversion people should avoid risk in this situation. An existing pupillometry dataset (Hochman and Yechiam, 2011; Study 1) in which these two problems were administered was used. Previous analyses of the data focused only on phasic (i.e., on-task) arousal (Hochman and Yechiam, 2011). We tested whether the association between tonic pupil size and risk taking would be more pronounced in risks with losses, even while the participants were loss neutral.

METHOD

Participants

Twenty-five undergraduates from the Technion (13 men and 12 women) participated in the study. The participants were given a fixed fee and were also compensated according to the number of points earned in the experimental task, at a rate of 0.1 Israeli Shekel per 1 point earned (they were informed of the conversion rate beforehand).

Behavioral task

All participants completed two experience-based decision tasks involving 60 trials. Approximately half of them performed the Mixed condition task followed by the Gain condition task and the other half performed the tasks in reverse order. The instructions were as in Study 1. The tasks involved operating a “money machine” with two choice alternatives. The payoffs were drawn from the outcomes of the Gain and Mixed conditions above. In order to make the incentive structure less obvious, a constant of 0.1–0.5 (in 0.1 intervals) was randomly added or subtracted from the sampled payoff in every trial. Additionally, to eliminate possible surprise effects that would be non-symmetric with respect to gains and losses, payoffs were delivered in a deterministic fashion. Each choice alternative initially produced either a gain/relative-gain or a loss/relative-loss, which was switched to a payoff from the opposite domain on each selection. About half of the participants were presented with a gain/relative-gain in the first selection, while for the other participants this order was reversed.

PD measure

Pre-task pupil size was examined as in Study 1. Due to a technical problem we did not get pre-task results from two of the participants. Thus, all correlations with tonic PD are based on a sample size of 23.

RESULTS AND DISCUSSION

As reported in Hochman and Yechiam (2011), the average proportion of risky selections in the Mixed condition was not significantly different from 0.5 (Mean = 0.54, SD = 0.15). Clearly, the participants did not avoid the alternative incurring larger losses. Additionally, the average proportion of risky selections in the Mixed condition and in the Gain condition (Mean = 0.49, SD = 0.23) was quite similar, $t(24) = 1.07$, $p = 0.30$. Thus, the participants exhibited no loss aversion in this experience-based choice task.

Differently from Study 1, the correlation between risky choices in the two task conditions was close to zero ($r = -0.02$, $p = 0.91$). This is consistent with previous results showing that consistency across domains is impaired when there is no sure thing alternative (Yechiam and Ert, 2011).

Scatter plots of risk taking proportions by pre-task PD appear in **Figure 3**. As illustrated in the figure, individuals with high pre-task PD tended to take less risk in the Mixed condition. In the Gain condition a surprising reverse trend was observed: those with higher pre-task PD actually took more risk. Correlation analyses showed that in the Mixed condition the pre-task PD was negatively correlated with the proportion of risky choices, $r = -0.37$, $p = 0.04$ (one tailed), while in the Gain condition, pre-task PD was *positively* correlated with risky choices, $r = 0.47$, $p = 0.02$.

We examined whether the positive effect found in the Gain condition is a product of boredom at the end of the task. Previous findings suggest that in monotonous tasks that have little cognitive requirement, individuals with moderate levels of arousal seek to maintain their arousal (Fischer et al., 2008). One way to increase arousal may be to explore both alternatives and thus to also take risk (see Iglesias-Parro et al., 2001). Possibly, this situation was more likely to develop in the Gain condition because losses are more arousing. Also, recall that the task in Study 2 was more monotonic than in Study 1 because of the gain–loss–gain–loss pattern. In the first half of the task, the negative correlation for the Mixed condition remained about the same, $r = -0.41$, $p = 0.05$. By contrast, the positive correlation in the Gain task was found to be non-significant, $r = 0.30$, $p = 0.17$. Thus, consistent with the boredom-based explanation, the positive correlation for the Gain condition emerged only in the second half of the task (Gain: $r = 43$, $p = 0.04$; Mixed: $r = -0.40$, $p = 0.06$). For both halves of the task, the negative correlation predicted by personality theories was only apparent when the risk involved losses, and this was found simultaneously with no loss aversion.

We also examined gender differences in the studied variables. The pre-task PD in women (Mean = 4.59 mm, SD = 1.59) was larger than that of the men (Mean = 3.92 mm, SD = 0.85) but not in a significant manner, $t(21) = 1.24$, $p = 0.22$. Additionally, there were no significant gender differences in the proportion of risky selections in the Mixed and Gain conditions. In fact, when aggregating the results across the two studies, the PD for both genders was quite similar (mean difference of 0.09 mm).

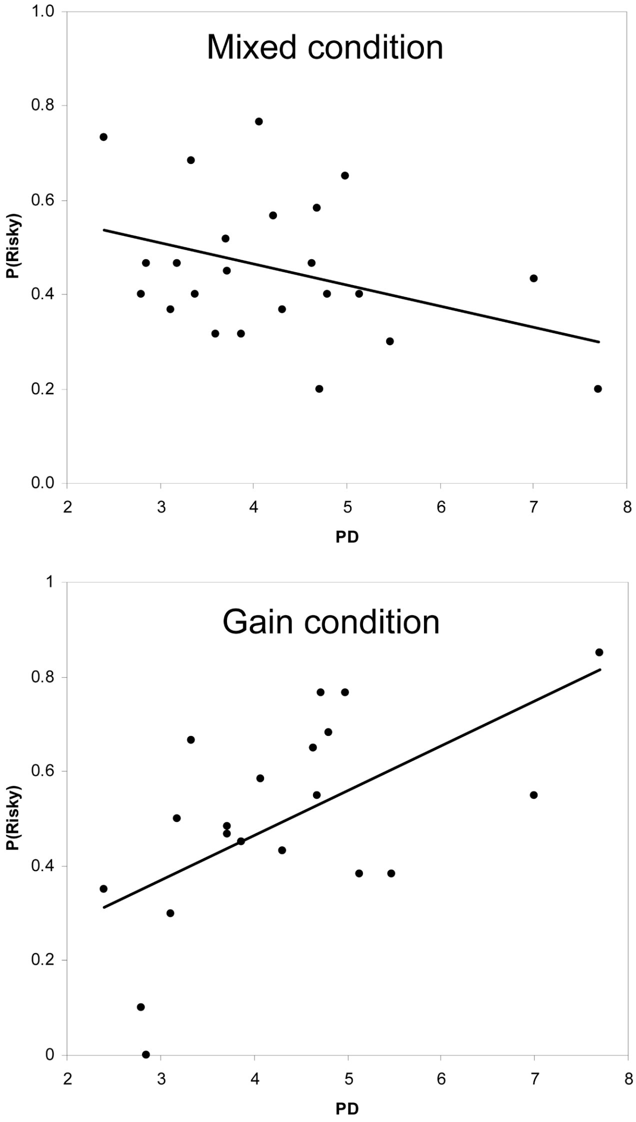

FIGURE 3 | Scatter plot and regression lines of the proportion of risky selections across trials by pre-task PD in Study 2. Top: Mixed condition. Bottom: Gain condition.

STUDY 3: REPLICATION USING MIXED GAINS AND LOSSES

To examine the interpretation that the positive correlation in the Gain condition was a product of low task demands, we replicated Study 2 with time pressure and a secondary requirement to perform an arithmetic task between choice trials. We expected to replicate the negative correlation observed in Study 2 for risky losses, but not the positive correlation observed for risky gains.

METHOD

Participants

Forty undergraduate students from the Technion (20 women and 20 men) participated in the experiment. Their average age was 24 (ranging from 19 to 28). Participants were given a fixed fee and were also compensated according to the number of points earned in the experimental task, with a conversion rate of 0.1 Israeli Shekel per 1 point earned.

Behavioral task

The decision task consisted of two buttons and two counters, as in Study 2. Participants performed 30 trials in each of the two experimental conditions (Mixed and Gain). The order of the Mixed and Gain task conditions was counter-balanced so that half of the participants performed each task first. The choice outcomes were as in Study 2. The participants received no prior information concerning the choice outcomes, and learned to make choices from their experience. An arithmetic task was administered along with the decision task, as follows.

In each trial participants made their decision and afterward performed an arithmetic task. They were required to accomplish both tasks in 7.5 s, and failure to do so resulted in a loss of three points. The arithmetic problems were presented in the upper section of the screen. The answers were typed using a virtual keypad. The task involved adding or multiplying a single-digit number with a two-digit number. The exact numbers were randomly generated in each trial (the single-digit number was chosen from a uniform distribution ranging from 2 to 6, and the two-digit number was chosen from a uniform distribution ranging from 10 to 17). If participants answered the arithmetic question incorrectly they received an "incorrect answer" feedback but could give other answers within the 7.5 s time window. The task included a time meter which noted the time left until the end of each trial. When participants answered the arithmetic problem correctly the screen elements of that task were darkened. Each participant was randomly allocated to receive either addition or multiplication questions. As the allocation of the participants into the addition or multiplication questions had no effect on the studied correlations, we pooled across this manipulation.

PD measure

Pre-task pupil size was examined as in Study 1. Due to a technical problem we did not get pre-task results from one of the participants, leaving a total of 39 participants.

RESULTS AND DISCUSSION

We first examined the difference between risk taking patterns in the Mixed and Gain conditions. As in Study 2, the proportion of risky selections in the two task conditions was quite similar, 0.46 (SD = 0.19) in the Mixed condition and 0.46 in the Gain condition (SD = 0.25), $t(37) = 0.02$, $p = 0.98$. Scatter plots of risk taking proportions by pre-task arousal levels (in PD) appear in **Figure 4**. In the Mixed condition the participants' pre-task PD was negatively correlated with the proportion of risky selections ($r = -0.34$, $p = 0.02$, one tailed). However, in the Gain condition there was no significant correlation between the two measures ($r = 0.07$, $p = 0.33$, one tailed). Thus, the positive association in the Gain condition found in Studies 1 and 2 did not emerge in a statistically significant manner in Study 3[3].

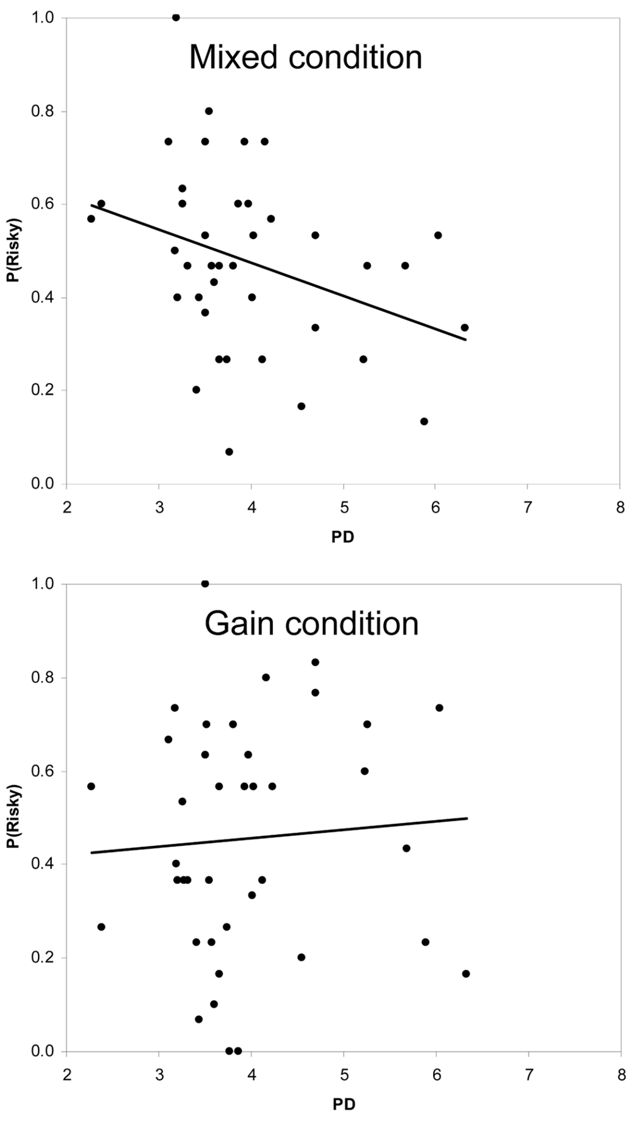

FIGURE 4 | Scatter plot and regression lines of the proportion of risky selections across trials by pre-task PD in Study 3. Top: Mixed condition. Bottom: Gain condition.

To sum up, in this study where the decision task was performed with moderate time pressure and with an additional cognitive requirement, we replicated the negative correlation between tonic PD and risk taking with losses. However, as opposed to Study 2, there was no positive association between arousal and risk taking in the gain domain. The findings are therefore consistent with the prediction of the attentional model of losses, which implies that

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[3] An examination of possible gender effects revealed that the pupil size of women (Mean = 3.83 mm., SD = 0.83) was not significantly different from that of the men [Mean = 4.02 mm., SD = 1.08], $t(37) = 0.59$, $p = 0.56$. There were also no significant gender differences in risk taking both in the Mixed and Gain conditions.

losses do not reverse the association between tonic PD and risk taking but rather, accentuate it.

GENERAL DISCUSSION

Several theories of personality and traits predict a negative association between arousal level and risk taking (e.g., Zuckerman et al., 1964; Gray, 1987; Zuckerman, 1990; Eysenck, 1992). Though the exact mechanisms that lead to this negative correlation are different in each theory, their general idea is similar: they suggest that people exhibiting lower levels of internal arousal seek stimulation by taking risk. Here, we hypothesized that the negative association between tonic arousal and risk taking would be enhanced in risks with losses, due to the simple fact that losses increase arousal and on-task attention (Yechiam and Hochman, 2011).

The results of our three pupillometry studies supported the predicted moderating effect of losses. In Study 1 we have shown that in a loss-domain task there was a significant negative correlation between pre-task PD and the proportion of risky selections. In an equivalent gain domain task this negative correlation was much lower and not statistically significant. In Study 2 we examined whether these effects of losses on arousal–behavior relationship are due to loss aversion. For this purpose we studied a previous pupillometry database (Hochman and Yechiam, 2011) which included a choice task with symmetric gains and losses, and an equivalent task in the gain domain. While the participants showed no loss aversion on average, a negative correlation between pre-task arousal and risk taking was only observed in the condition with losses.

Somewhat surprisingly, in this second study we found that across all trials there was a positive correlation between pre-task arousal and risk taking in the gain domain. We argued, however, this positive association did not represent a general pattern. This was supported by a block by block analysis, which showed that the positive association only appeared in the second half of the task. We explicitly examined this assertion in Study 3, where we showed that administering the decision task in a more demanding environment (involving time pressure and a secondary task) eliminated the positive correlation in the gain domain. In this study, as in Study 1, in the absence of losses there was a zero correlation between arousal and risk taking, and the addition of losses produced a negative correlation between these measures.

We proposed that the negative correlation between tonic arousal and risk taking in the conditions with losses reflects the effect of losses on arousal and attention. This explanation was supported by our findings that losses led to significantly elevated pupil size and response time compared to equivalent gains during the decision task. Our results are consistent with past findings on the effect of losses on arousal (e.g., Hochman and Yechiam, 2011).

Taken together, the current results suggest that losses are an inherent part of what makes things risky. Indeed, the dictionary definition of risk equates it with loss. For example, In Merriam Webster (2011) risk's first definition is "possibility of loss or injury (peril)." Similarly, the Oxford English Dictionary (OED, 1982) defines risk as "hazard, danger, exposure to mischance, or peril." Indeed, while there is some disagreement about the ancient origin of the word, it is considered to have come to the English language from the French word *risque*, and in this language it was adapted from Italian *risco*, which stands for "navigating among dangerous rocks" (Timmerman, 1986). In Hebrew the word "*sikun*" which denotes risk is derived from *sakana*, or danger. The economic definition of risk, which is based on the variance of the outcomes and is almost universally accepted as a way of operationally defining risk, ignores the relation between risk and losses.

Here we have shown that losses matter. When individuals with low tonic arousal take risk they only do so for risks that involve losses. Therefore, in adjusting their behavioral responses to their arousal states, people "acknowledge" things as risky only when losses are part of them. In risks that do not include losses, the link between arousal and risk taking is severed. We have also shown that this property of losses does not depend on loss aversion, and emerges in experience-based tasks, where typically and in our study as well, no loss aversion is exhibited (Erev et al., 2008). Thus, the studied effect of losses appears to be quite general. We have therefore suggested that it may be due to the effect of losses on arousal and attention, rather than due to an asymmetry in decision weights.

Our findings do not preclude, however, that there may be other factors which can serve as cues that a given situation is risky. Possibly, after a prolonged learning period individuals may learn to associate an alternative producing relative gains and relative-losses (or small gains) as risky. Yet in our study this did not happen in the course of 100 repeated choice trials. Factors such as the size of the relative-loss could play a part in this. Another important limitation of the current studies is the small sample sizes used. This issue is especially pertinent in the context of examining individual differences (see e.g., Stanovich and West, 2008).

The current findings may explain some of the mixed findings in the literature on the association between physiological indices of tonic arousal and sensation seeking. Gerra et al.'s (1999) study of healthy adults demonstrated a *positive* association between NE concentration and sensation seeking on Zuckerman et al.'s (1964) scale, whereas similar studies of clinical populations reported negative correlations (Ballenger et al., 1983; Arque et al., 1988; Zuckerman, 1994). Studies of tonic endocrine levels in pathological gamblers also obtained mixed results (Ramirez et al., 1988; Roy et al., 1988; Schmitt et al., 1998). The Sensation Seeking Scale is a list of activities (e.g., "I would like to take the sport of water skiing," "I would not like to learn to fly an airplane") without explicit information concerning the perceived outcomes of those activities. Possibly, some individuals find these activities more dangerous; and this activates the negative association between tonic arousal and risk taking. Yet for others who find these activities less dangerous, this may not occur.

The current findings may also be relevant to the issue of risk communication. The experimental results suggest that presenting the negative side effect of risky products (e.g., cigarets) is a double edged sword. On the one hand, it reduces the attractiveness of the risky alternative; but on the other hand it may increase the arousal associated with it and this can actually attract some individuals.

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Physiological plausibility and boundary conditions of theories of risk sensitivity

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A commentary on

To take risk is to face loss: a tonic pupillometry study
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The contribution by Yechiam and Telpaz (Y&T) published in Frontiers in Cognitive Science places it in a corpus of literature which bridges at least three different disciplines, i.e., psychology, economics, and neuroscience. The goal of this line of research is to explore the neurological and physiological underpinnings of one of the central topics in judgment and decision-making (JDM) research – choice behavior in decisions from experience. Y&T successfully contributes to this goal by demonstrating a novel effect that losses increase experimental participants' arousal as measured by pupil dilatation, which in turn positively correlates with a risk aversion behavior. They hypothesize that participants' attention is increased in decision problems involving losses, which trigger an innate prudent behavior in situations entailing danger and/or hazard. Interestingly, Y&T find that the nature of attention is not selective, i.e., when losses are present, participants are shown to devote more attention to the task as a whole rather than to the single negative outcomes, in contrast to Prospect Theory's loss aversion.

Y&T's contribution can be highlighted in the context of research on the neural mechanism underlying loss aversion (see, for example, Breiter et al., 2001; Tom et al., 2007). These studies suggest that behavioral loss aversion in decisions from description reflects an asymmetric response to gain and losses in the neural system encoding for reward values (the ventromedial prefrontal cortex, orbitofrontal cortex, and ventral striatum). What makes Y&T's contribution particularly noteworthy is their mediating attentional hypothesis, which links physiological mechanisms to the psychological processes involved in experience-based decisions.

One of the possible future developments from Y&T's work is that of drawing on their attentional hypothesis to explain dependence of risk aversion on the payoff level, as observed in the Experimental Economics literature (Harrison et al., 2005; Holt and Laury, 2005). Specifically, it has been observed that participants' degree of risk aversion increases significantly as actual positive payoffs are scaled up, and that this effect is negligible when payoffs are hypothetical. These findings provide an opportunity to widen the scope of the attentional hypothesis. Specifically, payoffs corresponding to large cash amounts might have the analogous effects of losses of increasing arousal and of triggering a higher level of risk aversion; whereas hypothetical payoffs might result in a substantial inhibition of attention. Therefore, the motivation implied by real stakes can be interpreted as one of the possible boundary conditions (see below) for Y&T's attentional hypothesis, giving rise to a question of the relative weight of attention and motivation in shaping risk attitudes.

Y&T's report can also be contextualized within the wide literature on individual differences in reasoning, judgment and decision making (e.g., Stanovich and West, 2000) and their implications to the rationality debate. The prototypical finding in that literature is the correlation between cognitive ability and normative responding, with a strong emphasis on normative evaluation of rationality. This so-called "normativist" approach has recently been subject to criticism (Elqayam and Evans, 2011) as unhelpful in developing a *psychological* theory of human rationality. It is therefore noteworthy that Y&T take their individual differences work in a completely different direction, with what seems to be a purely 'descriptivist' approach, with no normativist connotations. As one reviewer of this manuscript put it, any behavior in this setting could be justified as 'rational'. The behavioral patterns described vary qualitatively rather than quantitatively. This is typical of descriptivist approaches to cognitive variability higher mental processing (Evans and Elqayam, 2011). Given the dearth of such focus in higher mental processing, this is a welcome development.

Lastly, a potentially significant issue here is the implications to risk aversion as originally portrayed in prospect theory (Kahneman and Tversky, 1979). One could argue that Y&T contribute to defining boundary conditions for Prospect Theory, by proposing an alternative explanation for specific settings in which Prospect Theory is not supported by empirical evidence[1]. Indeed, as a unified theory of risk aversion is not yet at hand, knowing the range of application of each of the existing theories is crucial.

One reason that Y&T in particular, and decisions from experience in general, can define boundary conditions, is their focus on the processing level of analysis. Marr (1982) famously distinguished between three levels of analysis regarding any information processing system: The computational level, which portrays the function computed by the system (e.g., arithmetic is a pocket calculator's function); the algorithmic level, which has to do with processes (e.g., the calculator's software); and the implementational level, which explores the physical underpinnings of the system – its hardware/wetware characterization (e.g., the calculator's

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[1] Note that Prospect Theory cannot explain the typical behavioral patterns found in decisions from experience studies (see, for example, Barron and Erev, 2003, and Erev and Haruvy, 2010), unless one assumes parameter values that imply no loss aversion, linear value function (at least with low stakes), and underweighting of rare events. We are grateful to an anonymous reviewer for pointing this out.

chip). Viewed in these terms, we see prospect theory as portraying behavior mainly on the computational (i.e., functional) level of analysis; or, as some authors put it – an "axiomatic" system (see Wakker, 2010). In contrast, Y&T explore the attentional processes (algorithmic level), and their physiological underpinnings (implementational level). As Marr commented, levels of analysis interact, with different processes sometimes computing different functions, as is the case here. Research questions about processing and physiology are much rarer in judgment and decision making research than computational level questions (although see, e.g., Breiter et al., 2001; Tom et al., 2007), and studies that combine several levels of analysis, as Y&T have done, are even rarer. This makes Y&T's contribution of particular interest to scholars of human thinking and decision making.

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Processing differences between descriptions and experience: a comparative analysis using eye-tracking and physiological measures

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Do decisions from description and from experience trigger different cognitive processes? We investigated this general question using cognitive modeling, eye-tracking, and physiological arousal measures. Three novel findings indeed suggest qualitatively different processes between the two types of decisions. First, comparative modeling indicates that evidence-accumulation models assuming averaging of all fixation-sampled outcomes predict choices best in decisions from experience, whereas Cumulative Prospect Theory predicts choices best in decisions from descriptions. Second, arousal decreased with increasing difference in expected value between gambles in description-based choices but not in experience. Third, the relation between attention and subjective weights given to outcomes was stronger for experience-based than for description-based tasks. Overall, our results indicate that processes in experience-based risky choice can be captured by sampling-and-averaging evidence-accumulation model. This model cannot be generalized to description-based decisions, in which more complex mechanisms are involved.

Keywords: risky choices, description vs. experience gap, sampling, eye-tracking, evidence-accumulation, prospect theory

INTRODUCTION

According to standards of rationality, choices between risky prospects should depend on the utility of possible outcomes and their respective probabilities. Choices should thus be invariant to different formats of information presentation. Classic work, however, has shown that this invariance assumption is systematically violated: for example, framing effects (e.g., presenting information in terms of gains vs. losses) have a profound effect both on choice behavior (e.g., Tversky and Kahneman, 1981; Kühberger, 1998; Maule and Villejoubert, 2007) and judgments (e.g., Hilbig, 2009, 2012). Recently, there has been an upsurge of interest in the influence of one specific aspect of information presentation, namely whether choice-relevant information is exhaustively described or actively sampled, that is, experienced.

A growing body of research suggests a "gap" between decisions that are based on description and decisions that are based on experience (Barron and Erev, 2003; Hertwig et al., 2004; Erev and Barron, 2005; Yechiam et al., 2005a; Jessup et al., 2008). Indeed, this gap was recently corroborated on a neuronal level (FitzGerald et al., 2010). In description-based risky choice, the outcomes and their respective probabilities are fully described for both options. By contrast, in experience-based decisions, no such conclusive information is provided; rather, participants have to learn which outcomes might occur and what their approximate probabilities are through experience. For example, Barron and Erev (2003) presented the following choice problem to participants: get three points for sure vs. get four points with 0.8 probability, and zero points otherwise. Instead of receiving such a full description of the options, participants were required to make 400 selections between the two gambles by pressing one of two unmarked buttons. Each selection returned an outcome drawn from the underlying payoff structure of the corresponding option. The accumulated outcomes were converted into money and paid to the participants. According to previous findings, participants in an all gain domain should prefer the safer option due to (myopic) risk aversion (e.g., Kahneman and Tversky, 1979). By contrast, Barron and Erev (2003) found a preference for the riskier option (66%) when participants based their choices on experience. This difference between description vs. experience-based decisions concerning the preference for risky options (and other choice phenomena) is considered the descriptions-experience-"gap" (Hertwig and Erev, 2009)[1].

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[1] Note, however, that the choice problem in Barron and Erev (2003) differed from a description-based task not only by in terms of how information was acquired. Rather, whereas description-based tasks usually require a one-shot decision, the *feedback task* used in Barron and Erev required participants to make repeated choices with feedback, all of which had monetary consequences. To rule out that specifically this feedback aspect may have driven the "gap," subsequent research replicated the "gap" in a one-shot experience-based task (i.e., *sampling task*): Participants again sample single outcomes drawn from each of the choice options. However, none of these samples is consequential. Instead, after the sampling phase, participants make a single consequential choice (e.g., Hertwig et al., 2004). Although both experience-based paradigms reveal choice patterns that differ from those typically found in the description-based paradigm, recent research also indicates considerable differences between the two experience-based tasks. Specifically, the

While the description-experience "gap" has been found consistently, there still are open questions concerning the underlying cognitive mechanisms (Hertwig and Erev, 2009; Ungemach et al., 2009). In particular, it is unsolved whether choices in both formats are essentially governed by the same processes. Alternatively, and on top of obvious differences resulting from the fact that information might have to be transformed before integration, they might trigger qualitatively distinct cognitive processes. To address these questions we herein test hypotheses concerning the processes underlying one-shot experience-based decisions in comparison to decisions from descriptions.

For an in-depth process analysis we resort to measurement of information sampling using eye-tracking and analyze differences in physiological arousal in response to specific task characteristics. While previous research was limited to the analyses of information sampling for experience-based decisions only (i.e., by looking at button-press behavior), an eye-tracking approach provides insight concerning information sampling in both paradigms. To the best of our knowledge, we are the first to apply fixation-based-sampling models to *both* experience- and description-based risky choice. In addition, we directly test whether the degree of attention given to outcomes corresponds to their actual probability of occurrence – as is a cornerstone assumption of prominent sampling models for risky choice (Busemeyer and Townsend, 1993; Roe et al., 2001; Johnson and Busemeyer, 2005). Findings from other eye-tracking studies in the description paradigm indicate that there is at least some relation between objective probability and attention in risky choice (Fiedler and Glöckner, submitted) and in the valuations of single gambles (Ashby et al., 2012). Nevertheless, other factors such as outcomes (Ashby et al., 2012; Fiedler and Glöckner, submitted) and emerging preference (Innocenti et al., 2010; Glöckner and Herbold, 2011; Glöckner et al., 2012; Fiedler and Glöckner, submitted) have been shown to influence attention as well (see also Armel et al., 2008; Milosavljevic et al., 2010; Krajbich and Rangel, 2011).

UNDERWEIGHTING AND OVERWEIGHTING OF SMALL PROBABILITY OUTCOMES

One of the main differences between decisions from experience and decisions from descriptions concerns the implications of observed choice behavior for the subjective evaluation of rare events (i.e., outcomes with small probabilities). According to Cumulative Prospect Theory (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992), the most prominent model for risky choice, there should be an overweighting of rare events. By contrast, it has been argued that the choice patterns observed in decision from experience imply that rare events are underweighted (Hertwig et al., 2004; Erev and Barron, 2005; Hertwig and Erev, 2009). Specifically, analyses of choices suggest that in description-based tasks, people behave *as if* they overweight small probabilities, whereas they behave *as if* they underweight small probabilities in experience-based tasks. As described above, in description-based tasks, participants mostly (64%) prefer a certain-outcome option with an intermediate expected value (e.g., 100%, 3€) over an option with higher expected value but comprising an undesirable rare event (e.g., 80%, 4€, 20%, 0€); however, they show a reversed pattern in an experience-based task (12% choices for the certain alternative; Hertwig et al., 2004). Since the rare event is undesirable, this is in line with underweighting the probability of rare events in experience-based tasks but overweighting them in description-based tasks. Vice versa, when the rare event was desirable (e.g., 20%, €32, 80% €0), the risky alternative was preferred by the majority of participants in the description-based task, but only by the minority of the participants in the experience-based task.

MODERATORS AND POTENTIAL EXPLANATIONS

Two potential explanations of the description-experience "gap" that were previously proposed are sampling bias and recency effects[2]. Sampling bias refers to the tendency of individuals to draw small (and thus biased) samples. In Hertwig et al. (2004), for example, participants in the experience condition sampled only a median of 7.5 outcomes per option, even though they could have sampled endlessly without (monetary) costs. As a result, most based their final choice on a biased sample, which contained the rare event less often than its objective probability[3]. In view of these results and similar findings, some authors have proposed that the description-experience gap is little more than sampling error plus Prospect Theory (Fox and Hadar, 2006), suggesting that "people make equivalent choices when they use equivalent information to base their decision (on), regardless of presentation mode" (Camilleri and Newell, 2011a, p. 282). Indeed, recent studies show that the description-experience gap reduces under conditions in which more representative sampling is induced (e.g., Ungemach et al., 2009; Camilleri and Newell, 2011a) or when large representative samples can be drawn in parallel and very speedily (Hilbig and Glöckner, 2011). However, although the ubiquitous importance of sampling biases is out of question (e.g., Fiedler, 1996, 2008; Fiedler et al., 2000; Kareev and Fiedler, 2006), it has been found that even when individuals draw on large and representative samples the "gap" – though reduced – is not eliminated (Ungemach et al., 2009). Ungemach et al. (2009) argue that sampling bias alone can thus not account for the "gap."

Recency effects refer to the tendency to focus on events more recently encountered (e.g., Hogarth and Einhorn, 1992). Particularly, only a subset of the most recent samples could be taken into account in choice. Since rare events have a lower probability to be included in these recent samples (simply because they are rare; see

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description-experience "gap" is much stronger in the feedback task as compared to the sampling task (Camilleri and Newell, 2011b). In addition, the differences between the two experience-based paradigms are actually larger than between sampling and description.

[2] Two explanations that have also been suggested but will not be considered further herein are that individuals might underestimate the probabilities of rare events (i.e., estimation error; Hertwig and Erev, 2009) and that individuals might use different decision policies (Hills and Hertwig, 2010) reflected in either often switching between options (i.e., piece-wise sampling) or continuous sampling within one option (i.e., comprehensive sampling).

[3] In Hertwig et al. (2004) 78% of the participants made choices based on a sample of information which contained the rare event less often than its objective probability. Note that this is not caused by unequal (biased) sampling between options but due to a mere statistical effect that in small samples the majority of individuals often do not get to see the rare event at all. More precisely, the mean of the relative sampling frequency of the rare events equals their objective probability but due to the skewness in the distribution the median falls below the mean.

also text footnote 3), choices are likely to imply underweighting of these events. However, findings concerning this recency effect are equivocal. Some studies found that the second half of the samples drawn by participants predicted choices better than the first half (Hertwig et al., 2004), while others failed to find evidence for such recency effects (e.g., Ungemach et al., 2009).

Thus, the accumulated empirical evidence suggests that rare events are treated differently in description vs. experience-based decision making (Hau et al., 2010). However, it has been argued that biased sampling and recency cannot fully account for the description-experience gap (Ungemach et al., 2009). As such, knowledge on the mechanisms that contribute to the description-experience gap is incomplete (Hertwig and Erev, 2009; Ungemach et al., 2009; Ludvig and Spetch, 2011) which, in turn, highlights the importance of directly examining underlying processes.

Hertwig and Erev (2009) consider the possibility that the different statistical formats of information presentation (i.e., stated probabilities vs. experienced events) might trigger qualitatively different cognitive processes. The current study aims to identify such qualitative differences in processing, which stand in contrast to obvious differences that merely result from the fact that information has to be transformed in different ways before it can be integrated into a decision. For example, participants may first need to form an estimate of the outcomes' probabilities in the experience format, but then integrate outcomes and probabilities based on the same cognitive process as participants who are provided with the exact probabilities (in the description format). Therefore, we focus on qualitative differences in terms of information integration. An example would be that in one format participants might rely on deliberately multiplying outcomes and (weighted) probabilities and adding them up whereas in the other format they may rely on automatic processes of memory retrieval in order to decide which option is better.

THEORETICAL BACKGROUND AND METHODOLOGICAL APPROACH

Herein, we investigated decisions from the perspective of evidence-accumulation models (e.g., Busemeyer and Townsend, 1993; Roe et al., 2001; Johnson and Busemeyer, 2005; Raab and Johnson, 2007; Armel et al., 2008; Milosavljevic et al., 2010; Pleskac and Busemeyer, 2010), an important class of process models for decision making (see also Rieskamp, 2008; Hilbig and Pohl, 2009; Glöckner and Herbold, 2011; Hilbig and Glöckner, 2011). To better understand the underlying processes of description-based and experience-based decisions, we used a combination of process-tracing techniques, including recording of eye-fixations (via eye-tracking), cognitive modeling, and physiological arousal measurement (indexed by skin conductance response and pupil dilation). Moreover, these measures were used on a set of decisions that were randomly generated and somewhat more complex than in previously used tasks (see also Hilbig and Glöckner, 2011). This simultaneous reliance on multiple measures in a complex set of stimuli extends the scope of previous examinations and enables direct tests of (i) whether individuals indeed treat rare events differently under experience vs. description, and (ii) which types of processing differences contribute to this "gap."

Eye-fixation can provide important information about the weight (or importance) given to different pieces of information during the decision process (e.g., Raab and Johnson, 2007; Krajbich and Rangel, 2011; Glöckner et al., 2012). Since several evidence-accumulation models suggest that attention to outcomes should be proportional to its importance or subjective probability (Busemeyer and Townsend, 1993; Busemeyer and Johnson, 2004; Johnson and Busemeyer, 2005), eye-fixations can be used to investigate whether there are differences in the visual attention given to the rare events in both paradigms. If individuals overweight rare events, then these events are expected to receive a higher relative proportion of attention as compared to their objective probability. By contrast, if rare events are underweighted, they will receive a lower relative proportion of attention. Our data also allows testing whether overt attention is related to probability of outcomes at all. As mentioned above, some (but not all; see e.g., Armel and Rangel, 2008, for a different approach) evidence-accumulation models predict that attention to an outcome should increase with its probability and predict that "the outcome probabilities dictate where attention shifts, but only the outcome values are used in determining the momentary evaluation" (Johnson and Busemeyer, 2005, p. 843)[4].

Cognitive modeling and model comparisons additionally yield insight on how (and with which properties) the underlying processes employed by decision-makers can best be described (e.g., Yechiam and Busemeyer, 2005; Yechiam et al., 2005b; Yechiam and Ert, 2007). For example, evidence-accumulation models assume that individuals repeatedly sample information about the available options, and use these samples to evaluate the options. The sampled information is automatically accumulated in a serial manner, until one option is perceived as sufficiently better than the other, and thus chosen. In the following, we rely on naïve implementations of evidence-accumulation models (i.e., averaging and summing models) to examine whether one-shot choices that are made from description vs. experience can be captured by different process models and how well the models explain behavior overall. Averaging models assume that decision-makers average the sampled outcomes for both alternative, and choose the option with the higher average. By contrast, summing models assume that decision-makers sum the sampled outcomes of each alternative, and choose the option with the higher sum.

In both paradigms "samples of information" were operationalized by the number of eye-fixations to respective outcomes. These models were contrasted with a baseline Expected Value Model and Cumulative Prospect Theory assuming objective probabilities and outcomes of gambles. In the experience condition we additionally tested a strategy assuming that participants chose the option with the highest average outcome based on the subjectively sampled outcomes. In addition, to test the recency account for decisions from experience, this averaging model was also applied using only recent subsets of samples. A previous model comparison by Erev et al. (2010) indicates that (probabilistic implementations of) Cumulative Prospect Theory predict choices best in decisions

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[4] Note that this model statement is concerned with mental sampling. Therefore our test necessitates accepting the empirically well supported eye-mind hypothesis (Just and Carpenter, 1976) stating that individuals fixate the information they process. Also note that Prospect Theory (Kahneman and Tversky, 1979) is an as-if model, which does not necessarily imply a relation between decision weights and attention.

from descriptions but that the same theory performs poorly in predicting decisions from experience. Decisions from experience, in contrast, were found to be best described by an "Ensemble model" relying on the average prediction of four models including sampling models and Cumulative Prospect Theory.

Finally, potential differences in arousal between descriptions and experience were investigated. We were interested in the influence of the "difficulty" of the decision on arousal in the two paradigms, where difficulty is indicated by the similarity of options in expected values. Previous studies on probabilistic inferences (Hochman et al., 2010) and risky choice (Glöckner and Hochman, 2011) show that arousal increases with increasing conflict between the available information. Generalized to the risky choice paradigm used in the current study, arousal should be high (vs. low) if both gambles are similar concerning their expected value and/or expected utility since "pros" and "cons" for the alternatives are about equally strong in such a case (vs. one alternative being clearly better than the other). Thus, differences in the pattern of arousal for "easy" vs. "difficult" choices between the two paradigms should be an indicator for different underlying processes[5]. Such a comparison is critically informative concerning the question whether the "gap" is caused by relatively trivial differences in preprocessing of information only. If this were the case, a similar effect of difficulty on arousal would be expected in the experience and the description condition.

MATERIALS AND METHODS

PARTICIPANTS AND DESIGN

Forty-four students from the University of Bonn took part in the experiment (52.3% female, mean age 23 years) and were randomly assigned to the *experience* or the *description* condition. We manipulated within-subjects whether the rare event was more or less desirable and whether there was a high or a low difference in expected value (EV-diff) between gambles resulting in a 2 (experience vs. description) × 2 (rare event more vs. less desirable) × 2 (EV-diff low vs. high) mixed design. The experiment lasted about 45 min. Participants were students recruited from the MPI Decision Lab subject pool using the database-system ORSEE (Greiner, 2004). Participants received a show up fee of 5€ plus a performance-contingent payment for the study yielding additional payoffs between 0.1 and 29.8€ (average total: 18.3€ which equals approximately 25.7 USD). The experiment was hence incentivized and there was no deception involved.

MATERIAL

Participants made 60 decisions between two gambles with two outcomes each that had an average EV of 10€. In 38 target trials an option comprising a rare event (low-probability outcome) was paired with an option comprising intermediate-probability outcomes only (i.e., between 0.33 and 0.66). The remaining 22 decisions were filler tasks with options comprising intermediate-probability outcomes only (all between 0.33 and 0.66). For 20 of the 38 target decisions, the low-probability outcome was desirable (i.e., the rare outcome was more than twice as large as the non-rare outcome), while for the other 18 target decisions it was undesirable (i.e., the rare outcome was less than half as large as the non-rare outcome). Half of the tasks were constructed so as to yield a small difference in EV between gambles (EV-diff < 0.50€), whereas the other half had a higher difference in EV (i.e., 3€ < EV-diff < 4€). All decisions were randomly generated under the above restrictions using gambles with positive outcomes only, the values of which ranged from 0.10€ to 30€. One of the target decisions had to be excluded due to a programming error leaving us with a total of 814 (22 participants × 37 decisions) choices per conditions as basis for the analyses. All decision tasks, their assignment to the within-subjects conditions, and average choices are listed in Appendix A.

APPARATUS

Eye movements were recorded using the Eyegaze binocular system (LC Technologies) with remote binocular sampling rate of 120 Hz and an accuracy of about 0.45°. Images were presented on a 17″ color monitor (Samsung Syncmaster 740B, refresh rate 60 Hz, reaction time 5 ms) with a native resolution of 1280 × 1024. Fixations were identified using a 30 pixel tolerance (i.e., added max-min deviation for x and y-coordinates) and a minimum fixation time of 50 ms. Physiological arousal was measured by recording skin conductance responses using a NEXUS-8 system with a sampling rate of 32 samples per second. We used Butterworth (first order) filters to correct for high frequency and low frequency noise in the data[6].

PROCEDURE

In the description condition we relied on a procedure similar to the one used in Glöckner and Herbold (2011) which was slightly adapted by including a new decision screen to make it as similar as possible to the experience condition (**Figure 1**). Upon arrival, participants were familiarized with the decision task by reading a comprehensive instruction including screenshots of the paradigm. In both conditions, they were instructed to sample information as long as they liked. The decision screen was shown once participants pressed the space bar. Decisions were made by pressing buttons marked with "A" and "B" on the keyboard. In the experience condition, participants were additionally told that sampling also worked through pressing buttons "A" and "B" (see **Figure 1**). Individuals were calibrated and connected to the NEXUS (using the middle finger and the ring finger of the non-dominant hand). The experiment started with a test trial followed by the 60 decisions[7]. In both conditions, the position in which the two gambles were presented on screen (i.e., left or right) was counterbalanced between subjects.

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[5] These differences may thereby be explained by multiple process accounts. We do not aim to distinguish between them and they have to be further dissected in future research.

[6] We used a filter allowing a band from 0.1 to 1 Hz. To test the robustness of our findings we also conducted the analysis using a FIR Bandpass 128 filter [Parks–McClellan (optimal)] with the same band which essentially led to the same results.

[7] Due to a programming error, order was randomized only in the experience condition but it was fixed in the description condition (using the order presented in Appendix A). Note, however, that gambles were randomly generated, half of them were side-reversed which was counterbalanced between subjects, and they were intermixed with blocks of distractors. We therefore consider it very unlikely that this difference could have influenced our results. We nevertheless cannot completely rule out this possibility.

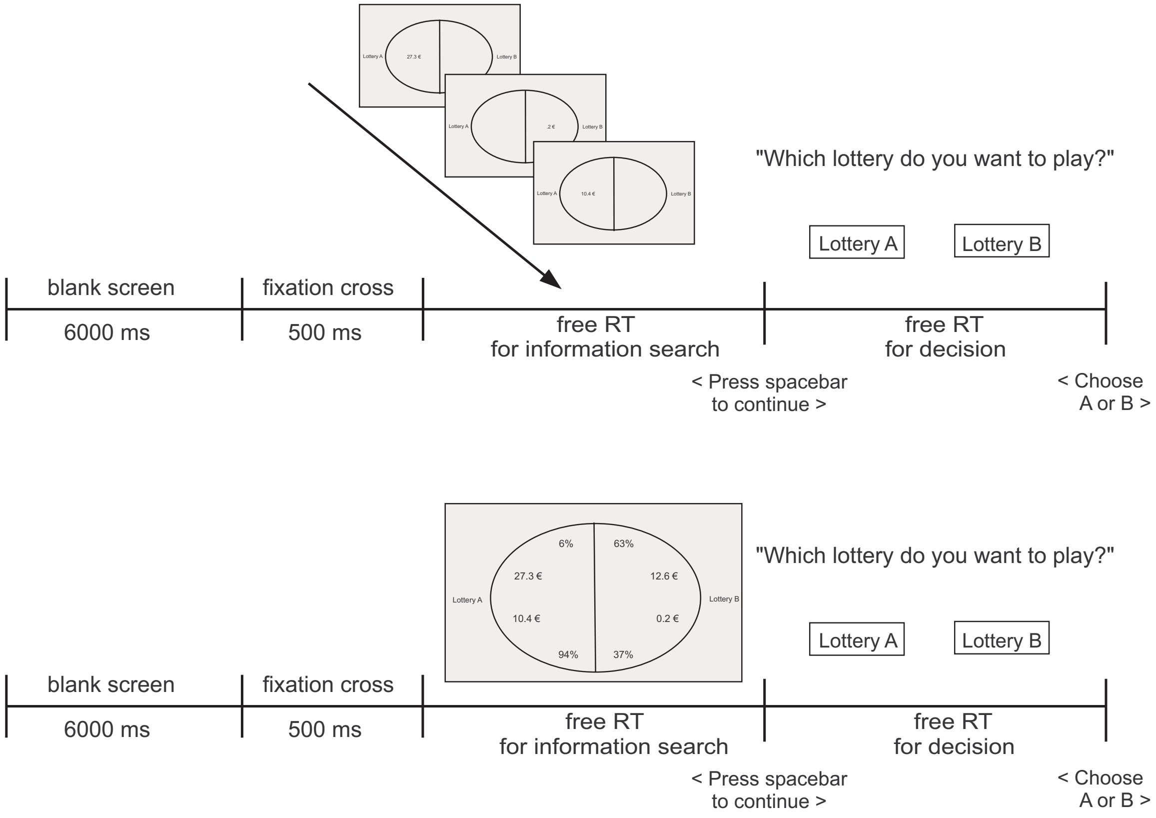

FIGURE 1 | Procedure in the experience (top panel) and the description (bottom panel) condition. Note. RT means response time.

Each decision started with a blank screen (6 s) followed by a fixation cross (0.5 s) to center attention on the middle of the screen. Next, the gambles were presented in an ellipsoid display which ensured that information was equally distant from the initial fixation point in both conditions (**Figure 1**). Information for one gamble was presented on the left and for the other on the right side. After (explicit or implicit) sampling (*information search phase*) and pressing the space bar the decision screen appeared and individuals made their decision (*decision phase*). The analysis of fixations was done for the information search phase, whereas the analysis of arousal was done separately both for the information search phase and the decision phase. The decision phase was exactly identical in the two conditions.

RESULTS

SAMPLING OF RARE EVENT

In the experience condition we observed an average of 32 (Md = 30) information inspections, that is, for each decision, individuals pressed each of the two buttons about 16 times, which took them 12.8 s on average. The sampling rate is on the upper end of the spectrum observed in previous investigations which may be due to the relatively large monetary incentives (Hau et al., 2010 report median total sampling rates between 11 and 33 in a review of several previous studies). Consequently, sampling rates of low-probability outcomes ($M = 0.084$, SE = 0.0045) were relatively unbiased and reflected the average objective probabilities of these outcomes well ($M = 0.0745$).

As described above, we use fixations to outcomes as a proxy for information sampling in both paradigms. Note that the information display was much richer in the description condition containing eight pieces of information (i.e., four outcomes and four probabilities) than in the experience condition only showing one outcome at a time (see **Figure 1**). In the experience paradigm, there was an average of 53.5 fixations to outcomes per decision (Md = 48). Fixations also showed relatively unbiased sampling of rare events which received 0.08 of the fixations to the respective gamble. This proportion is calculated as the number of fixations to the rare event divided by the total fixations to the rare event and the alternative outcome of the respective gamble (**Figure 2**). As pointed out in the previous section, the presentation rate of the rare event (i.e., how often the rare event was shown in the gambles containing a rare event) was 0.084. Hence, participants did not show particularly increased or decreased fixation rates to rare events. Fixations roughly reflected the presentation (=sampling) rate and were thus also in line with the objective probability of the rare events. In the description condition, we observed 43.9 fixations on average (Md = 35) per decision with more fixations directed to outcomes (58%) than to probabilities (42%). In contrast to the experience condition, rare events were strongly oversampled in the description condition: the low-probability outcomes received 0.50 of all fixations within the

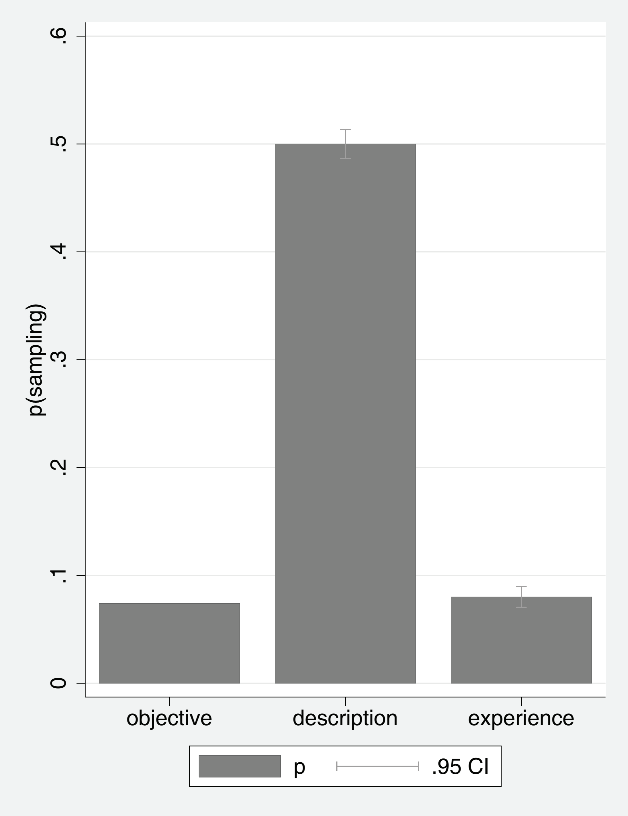

FIGURE 2 | Proportion of fixations to the rare events compared to their objective probability. Note. Proportions of fixations are calculated using fixations to outcomes only. Proportions are calculated within gambles as the number of fixations to the rare event divided by the total fixations to the rare event and the alternative outcome of the respective gamble. Note that in the experience condition, the sampling rate of the rare event was 0.084, which is roughly reflects in the fixation rate.

respective gamble which is significantly higher than their objective probability, $t(21) = 65.7$, $p < 0.001$ (**Figure 2**)[8]. Note, that a fixation rate of 0.50 is expected if both outcomes receive equal attention. For all 22 participants, the (fixation-based) sampling percentage of rare events was higher than the objective probability of these events.

In sum, there was relatively unbiased sampling of rare events in the experience condition but "oversampling" of rare events in the description condition in terms of attention. In fact, there seems to be no contingency between probability of the rare outcome and the proportion of attention it receives in the descriptions format (but, see Fiedler and Glöckner, submitted, for a more general analysis). In contrast, in the experience condition when only one piece of information is presented at a time, sampling rates measured by button-press and by fixation show a high degree of convergence. We nevertheless use both in the model comparison described below.

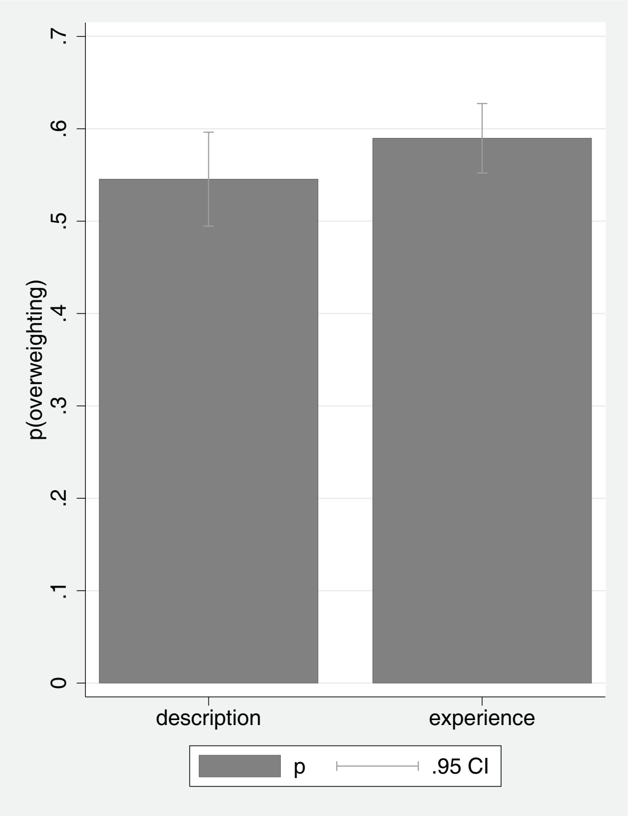

FIGURE 3 | Choices in line with overweighting of small probabilities. Note. Higher scores in *p*(overweighting) indicate stronger overweighting of rare events.

CHOICES

Overall analysis

We coded choices to indicate overweighting of small probabilities (i.e., 1 = choice for the gamble indicating overweighting; 0 = otherwise; see Appendix A) and plot this variable in **Figure 3**. Surprisingly, the option that – if chosen by the participants – would indicate overweighting of small probabilities was not chosen more often in the description than in the experience condition. The experience condition even shows a tendency toward stronger overweighting of small probabilities as compared to the description condition.

Note that placing more weight to an undesirable outcome of a gamble (i.e., an outcome with a relatively low monetary value) necessarily implies placing less weight on the more desirable outcome in this gamble (holding expected value constant). Hence, if the low-probability outcome were overweighted, the gamble with the rare event should become more attractive with increasing values of the low-probability outcome (c.f. Hilbig and Glöckner, 2011). Consider, for example, a gamble paying 4€ with 80% probability and otherwise nothing. Overweighting the (undesirable) 0€ outcome would reduce the probability of choosing this option as compared to an option comprising the same expected value, but with only one sure outcome (e.g., 3.2€). Vice versa, if the 0€ outcome were replaced by, say, a 10€ (and thus desirable) outcome,

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[8] Analyzing total fixation durations instead of number of fixations led to the same conclusions.

overweighting this rare event would increase the probability of choosing this gamble (again compared to an option comprising the same expected value, but with one sure outcome).

We therefore analyzed whether low-probability outcomes are over- or underweighted by conducting a logistic regressions predicting choice of the option comprising the low-probability outcome by its value (i.e., desirability; values are outcomes in Euro as described in Appendix A), controlling for differences in expected value. If low probabilities are overweighted, the proportion of choices of the corresponding option should increase with increasing value of the outcome (c.f. Hilbig and Glöckner, 2011). That is, the odds-ratio coefficient for Low-Probability Outcome should be above one indicating that the probability for choosing the gamble increases with the value of the low-probability outcome[9].

As expected, significant overweighting was observed in decision from description (**Table 1**, model 1; considering a one-sided test which is justified due to our *a priori* hypothesis, see Baron, 2010). Interestingly, however, we observed significant overweighting also for the experience condition (**Table 1**, model 2). The overall analysis indicated that there was no difference concerning overweighting between conditions as indicated by the non-significant interaction term (**Table 1**, model 3).

In sum, although we find oversampling of rare events in the description condition as compared to the experience condition, choice patterns in *both* conditions indicated overweighting of rare events. Interestingly, this result speaks against the hypothesis that decisions in both conditions are based on the same evidence-accumulation process of fixation-sampled information, since according to such models, low-probability outcomes should have had much more relative influence on choices in descriptions as compared to experience due to the strong oversampling in the former (as reported in the previous section).

Table 1 | Logistic regression of choices for the gamble comprising the rare event (p_{choice}).

	(1) p_{choice} description	(2) p_{choice} experience	(3) p_{choice} overall
Low-probability outcome	1.025^{+}	1.045^{***}	1.035^{***}
(centered)	(1.95)	(4.03)	(4.30)
Presentation format†			0.982
			(−0.09)
Presentation format × low-probability outcome			1.022
			(1.30)
EV-difference	1.563^{***}	1.422^{***}	1.488^{***}
	(10.57)	(6.12)	(10.56)
N	814	814	1628
Pseudo R^2	0.185	0.151	0.166

Exponentiated coefficients representing odds-ratios (z statistics in parentheses); cluster correction used at the level of participants to account for dependencies due to repeated measurement.

†Coding: 0 = descriptions, 1 = experience (centered).

$^{+}p < 0.10$, $^{***}p < 0.001$ (all two-sided test).

Determinants of choices in the experience condition

We split tasks depending on whether the rare event was sampled (i.e., shown on the screen) (a) never, (b) once, or (c) more than once and reran the logistic regression predicting choices of the option comprising this low-probability outcome (again, with the value of the low-probability outcome and EV-difference as predictors). We found significant underweighting of low-probability outcomes for trials in which the rare event was not sampled (odds-ratio = 0.97, $z = -2.33$, $p = 0.02$), but overweighting for trials in which it was sampled once (odds-ratio = 1.08, $z = 5.50$, $p < 0.001$) or several times (odds-ratio = 1.11, $z = 7.44$, $p < 0.001$). Overweighting of rare events thus increases with the number of times they are sampled as indicated by a significant Number of Samples × Value of the Low-Probability Outcome interaction (odds-ratio = 1.05, $z = 5.21$, $p < 0.001$). The description-experience "gap" hence reduces with increasing number of samples drawn and might heavily depend on the fact that, in typical studies, many individuals do not sample the rare event at all. Thus, the high overall number of samples drawn in the current study might contribute to the fact that no evidence for underweighting of small probabilities is implied by the choice patterns in the experience condition.

COMPARING MODELS FOR RISKY CHOICES IN EXPERIENCE – AND DESCRIPTION-BASED DECISIONS

Model specification

To investigate the underlying processes more closely we calculated the predictive power of different naïve implementations of evidence-accumulation models and compared them against several competitors. Thereby, all models were implemented in a stochastic manner using a logistic choice rule (details see below) in which the probability of choosing a gamble increases with the difference in value (V_{diff}) between gambles. The models only differ in the way in which values V for each gamble are calculated and therefore in V_{diff}.

As basic comparison standard, we used two models that relied on objective probabilities and outcomes or transformations of these. Specifically, we considered an expected value model ($\text{EV}_{\text{objective}}$), and an implementation of Cumulative Prospect Theory ($\text{CPT}_{\text{objective}}$) with the parameters from Tversky and Kahneman, 1992 (i.e., $\alpha = 0.88$, $\gamma = 0.61$, $\lambda = 2.25$; all outcomes positive).

For the experience condition, participants might simply choose the option with the higher average of outcomes that was sampled by pressing buttons. We calculated predictions from such sampling-based models, which rely on the sampled outcomes for each gamble (or subsets of them). The first implementation takes into account all samples ($\text{SampAver}_{\text{All}}$). Note that participants have no other information than the sampled outcomes. Given this information deficit (and ignoring opportunity costs), $\text{SampAver}_{\text{All}}$ is the optimal strategy to maximize chances to win

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[9] Here and in all following regressions we used cluster correction on the level of subjects to correct for dependencies in errors caused by the repeated measurement design (Rogers, 1993). We also conducted the analyses using multi-level random effects models (i.e., random intercept), which leads to the same conclusions.

money in this paradigm. As mentioned in the introduction, sampling average models might also be implemented using the most recent samples only. To test these alternative implementations, two further models that average over the last 10 ($\text{SampAver}_{\text{Rec10}}$) or the last five samples ($\text{SampAver}_{\text{Rec5}}$) per decision were calculated. These sample sizes were used since estimated average samples for recency (and also other sampling-based) models in Erev et al., 2010, e.g., see Table 3C) were between 5 and 10 (but see Discussion for limitations of this approach). To test whether summing instead of averaging of outcomes can account better for the data, we also included a model assuming summation of all sampled outcomes (SampSum). Note that for all sampling-based models introduced in this section one sample refers to one sampled outcome, independently of how often individuals looked at them.

More importantly, we considered averaging and summation models implementing evidence-accumulation based on participants actual fixations. In these model variants, valuations of gambles are based on the distribution of fixations to specific outcomes. Conceptually, fixation-based summation models (FixSummation) assume that preferences are constructed in a dynamic process in which each fixation to an outcome adds evidence for the respective gamble which is proportional to the value of the outcome. Fixation-based averaging models (FixAveraging) do the same but additionally correct for the number of fixations to each gamble so that the option with the higher average evidence is selected[10]. Appendix B provides a formal description of the models implemented.

For all models, we used a multi-level logistic regression model to predict individual choices of the option comprising the rare event based on difference in value between gambles (V_{diff}).

Model estimation

We estimated the model fit to the choice data using multi-level (mixed-effect) logistic regressions assuming normally distributed $N(0, \sigma_u^2)$ random intercept u_i according to:

$$f(z) = \frac{1}{1 + \exp(-z)} \tag{1}$$

and

$$z = \beta_0 + \beta_1 (V_{\text{diff}})_{it} + u_i \tag{2}$$

with i indexing subjects and t indexing tasks.

All models have three estimated parameters (β_0, β_1, σ_u^2). The best model was selected based on the Bayesian Information Criterion (BIC, Schwarz, 1978). To test the stability of the estimation we also reran the analyses using a logistic regression with cluster correction for standard errors which provides pseudo R^2 values indicating how much variance can be explained by a model.

Model fitting results

In the experience conditions, the fixation-based averaging model (FixAveraging) provided the best fit to the data (**Table 2**). The sampling-based averaging model taking into account all samples ($\text{SampAver}_{\text{All}}$) performed nearly as well, whereas all other models turned out considerably worse. Models relying on only the most recent samples performed poorly, as did the sampling-based summation model and the fixation-based summation model.

In the description condition, by contrast, Cumulative Prospect Theory ($\text{CPT}_{\text{objective}}$) performed best, whereas both fixation-based models performed poorly. Overall, these findings indicate that attention-based evidence-accumulation models can account better for experience-based choices than for description-based choices.

Robustness checks and further analyses

In the experience condition, sampling of outcomes and fixations to the respective outcomes are necessarily highly correlated. As one would expect, the predictions of the two best models in the experience paradigm $\text{SampAver}_{\text{All}}$ and FixAveraging were therefore also highly correlated ($b = 0.93$, $t = 93.60$, $p < 0.001$). We tested whether, despite this high degree of overlap, both models make unique contributions in predicting choices by including both predictors simultaneously in a logistic regression (clustering at the participant level and correcting for individual differences using dummies). The predictors of both models remained significant at $p < 0.05$ indicating that both models have unique predictive power.

We conducted further tests of whether modified implementations of the models mentioned above improve model fit. First, one might suspect that our implementations of fixation-based models

Table 2 | Model comparison predicting choices for the rare event.

Model class	Description		Experience	
	BIC	**Pseudo R^2**	**BIC**	**Pseudo R^2**
OBJECTIVE PROBABILITY AND OUTCOME-BASED MODELS				
$\text{EV}_{\text{objective}}$	871	0.18	858	0.12
$\text{CPT}_{\text{objective}}$	**832**	**0.21**	799	0.18
SAMPLING-BASED MODELS				
$\text{SampAver}_{\text{All}}$			768	0.21
$\text{SampAver}_{\text{Rec10}}$			872	0.11
$\text{SampAver}_{\text{Rec5}}$			867	0.12
SampSum			876	0.11
FIXATION-BASED MODELS				
FixAveraging	1009	0.05	**767**	**0.22**
FixSummation	991	0.07	828	0.17
Observations	813		751	

BIC scores are from multi-level logistic regressions described in Equations 1 and 2; Pseudo R^2 are from a logistic regression with cluster correction using the same predictors. Low BIC scores and high pseudo R^2 indicate a better fit of the model to the data. The best fitting models for both conditions are in bold. Trials were excluded from the comparison if there were no fixations recorded to any outcome within the respective trial.

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[10] Note that – in contrast to averaging models – summation models take into account biased sampling toward one of the options. For decisions with all non-negative outcomes increased attention toward one option should lead to a choice bias in favor of this option. This implementation of fixation-based summation models is similar to evidence-accumulation models suggested by Rangel, Krajbich and colleagues (Armel et al., 2008; Krajbich and Rangel, 2011).

might be suboptimal since they take into account frequency of fixations only and ignore the duration of these fixations. To test this hypothesis, we calculated model implementations for the Fix-Averaging and the FixSummation models in which each fixated outcome is weighted by the duration of the respective fixation. In both conditions, model fit decreased when weighting fixation by duration compared to using frequency of fixations. Second, in the description condition, fixations to outcomes and their probabilities might both be considered to provide evidence of attention to the respective gamble. We therefore implemented fixation-based models in which each fixation to a probability was also counted as evidence for the outcome connected with this probability. In both implementations, the model fit improved slightly (by about three BIC points), which, however, does not change any of above conclusions.

AROUSAL MEASURES: PUPIL DILATION AND SKIN CONDUCTANCE RESPONSE

Finally, we analyzed increases in physiological arousal between conditions and tasks as measured by (a) pupil dilation and (b) skin conductance response. A focus was placed on differences in affective responses to our manipulation of EV-difference between conditions, indicating differences in processing. As dependent measures we calculated peak arousal scores, that is, the maximum increase of arousal as measured by pupil dilation and skin conductance from baseline (i.e., measured at fixation cross presentation) in the respective part of the decision process. We thereby conducted analyses separately for the information search phase (i.e., in which the information about the options was presented and sampled) and the decision phase (i.e., in which the decision screen was presented). Due to unsystematic breakdowns of the NEXUS system, we lost parts of the data for several participants, leaving us with 33 (out of the 44) complete sets for the analysis of skin conductance (15 experience, 18 description). Peak arousal scores for pupil dilation and skin conductance response showed a medium correlation [$r = 0.34$, $t(35) = 2.13$, $p < 0.05$; scores aggregated at the task level].

Pupil dilation

For both conditions, we regressed pupil dilation scores on absolute EV-difference (based on objective probabilities and outcomes), controlling for effects of trial order by including trial number as predictor, and differences between subjects by including subject dummies. In the description condition, pupil dilation decreased with increasing EV-difference, which was not the case in the experience condition (**Figure 4**, left). The effect in the description condition turned out significant both in the information search phase [$b = -0.014$, $t(21) = -3.03$, $p = 0.006$] and the decision phase [$b = -0.010$, $t(21) = -2.11$, $p = 0.047$]. In the experience condition, the effect was not significant [information search phase: $b = -0.00097$, $t(21) = 0.29$, $p = 0.77$; decision phase: $b = -0.0029$, $t(21) = -0.66$, $p = 0.518$][11] which also holds when using experienced (i.e., subjectively sampled) probabilities to calculate EV-difference instead of objective probabilities (both $p > 0.25$).

Skin conductance response

We regressed skin conductance response scores on absolute EV-difference, controlling for effects of trial order, and differences between subjects by including subject dummies. The results nicely converge with the findings concerning pupil dilation: skin conductance response decreased with increasing EV-difference in the description condition but not (or much less so) in the experience condition (**Figure 4**, right). EV-difference did not predict arousal for the experience condition, neither in the information search phase nor in the phase in which the decision screen was shown (both $p > 0.23$). In the description condition, by contrast, we found strong corresponding effects in both the search phase [$b = -0.034$, $t(17) = -2.31$, $p = 0.034$] and the decision phase [$b = -0.022$, $t(17) = -3.04$, $p = 0.007$]. Since the decision phase was exactly identical in both conditions, the difference between conditions indicates that there might be qualitative differences in processing between both conditions that do not only concern trivial differences in information search but also the way in which information is integrated. We will discuss this issue in more detail the Section "Discussion."

Note, however, that the general level of arousal did not differ significantly between conditions, neither for pupil dilation [$b = -0.009$, $t(43) = 0.5$, $p = 0.62$] nor for skin conductance response [$b = 0.023$, $t(32) = 0.87$, $p = 0.40$], and coefficients even pointed in opposite directions (condition dummy coded with Experience = 1).

DISCUSSION

In the current work, we examined processing differences between one-shot decisions from description vs. experience using eye-tracking, cognitive modeling, and physiological arousal. Concerning choices, we did not find underweighting of low-probability outcomes in experience-based decisions and therefore our results do not replicate the description-experience gap in choices. It is noteworthy that this also holds when considering the 37 decisions independently (see Appendix A). Although we did not expect this result, it is interesting since it is in line with recent evidence pointing at important moderators for observing the descriptions-experience "gap[12]."

First, our findings are in line with Camilleri and Newell (2011b) who find that behavior in one-shot experience-based decisions (i.e., sampling information and then making one decision that is incentivized) leads to behavior more in line with decisions from description compared to repeated experience-based decision (i.e., each sample is incentivized and individuals receive immediate

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[11] In the description condition trial order (jointly calculated over search and decision phase) turned out significant as well, $b = -0.0022$, $t(21) = -4.16$, $p < 0.001$, which was not the case in the experience condition, $b = 0.0002$, $t(21) = 0.47$, $p = 0.644$. A further regression analysis was conducted including two-way interaction terms for condition by EV-diff and condition by trial number (all variables centered) in the model (but excluding subject dummies). As indicated by the trial order coefficients reported above, participants in the two conditions reacted differently on trial order [IE: $b = 0.0023$, $t(21) = 3.83$, $p < 0.001$]. Most importantly, however, the interaction effect of EV-diff and condition was significant even when controlling for this effect [IE: $b = 0.0117$, $t(21) = 2.58$, $p = 0.013$].

[12] Of course, it is also generally important to report non-replications to avoid the problem of publication bias (Renkewitz et al., 2011).

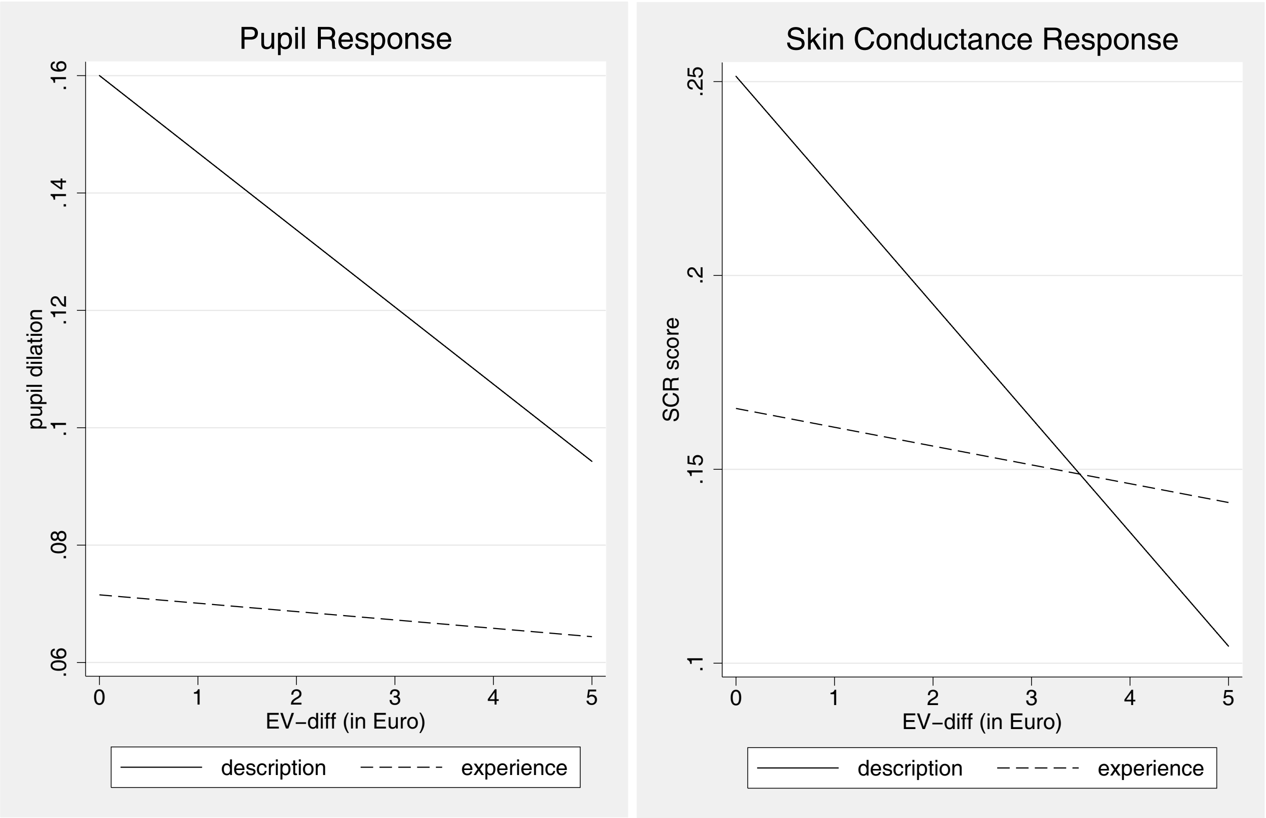

FIGURE 4 | Physiological arousal. Note. The graphs show predicted peak arousal scores for Pupil Dilation (left panel) and Skin Conductance Response (right panel) with high numbers indicating high arousal. Both scores are differences from baseline measured at presentation of the fixation cross preceding the respective trial. Pupil dilation scores are in millimeters and refer to changes in radius. Graphs are based on a joint analysis over information search phase and decision phase.

feedback; see also text footnote 1, above). Second, in our study, participants sampled more than twice as often as participants in the original study on one-shot experience-based decisions by Hertwig et al. (2004). As a consequence of this low sampling rate, 78% of their participants sampled the rare event less often than expected (Camilleri and Newell, 2011b). We did not observe such a bias in sampling. Therefore, our findings are in line with Ungemach et al. (2009) in showing that the gap reduces with increasing sample size and the argument that the effect is largely driven by biased samples (Fox and Hadar, 2006; Camilleri and Newell, 2011b).

Most importantly, even though choices did not reveal a "gap" between descriptions and experience, a more in-depth model comparison based on choices as well as an analysis of process measures suggest that the underlying cognitive processes in the two types of paradigms are markedly different.

EVIDENCE FOR QUALITATIVE PROCESSING DIFFERENCES BETWEEN DECISIONS FROM DESCRIPTION VS. DECISIONS FROM EXPERIENCE

Our findings indicate qualitative processing differences between decisions from description and decisions from experience that go beyond trivial differences concerning preprocessing of information. As such, the current results speak against the hypothesis that individuals merely transform information in an initial preprocessing stage, but later rely on the same integration process in both paradigms. This conclusion is based on three novel findings which we briefly summarize in what follows.

First, the model comparison for choices indicates that notably different models explain choices best in the two conditions, which replicates and extends findings from Erev et al. (2010). Evidence-accumulations models assuming sampling of outcomes by fixation and linear integration of these outcomes, which have been suggested as models for risky choices in general (Busemeyer and Townsend, 1993), can account well for decisions in the experience paradigm but not in the description paradigm. In the description paradigm, by contrast, Cumulative Prospect Theory was the best model, which converges with other recent findings from comprehensive model comparisons (Erev et al., 2010; Glöckner and Pachur, 2012).

Second, we find that an effect of EV-difference on arousal, as measured by pupil dilation and skin conductance response, can be found in description-based but not in experience-based choices. If the same cognitive processes had been at work for information integration in both conditions, the effect of EV-difference on arousal should have been comparable. Together with the modeling results, the physiological data suggests that decisions from descriptions involve more complex mathematical processes of computation such as coherence construction (Glöckner and Betsch, 2008; see Models for Decision from Description, for details) or other ways of subjectively weighting outcomes (Ayal and Hochman, 2009), which are highly affected by expected value differences (see Ayal and Hochman, 2009; Glöckner and Hochman, 2011). By contrast, experience-based decisions might involve simpler processes based on linear integration and a comparison of the averages of experienced outcomes[13]. These processes appear to be more similar to accumulation of fixation-sampled evidence until a certain threshold is reached (Busemeyer and Townsend, 1993; Raab and Johnson, 2007; Krajbich and Rangel, 2011). Alternatively, they might also be similar to memory prompting (Dougherty et al., 1999; Thomas et al., 2008) or instance-based learning (Lejarraga et al., 2012)[14]. Presumably, these types of processes essentially require little more than remembering what was previously seen. Since these types of decisions are more easily constructed, they are arguably less sensitive to task-difficulty manipulations (e.g., differences in expected values). Of course, this interpretation of the arousal results will require further tests in future research.

Third, the link between attention measured by overt fixations and weight placed on specific outcomes in the decision tasks seems to be much stronger in decisions from experience than in decisions from descriptions. In the latter, our findings indicate that despite substantial fixation-based oversampling of rare events, there was relatively little overweighting and thus, fixation-based models perform relatively poorly (despite predictive power well above chance-level). In the experience condition, by contrast, the good model fit for fixation-based models indicates that the relation between attention and weight is quite strong.

MODELS FOR DECISIONS FROM EXPERIENCE

The current findings speak to several important questions concerning the specific processes underlying decisions from experience in the sampling paradigm. Specifically, they support the idea that certain implementations of evidence-accumulation models (Busemeyer and Townsend, 1993; see also Roe et al., 2001; Raab and Johnson, 2007; Jessup et al., 2008; Krajbich and Rangel, 2011) can account well for processes in decisions from experience. In addition, our data provide relatively clear hints on which implementations should be preferred: first, models assuming averaging of outcomes are superior to models assuming summing. This speaks against models assuming evidence-accumulation without standardization for the number of samples. Prominent evidence-accumulation models for decision making are conceptually based on the idea that there is a mere process of accumulation which does *not* include standardization for number of samples (e.g., Busemeyer and Townsend, 1993; Johnson and Busemeyer, 2005; Raab and Johnson, 2007; Krajbich and Rangel, 2011). Second, models taking into account all samples account for behavior better than recency-based models which rely only on a subset of samples. Note, however, that our investigation did not address models which assume that the number of recently sampled outcomes is a free parameter that reflect individual differences in sampling size. Thus, we cannot rule out the possibility that such more complex models, as well as models which assume decreasing weights for outcomes that are less recent may further improve the predictive power for participants' behavior in decisions from sampling.

MODELS FOR DECISIONS FROM DESCRIPTION

In line with prior evidence, our results indicate that choices in risky decisions from descriptions can be described adequately by Cumulative Process Theory (e.g., Tversky and Kahneman, 1992; Glöckner and Pachur, 2012)[15]. Nevertheless, process implementations of this theory assuming serial stepwise calculations of weighted sums have been rejected (Glöckner and Herbold, 2011). Instead, processes that rely at least partially on more complex automatic-intuitive mechanisms have received support. Process measures in Glöckner and Herbold were most in line with implementations of coherence construction models. The suggested adaptation of the Parallel Constraint Satisfaction Model (Thagard, 1989; Holyoak and Simon, 1999; Simon et al., 2004; Betsch and Glöckner, 2010) to risky choice assumes that probability weighted outcomes are used as competing pros and cons (i.e., cues) speaking for one or the other option and that initial advantages of one option are accentuated by partially relying on automatic-intuitive processes. The effect of conflict manipulated by decreasing EV-difference (as opposed to coherence) on arousal observed in the current study provides further support for this approach, and is in line with previous findings demonstrating a link between coherence and arousal (Hochman et al., 2010; Glöckner and Hochman, 2011). As noted above, the arousal findings might, however, also be explained by other mechanisms and further research is needed to investigate the processes underlying risky choice from description.

SUMMARY

The current results demonstrate that there are considerable differences in the cognitive processes underlying one-shot decisions from experience vs. description. In experience-based decisions, individuals are not explicitly provided with probability information and therefore evaluate options in a way that can be well-captured by naïve evidence-accumulation models assuming averaging of all fixation-sampled outcomes. The process seems to be based on a linear integration and a comparison of the averages. Thus, the difference between expected values of options does not influence arousal. Decisions from descriptions, by contrast, cannot be described well by fixation-based evidence-accumulation. Choices are more in line with Cumulative Prospect Theory, which, however, does not claim to describe processes. The findings that (i) different models account for choices best in the two paradigms, (ii) arousal increases with difference in expected value between options only in descriptions but not in experience, and (iii) the link between attention and weight given to certain outcomes is much stronger in experience indicate that qualitatively different kinds of processes are at work.

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[13] One factor contributing to this might be the simpler information display in the experience condition (see **Figure 1**).

[14] For a more general classification of these kinds of processes and their role in decision making, see also Glöckner and Witteman (2010).

[15] It should be noted that CPT has been rejected in favor of competing models in complex multi-outcome risky choices (Birnbaum, 2006, 2008a,b) but it is nonetheless considered a good paramorphic model for risky choices between two options with two outcomes each.

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APPENDICES

APPENDIX A

Gamble comprising rare event	**Alternative gamble**	**Desirable rare event**	**EV-diff**	**Percentage choosing the low-probability option**	
				Description ($N = 22$)	**Sampling ($N = 22$)**
10.4€ (0.94)/27.3€ (0.06)[a,b]	12.6€ (0.63)/0.2€ (0.37)	Yes	High	1	0.818*
26€ (0.09)/10.4€ (0.91)[a,b]	11.7€ (0.60)/4.1€ (0.40)	Yes	High	1	0.864[+]
7€ (0.91)/18€ (0.09)[a]	3.4€ (0.61)/23.8€ (0.39)[b]	Yes	High	0.591	0.409
7.3€ (0.93)/23.8€ (0.07)[a]	3.9€ (0.60)/23€ (0.40)[b]	Yes	High	0.409	0.682[+]
7.3€ (0.94)/27€ (0.06)[a]	3.9€ (0.60)/23.5€ (0.40)[b]	Yes	High	0.318	0.591[+]
25.7€ (0.05)/10.6€ (0.95)[a,b]	19.7€ (0.40)/0.10€ (0.60)	Yes	High	1	0.955
10.6€ (0.92)/23.5€ (0.08)[a,b]	1.1€ (0.59)/17.9€ (0.41)	Yes	High	1	0.909
22.8€ (0.06)/7.6€ (0.94)[a]	5.9€ (0.55)/20.2€ (0.45)[b]	Yes	High	0.273	0.455
26.8€ (0.07)/10.3€ (0.93)[a,b]	13€ (0.60)/1.5€ (0.40)	Yes	High	1	0.909
23.7€ (0.06)/7.1€ (0.94)[a]	24€ (0.41)/3.6€ (0.59)[b]	Yes	High	0.409	0.682[+]
8.7€ (0.90)/1.6€ (0.10)[b]	1.2€ (0.35)/16.7€ (0.65)[a]	No	High	0.682	0.455
0.4€ (0.08)/8.4€ (0.92)[b]	8.6€ (0.39)/13.1€ (0.61)[a]	No	High	0.091	0.045
0.1€ (0.05)/9.3(0.95)	24.4€ (0.40)/3.5€ (0.60)[a,b]	No	High	0.273	0.364
6.1€ (0.09)/12.7(0.91)[b]	10€ (0.43)/7.2€ (0.57)[a]	No	High	0.864	0.909
1.7€ (0.08)/8.8€ (0.92)	9.8€ (0.47)/13.7€ (0.53)[a,b]	No	High	0.045	0.045
12.3€ (0.93)/0.70€ (0.07)[b]	9€ (0.54)/7.3€ (0.46)[a]	No	High	0.273	0.545[+]
6.1€ (0.05)/12.5€ (0.95)[b]	2.3€ (0.56)/16€ (0.44)[a]	No	High	1	0.864[+]
1.5€ (0.09)/12.5€ (0.91)[b]	12.7€ (0.61)/0.10€ (0.39)[a]	No	High	0.955	0.909
12.2€ (0.94)/3.7€ (0.06)[b]	2.3€ (0.39)/12.2€ (0.61)[a]	No	High	0.909	0.955
1.7€ (0.06)/8.4€ (0.94)	13€ (0.52)/10.3€ (0.48)[a,b]	No	High	0.045	0
24.4€ (0.07)/9€ (0.93)[a,b]	5.8€ (0.42)/12.8€ (0.58)	Yes	Low	0.682	0.818
29.4€ (0.10)/8€ (0.90)[a]	12.3€ (0.57)/7.3€ (0.43)[b]	Yes	Low	0.636	0.682
9.6€ (0.94)/22.9€ (0.06)[a,b]	12.1€ (0.43)/8.7€ (0.57)	Yes	Low	0.727	0.727
8.7€ (0.91)/18.3€ (0.09)[a]	15.5€ (0.46)/5.2€ (0.54)[b]	Yes	Low	0.545	0.773
26.5€ (0.09)/8.3€ (0.91)[a]	1.9€ (0.36)/15€ (0.64)[b]	Yes	Low	0.818	0.864
8.6€ (0.91)/22.7€ (0.09)[a]	5.5€ (0.43)/13.2€ (0.57)[b]	Yes	Low	0.682	0.636
29.8€ (0.07)/8.9€ (0.93)[a,b,c]	2.7€ (0.47)/17.1€ (0.53)	Yes	Low		
9€ (0.92)/18.2€ (0.08)[a,b]	5.3€ (0.48)/13.3€ (0.52)	Yes	Low	0.773	0.818
8.8€ (0.92)/24.2€ (0.08)[a]	5.4€ (0.35)/13.2€ (0.65)[b]	Yes	Low	0.591	0.773
9€ (0.91)/21.3€ (0.09)[a]	13.2€ (0.45)/8.4€ (0.55)[b]	Yes	Low	0.727	0.5
1€ (0.08)/10.7€ (0.92)	20.3€ (0.45)/1.9€ (0.55)[a,b]	No	Low	0.727	0.591
2.9€ (0.06)/10.6€ (0.94)	1.2€ (0.65)/27.5€ (0.35)[a,b]	No	Low	0.864	0.818
1.4€ (0.09)/10.3€ (0.91)	14.8€ (0.40)/6€ (0.60)[a,b]	No	Low	0.727	0.227*
4€ (0.06)/11.2€ (0.94)[b]	2.8€ (0.53)/18.3€ (0.47)[a]	No	Low	0.682	0.545
5€ (0.08)/10.8€ (0.92)[b]	2.1€ (0.57)/19.9€ (0.43)[a]	No	Low	0.591	0.591
2.2€ (0.08)/10.2€ (0.92)	4.4€ (0.47)/14.2€ (0.53)[a,b]	No	Low	0.591	0.864*
2.7€ (0.05)/10.6€ (0.95)[b]	5.5€ (0.57)/16.2€ (0.43)[a]	No	Low	0.773	0.636
9.8€ (0.92)/4.3€ (0.08)	1.1€ (0.37)/14.9€ (0.63)[a,b]	No	Low	0.909	0.682[+]

The table shows all gambles and the probabilities of choosing the gamble with the low-probability outcome. Two-sample z-tests for equal proportions were conducted comparing percentages between conditions.

[a] *Gamble should be more often chosen if small probabilities are overweighted.*

[b] *Gamble with the higher expected value.*

[c] *Decision excluded from analysis due to partially wrong information presentation caused by a programming error.*

[+] *$p < 0.10$; *$p < 0.05$.*

APPENDIX B

Summation models

To implement summation models we calculate V_{diff} as follows:

$$V_{\text{diff}} = \left(f_{\mathrm{A}_1}^{f}\,\mathrm{o}_{\mathrm{A}_1} + f_{\mathrm{A}_2}^{f}\,\mathrm{o}_{\mathrm{A}_2}\right) - \left(f_{\mathrm{B}_1}^{f}\,\mathrm{o}_{\mathrm{B}_1} + f_{\mathrm{B}_2}^{f}\,\mathrm{o}_{\mathrm{B}_2}\right) \tag{A1}$$

Where A and B represent the two choice options, O represent the outcome, 1 and 2 the first and second outcome of each option, and f_{X}^{f} indicate the number of fixations to the outcomes X.

Averaging models

For averaging models, the sums of sampled outcomes for each option were additionally standardized by the total number of fixations to the respective option according to:

$$V_{\text{diff}} = \frac{\left(f_{\mathrm{A}_1}^{f}\,\mathrm{o}_{\mathrm{A}_1} + f_{\mathrm{A}_2}^{f}\,\mathrm{o}_{\mathrm{A}_2}\right)}{f_{\mathrm{A}_1}^{f} + f_{\mathrm{A}_2}^{f}} - \frac{\left(f_{\mathrm{B}_1}^{f}\,\mathrm{o}_{\mathrm{B}_1} + f_{\mathrm{B}_2}^{f}\,\mathrm{o}_{\mathrm{B}_2}\right)}{f_{\mathrm{B}_1}^{f} + f_{\mathrm{B}_2}^{f}}. \tag{A2}$$

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The impact of deliberative strategy dissociates ERP components related to conflict processing vs. reinforcement learning

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We applied the event-related brain potential (ERP) technique to investigate the involvement of two neuromodulatory systems in learning and decision making: The locus coeruleus–norepinephrine system (NE system) and the mesencephalic dopamine system (DA system). We have previously presented evidence that the N2, a negative deflection in the ERP elicited by task-relevant events that begins approximately 200 ms after onset of the eliciting stimulus and that is sensitive to low-probability events, is a manifestation of *cortex-wide* noradrenergic modulation recruited to facilitate the processing of unexpected stimuli. Further, we hold that the impact of DA reinforcement learning signals on the anterior cingulate cortex (ACC) produces a component of the ERP called the feedback-related negativity (FRN). The N2 and the FRN share a similar time range, a similar topography, and similar antecedent conditions. We varied factors related to the degree of cognitive deliberation across a series of experiments to dissociate these two ERP components. Across four experiments we varied the demand for a deliberative strategy, from passively watching feedback, to more complex/challenging decision tasks. Consistent with our predictions, the FRN was largest in the experiment involving active learning and smallest in the experiment involving passive learning whereas the N2 exhibited the opposite effect. Within each experiment, when subjects attended to color, the N2 was maximal at frontal–central sites, and when they attended to gender it was maximal over lateral-occipital areas, whereas the topology of the FRN was frontal–central in both task conditions. We conclude that both the DA system and the NE system act in concert when learning from rewards that vary in expectedness, but that the DA system is relatively more exercised when subjects are relatively more engaged by the learning task.

Keywords: norepinephrine, dopamine, N2, feedback error-related negativity, anterior cingulate cortex, locus coeruleus, event-related potential, fusiform gyrus

INTRODUCTION

Adaptive decision making depends on both fast and efficient processing of stimulus events for effective responding (e.g., Servan-Schreiber et al., 1990) and slow trial-to-trial learning of action values for optimizing the selection process (e.g., Schultz et al., 1997). The catecholinergic neuromodulatory systems that distribute norepinephrine (NE) and dopamine (DA) have been implicated in these two groups of processes, respectively (Servan-Schreiber et al., 1990; Schultz et al., 1997). Further, putative manifestations of these systems have been identified in the human electroencephalogram (EEG; Holroyd and Coles, 2002; Nieuwenhuis et al., 2005a,b; Warren et al., 2011). However, the way these two systems interact has yet to be explored.

The locus coeruleus–norepinephrine system (NE system) is believed to play a key role in facilitating fast and effective processing of task-relevant stimuli (Usher et al., 1999). The locus coeruleus (LC) is a neuromodulatory nucleus in the midbrain that briefly enhances cortical processing in reaction to motivationally salient or conflict-inducing events (Usher et al., 1999; Gilzenrat et al., 2002). The LC is the primary source of NE to the cortex and other regions (Berridge and Waterhouse, 2003), where NE release increases the responsivity of individual neurons and improves the signal-to-noise ratio of associated neural networks (Servan-Schreiber et al., 1990). Single-cell recordings from the LC in monkeys show that the LC releases NE in phasic bursts to motivationally salient events, and periods of greater phasic release of NE are associated with better performance in target discrimination tasks (Usher et al., 1999). The NE system is also auto-inhibitory, such that phasic bursts of NE are followed by a refractory-like[1] period lasting ∼500 ms characterized by reduced or arrested NE supply to the cortex.

In a previous paper (Warren et al., 2011), we proposed that the impact of phasic bursts of NE on cortical processing manifests in the human EEG as an increase in amplitude of the N2, a negative deflection of the human event-related brain potential (ERP) occurring between about 200 and 300 ms after the onset

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[1] As opposed to the potassium-mediated refractory period common to individual neurons throughout the brain.

of the eliciting stimulus, the amplitude of which is exercised by unexpected or conflict-inducing events (e.g., Nieuwenhuis et al., 2003). This theory is a modification of a previous "LC–P3 theory" that holds that the phasic bursts of NE produce the P3 – a prominent, positive deflection in the ERP that immediately follows the N2 – rather than the N2 itself (Nieuwenhuis et al., 2005a). Thus, our "modified LC–P3 theory" develops this account by proposing that the LC burst impacts cortical activity somewhat earlier than originally proposed, during the time period of the N2 (∼250 ms post-stimulus), whereas the LC refractory period coincides with P3 generation.

A key prediction of our proposal is that any change in the ERP due to noradrenergic modulation should exhibit a variable scalp distribution dependent on relative engagement of the different cortical areas giving rise to the ERP. This position follows from two key characteristics of the NE system. First, the broadly dispersed efferent projection system of the LC distributes NE to all regions of the cortex, so any given phasic release can modulate neural activity (and the associated N2) anywhere in cortex (Berridge and Waterhouse, 2003; Nieuwenhuis et al., 2007). Second, NE-mediated *changes* in activity should be greatest in cortical areas that are most engaged by the task at hand because increasing the signal-to-noise ratio in the entire cortex will have the greatest impact in those areas (Nieuwenhuis et al., 2005a, 2011). This position contrasts with theories of the N2 which posit that the N2 is produced specifically by the anterior cingulate cortex (ACC) and should therefore exhibit a relatively fixed topology, maximal at frontal–central regions of the scalp (e.g., van Veen and Carter, 2002a,b; Yeung et al., 2004).

In previous work, we supported the modified LC–P3 theory by demonstrating that the scalp distribution of the N2 varies widely according to task changes that relatively engage different cortical areas (Warren et al., 2011). We presented subjects with pictures of male and female faces that were tinted either blue or yellow. Subjects attended to either the gender or the color of the faces and counted targets in an oddball task. The impact of frequency was isolated by subtracting frequent stimulus trials from infrequent stimulus trials, yielding a difference-wave representative of the change in neural activity specifically caused by differences in stimulus probability (and putatively due to differences in NE recruitment). When subjects attended to the color of the face, the N2 in the difference wave was maximal over frontal–central regions as is often observed in simple oddball tasks (e.g., Nieuwenhuis et al., 2003; Holroyd et al., 2008; but see Folstein and Van Petten, 2007), consistent with arguments that the N2 is generated in the ACC (van Veen and Carter, 2002a,b; Yeung et al., 2004). By contrast, when subjects attended to the gender of the faces the N2 in the difference wave was maximal over lateral-occipital regions, consistent with a relatively large change in activity within the fusiform face-processing area (FFA). This study demonstrated that identical task stimuli (colored faces) presented with identical task designs (standards and deviants) can nevertheless radically alter the topology of the N2 depending on which aspect of the stimuli participants are instructed to attend.

An interesting special case of the N2 occurs when the eliciting stimulus is a feedback stimulus in a reward/no-reward paradigm. A negative feedback stimulus (e.g., that indicates a potential reward was not received) elicits a frontal–central negative deflection in the same time range as the N2, but positive feedback does not (Miltner et al., 1997). This difference is called the feedback-related negativity (FRN), and is usually measured with a difference wave approach whereby the ERP to reward feedback is subtracted from the ERP to error feedback (Holroyd and Krigolson, 2007). It is important to note that the FRN may be characterized by variance in the ERP associated with *both* negative *and* positive feedback. Source localization studies suggest that the FRN is generated in, or very close to, the ACC (Gehring and Willoughby, 2002; Miltner et al., 2003; Hewig et al., 2007). Additionally, a neurocomputational theory of this ERP component is based on the seminal observation that rewarding events elicit phasic bursts of dopamine (DA) activity that are utilized by the targets of the DA system (including the ACC) for the purpose of adaptive decision making (Schultz et al., 1997; Holroyd and Coles, 2002). In particular, single-cell recordings from primates show increased phasic DA activity in response to unexpected rewards or reward predictors, and shallow dips from baseline DA activity in response to punishment or to the absence of expected rewards (e.g., Schultz, 2002). Holroyd and Coles (2002) proposed the reinforcement learning theory of the FRN, which holds that the FRN reflects the impact of these phasic DA signals on the ACC such that motor neurons in the ACC are inhibited and disinhibited by phasic increases and decreases of DA, respectively.

Recent evidence suggests that these phasic DA signals specifically modify the amplitude of the N2. According to this position, the ACC produces a negative deflection to unexpected task-relevant events (the N2), including unexpected negative feedback and unexpected reward feedback. However, unexpected reward feedback also elicits a dopamine-induced positive deflection ("the reward positivity") that is superimposed over the N2 and cancels it out (Holroyd et al., 2008). In other words, unexpected error and reward feedback elicit the N2, but unexpected reward feedback *also* elicits a reward positivity that obscures the N2, creating the difference observed between the ERPs to positive and negative feedback (the FRN).

To dissociate the reward positivity from the N2, a recent multi-experiment study presented subjects with complicated reward feedback that indicated not only whether a subject had won or lost money, but also what response was required of them for the subsequent trial (Baker and Holroyd, 2011). In one experiment, a stimulus-induced delay in reward processing caused the reward positivity to appear about 100 ms later than usual (peaking at about 350 ms), thereby exposing the N2 on those trials. When the reward-feedback stimulus was simplified in further experiments, the reward positivity appeared earlier and attenuated the N2. Furthermore, factors related to response conflict impacted N2 amplitude and reduced the reward positivity on high-conflict reward trials.

The ACC has been posited to be the neural generator of both the N2 (van Veen and Carter, 2002a,b; Yeung et al., 2004) and the FRN (Holroyd and Coles, 2002). Furthermore, here we have proposed that noradrenergic modulation enhances activity in the ACC and all across the cortex, amplifying the N2 in target areas. Thus, there are three factors that push the amplitude of the N2 at frontal–central scalp locations up and down: ACC activity, noradrenergic modulation, and dopaminergic modulation. If we have any chance of understanding how the frontal–central N2 provides insight into ACC function, we need to understand how these systems interact – otherwise we will be at a loss to interpret N2 data.

To investigate this issue, we employed the same paradigm used in our previous study (Warren et al., 2011), presenting subjects with male or female faces tinted either blue or yellow, with frequent or infrequent category presentations based on either the gender or the color of the faces. But here the stimuli also indicated reward or no-reward, allowing us to simultaneously examine the N2 and the FRN. We manipulated the amplitudes of the reward positivity and the N2 along two independent dimensions. Along one dimension, we varied (across subjects) the degree of participant engagement in a feedback task, which is known to affect FRN amplitude. For example, Yeung et al. (2005) manipulated the degree to which a deliberative strategy was required of subjects, from passively observing reward/no-reward outcomes, to actively making a decision that would result in either reward or no-reward. The FRN was significantly larger when subjects utilized the feedback to optimize their decisions, as opposed to passively collecting rewards (see also Holroyd et al., 2009; Li et al., 2011; Peterson et al., 2011). We implemented this manipulation across three experiments wherein subjects passively collected rewards in Experiment 1 (Passive Experiment), made a decision based on multiple stimulus feature-response combinations in Experiment 2 (Active Experiment), and intermediate to these, made a decision based on relatively simple response–reward contingencies in Experiment 3 (Moderate Experiment). We predicted that the FRN would be largest in the Active Experiment and reduced or absent in the others. By contrast, we predicted that the N2 would be smaller with increasing task engagement because of component overlap with the reward positivity elicited by infrequent rewards.

Along the second dimension we varied N2 amplitude by manipulating (within subjects) the attended dimension of the feedback: Subjects were required to attend to either the color or the gender of the feedback stimuli (male or female faces tinted either blue or yellow). We predicted that switching from color to gender would move the N2 from frontal–central to lateral-occipital regions of the scalp. By contrast, we predicted that the FRN would remain frontal–central irrespective of the attended dimension of the feedback. Further, we predicted that we would observe maximal interference between the two components in the color condition of the Active Experiment, where both the N2 and the reward positivity are frontal–central. These results would validate our claim that the N2 and FRN are produced by distinct neural mechanisms, one that produces a negativity to infrequent events that has a variable scalp distribution consistent with a noradrenergic origin, and one that produces a positivity to rewards and a negativity to no-rewards that has a frontal–central scalp distribution consistent with genesis in the ACC.

EXPERIMENT 1: PASSIVE LEARNING

In the Passive Experiment we sought to replicate the results of our previous study by engaging the NE system and the N2 in an oddball task with minimal involvement of reinforcement learning systems and therefore minimal interference from the FRN. We employed the exact same paradigm as reported in our previous work (Warren et al., 2011) except that instead of counting stimuli associated with a target category (e.g., male faces), subjects counted earnings accrued with each stimulus presentation (e.g., if subjects were told that they would be given 5 cents for each male face); they were asked to report the sum once during the block and a second time at the end of the block. Importantly, because participants were not required to make an overt response on each trial, we expected this task to elicit only a small FRN, if any (Yeung et al., 2005; Holroyd et al., 2009; Li et al., 2011). Further, as we observed previously, we predicted that relative engagement of the FFA in the attend-gender condition would enhance the N2 over lateral-occipital sites, whereas relative engagement of the ACC in the attend-color condition would enhance the N2 over frontal–central sites. Finally, we predicted that the FRN – to the extent that it was present – would not exhibit any changes in scalp topography.

METHOD

Methods were identical across all four experiments except where indicated.

Participants

Twenty-one people (three males) completed this experiment. For all experiments reported in this paper, participants signed up through the research participation system at the University of Victoria, Canada, and were compensated with extra credit in an undergraduate psychology course or were paid $20.00 Canadian for their time. This project (Experiments 1 through 4) was approved by the human subjects review board at the University of Victoria and conducted in accordance with the ethical standards prescribed in the 1964 Declaration of Helsinki.

Apparatus and procedure

Participants were seated comfortably, approximately 50 cm in front of a computer screen, in an electromagnetically shielded booth. Stimuli consisted of male or female faces (30 examples of each, lifted from black and white photos, excluding hair and contour of head) and tinted either blue or yellow (~4.4° visual angle). In a previous experiment (Warren et al., 2011), we used a larger set of the same stimuli (40 males and 40 females), but because the error rates in discriminating between male and female faces were high, here we selected a subset of those stimuli: The 75% that were most accurately discriminated previously. For both stimulus dimensions (color, gender), one stimulus type occurred infrequently (20% of all trials). The order of stimulus presentation was randomized with replacement. At the beginning of each block, subjects were instructed by the computer program to keep track of presentations of a specific target stimulus (blue faces, yellow faces, male faces, or female faces), which when presented would indicate a winning trial. The task consisted of eight blocks of 75 trials each (600 total trials), counterbalanced such that each of the four stimulus types (blue males, yellow males, blue females, yellow females) occurred in two blocks as the target, and of those two blocks, once as a frequent target and once as an infrequent target. Stimuli were presented for 1200 ms and were separated by a fixation cross displayed for 300 ms (see **Figure 1**, Passive Learning, for a graphic representation of the task).

Each presentation of the target stimulus category indicated that the subject won $0.05. Subjects were instructed to keep track of the

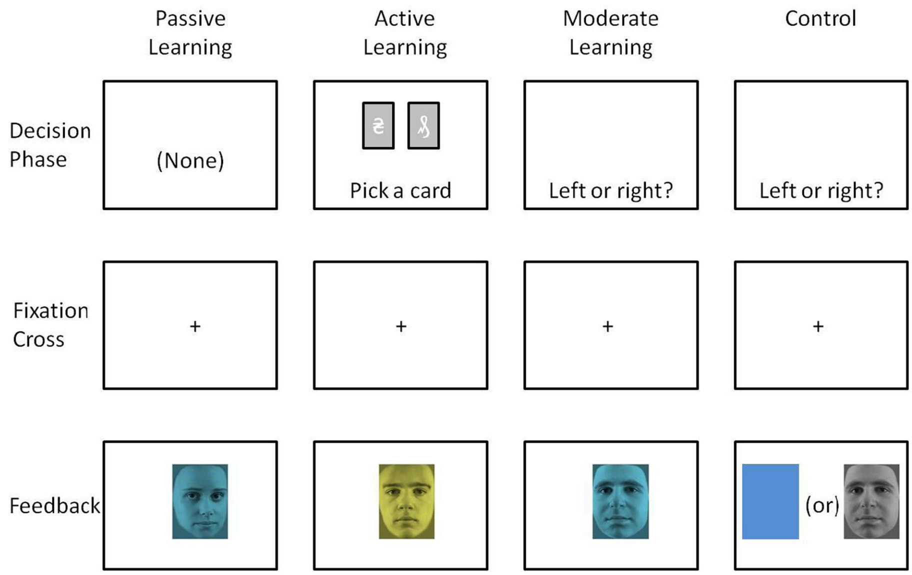

FIGURE 1 | Graphic representation of the four experiments.

money won and were required to report their count twice per block (at a random trial number about halfway through each block, and at the end of each block). This method yielded 16 reports of the subject's money count. Subjects reported their count by answering an eight-choice multiple choice question, choosing from several ranges within which the correct count fell (e.g., between \$0.30 and \$0.50, or between \$ 0.55 and \$0.75, etc.). We assessed accuracy by dividing the number of correct reports by the number of total reports.

Data acquisition

The EEG was recorded from 41 electrode locations arranged in the standard 10–20 layout using Brain Vision Recorder software (Version 1.3, Brain Products, Munich, Germany). During recording, the EEG data were referenced to the average voltage across channels, sampled at 250 Hz, and amplified (Quick Amp, Brain Products) and filtered through a passband of 0.017–67.5 Hz (90 dB octave roll off). Impedances were below 12 kΩ.

EEG data analysis

The EEG data were filtered off-line through a 0.1- to 20-Hz passband phase-shift-free Butterworth filter and re-referenced to linked mastoids. Ocular artifacts were removed using the algorithm described by Gratton et al. (1983). Trials in which the change in voltage at any channel exceed 35 μV per sampling point were removed. In total, 0.02% of the data were discarded. Thousand ms epochs of data were extracted from the continuous EEG from 200 ms before stimulus onset to 800 ms after. The data were baseline-corrected according to the average amplitude of the EEG over the 200-ms preceding stimulus presentation and ERPs were created by averaging the EEG data for each condition, electrode site, and participant.

To isolate the effect of reward independent of frequency, we subtracted the ERPs associated with reward from the ERPs associated with no-reward yielding an attend-color FRN and attend-gender FRN that were equated for the effect of stimulus probability. This method maximized the signal-to-noise ratio in the ERPs, as opposed to averaging the ERPs separately for the infrequent reward trials, frequent reward trials, infrequent no-reward trials, and frequent no-reward trials. Similarly, to isolate the effect of frequency independent of reward feedback, we subtracted the ERP associated with the frequently occurring stimuli from the ERP associated with the infrequently occurring stimuli, collapsed across reward condition, yielding a difference-wave N2 (dN2) for each task condition (attend-color, attend-gender). Thus, each of the infrequent and frequent ERPs contained equal numbers of reward and no-reward trials such that the difference between these ERPs were equated for the effects of reward. Note that because NE system activity causes a change in the relative activation of the underlying cortical systems (i.e., making ERP components larger), the impact of NE on the ERP is most appropriately measured in a difference wave that isolates that change. We distinguish between the dN2, and the "raw" N2 in light of this consideration. The interaction of the raw N2 and the reward positivity to the four individual conditions was examined separately in an across-group comparison (below).

The amplitudes of the dN2 and FRN were assessed using a base-to-peak measure as follows: For each subject in each condition, the most negative peak between 200 and 280 ms in the attend-color condition, or 300 vs. 380 ms in the attend-gender condition was identified and recorded as the dN2/FRN peak amplitude. The base amplitude of the dN2/FRN was then taken as the most positive voltage prior to the dN2/FRN and these values were subtracted from the dN2/FRN peak amplitude, yielding our base-to-peak measures. This procedure controls for overlap with the P2, a positive deflection that typically immediately precedes the dN2 and that can push the dN2 into positive peak values. Note that because the FRN is not typically preceded by any notable deflection in the difference wave, the base measure is approximately 0 μVs; for this reason the base-to-peak measure of the FRN is equivalent to a peak amplitude measure. However, we chose to assess FRN base-to-peak for consistency with our method for assessing dN2 amplitude.

In assessing the change in component topology across task conditions, we focused on two electrode sites representative of frontal–central and lateral-occipital scalp regions as we did in our previous study, specifically at channel locations FCz and P8. Both the FRN and the dN2 are typically maximal at channel FCz (e.g., Holroyd et al., 2008) and the dN2 was maximal at channel P8 in the attend-gender condition of our previous study (Warren et al., 2011). Single-tailed t-tests were applied to assess the amplitudes of these ERP components at these channels because of our *a priori* hypotheses of the direction of each difference. For example, we predicted that the dN2 would be larger at channel P8 than at channel FCz for the attend-gender condition; a dN2 that was larger at FCz than at P8 would run contrary to our hypothesis.

RESULTS

Behavioral results

Mean accuracy was 79.2% (SD = 14.4%) for the attend-color condition and 68.5% (SD = 21.2%) for the attend-gender condition. The data of one subject were eliminated from further analysis because the accuracy score was more than 2 SD below the mean in the attend-color condition. For the remaining 20 subjects, mean accuracy was 80.6% (SD = 13.1%) for the attend-color condition and 70% (SD = 20.4%) for the attend-gender condition. This difference approached significance using a two-tailed t-test, $t(19) = -2.0$, $p < 0.10$.

EEG results

The raw ERPs, difference waves and scalp distributions are shown in **Figure 2**. Inspection of the scalp distributions suggests that the attend-color dN2 was maximal over frontal–central sites (FCz, $-4.5\ \mu V$) whereas the attend-gender dN2 was maximal at lateral-occipital regions (PO8, $-3.5\ \mu V$). This impression was confirmed with a 2 × 2 ANOVA on dN2 amplitude with electrode (FCz vs. P8) and task (attend-color vs. attend-gender) as repeated factors. There was an effect of task such that the dN2 was larger in the attend-color condition ($-4.0\ \mu V$) than the attend-gender condition ($-2.8\ \mu V$), $F(1, 19) = 10.8$, $p < 0.01$, $\eta^2 = 0.36$. There was also an interaction of electrode and task, $F(1, 19) = 6.8$, $p < 0.05$, $\eta^2 = 0.26$, and one-tailed paired samples t-tests revealed that in the attend-color condition, the dN2 was larger at FCz than P8 (-4.5 vs. $-3.4\ \mu V$), $t(19) = -2.0$, $p < 0.05$, whereas in the attend-gender condition the dN2 was larger at P8 than at FCz (-3.2 vs. $-2.5\ \mu V$), $t(19) = 2.0$, $p < 0.05$.

Inspection of the scalp distributions in **Figure 2** further indicates that the FRN was distributed over posterior, rather than frontal, regions of the head in both the attend-color (Pz, $-5.2\ \mu V$) and attend-gender (POz, $-4.0\ \mu V$, followed by Pz, $-4.0\ \mu V$) conditions. A 2 × 2 ANOVA on FRN amplitude with electrode and task as repeated factors revealed an effect of electrode such that the FRN was larger at FCz than at P8 (-3.5 vs. $-2.9\ \mu V$), $F(1, 19) = 4.8$, $p < 0.05$, $\eta^2 = 0.20$. There was a trend toward a main effect of task such that the attend-color task yielded a larger FRN than the attend-gender task (-3.5 vs. $-2.9\ \mu V$), $F(1, 19) = 4.0$, $p < 0.10$, $\eta^2 = 0.18$. There was also a trend toward an interaction of electrode and task, $F(1, 19) = 3.2$, $p < 0.10$, $\eta^2 = 0.14$, and one-tailed paired samples t-tests revealed that in the attend-color condition, the FRN was larger at FCz than P8 (-4.1 vs. $-3.0\ \mu V$), $t(19) = -2.3$, $p < 0.05$, whereas there was no significant difference in the attend-gender condition (FCz: $-3.0\ \mu V$; P8: $-2.9\ \mu V$, $p > 0.05$). An additional check indicated that the FRN was larger at Pz than FCz in the attend-gender condition, $t(19) = 2.9$, $p < 0.01$, but not in the attend-color condition, $t(19) = 1.4$, $p > 0.05$.

DISCUSSION

We proposed that the dN2 is a manifestation of cortex-wide NE neuromodulation, and predicted that the impact of NE modulation on cortex and therefore the topology of the dN2 should vary according to task demands. By contrast, a standard theory of the FRN holds that it is produced by the impact of DA signals on ACC activity, and therefore that the FRN should appear with a consistent frontal–central scalp topology across task conditions. Here, we replicated our previous finding that the dN2 changes from exhibiting a primarily central scalp distribution when subjects categorize tinted faces based on color to a more lateral-occipital distribution when subjects categorize the same face stimuli based on the gender of the face. Further, although the FRN was larger at frontal central regions in both the attend-color and attend-gender conditions, it was not significantly larger at FCz than P8 in the attend-gender condition, it was relatively small overall (ranging from -2.9 to $-4.1\ \mu V$), and it exhibited a scalp distribution that was mostly posterior (see **Figure 2**). These results are inconsistent with the identification of this component with the FRN (Miltner et al., 1997) and indicate that (as predicted) this task did not produce a robust FRN. We conclude that, with minimal interference from the FRN, the dN2 exhibits a prominent yet variable scalp distribution.

EXPERIMENT 2: ACTIVE LEARNING

The Active Experiment maximized engagement of the system underlying the FRN by presenting subjects with an apparently complex decision task that encouraged deliberation. Subjects were asked to choose between two elaborate images of tarot cards presented side-by-side on a computer screen by pressing either a left or right key on a keyboard. Six different cards were paired a total of 15 different ways. The subjects were told that with each pairing one card had a better chance of winning than the other, and that they were required to learn which card to pick in any specific pairing (as opposed to finding which of the six cards had the best chance of winning overall). The complexity of the stimulus displays was intended to cultivate a sense that the task was challenging yet learnable (when in fact it was not). In so doing we expected the feedback stimuli to elicit a relatively large FRN with a frontal–central scalp topography for both the attend-gender and attend-color conditions. We further predicted that the FRN would interfere with the production of the dN2 in both the attend-color and attend-gender conditions.

METHOD

Participants

Twenty people (six males) participated in this study.

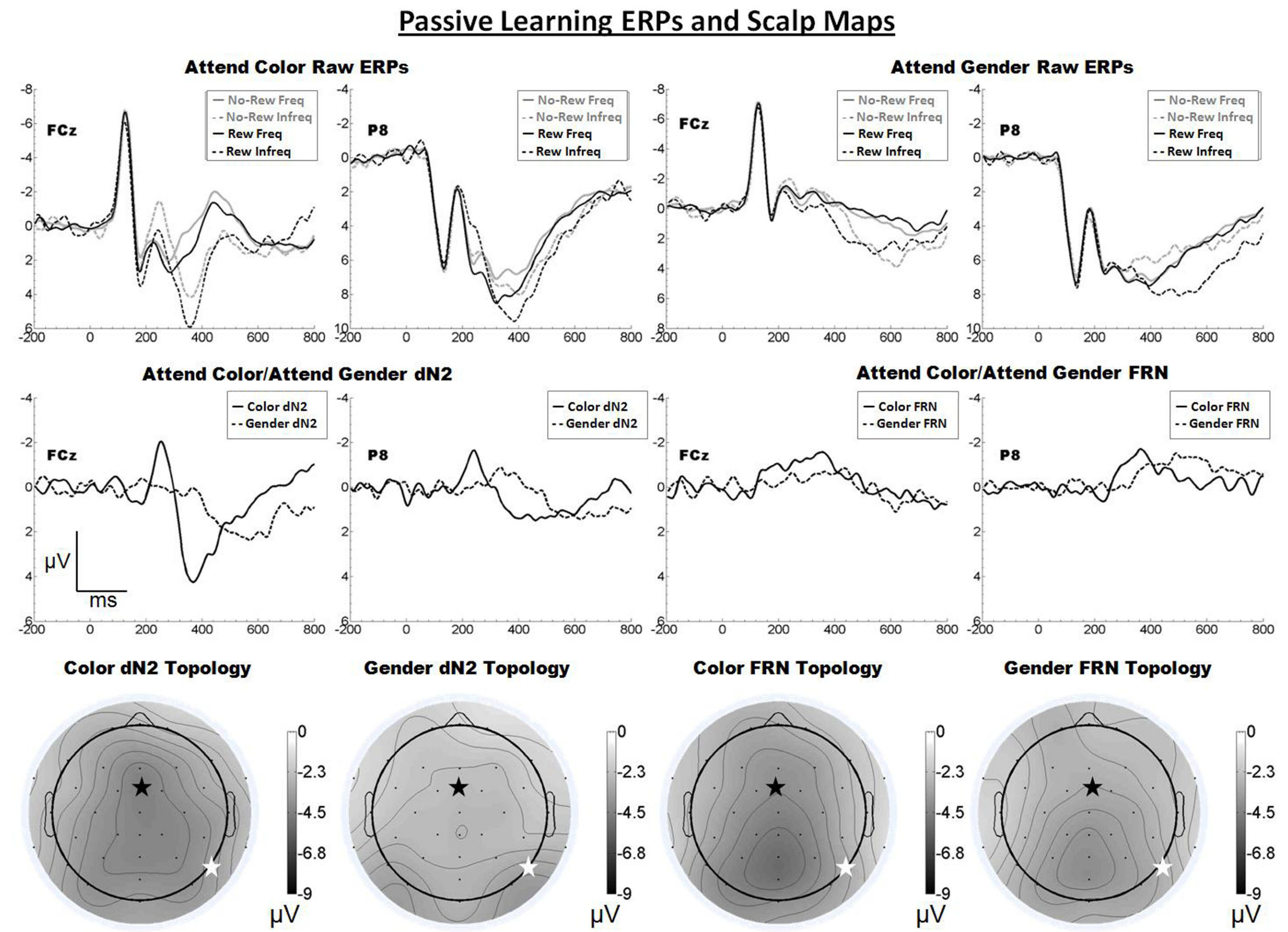

FIGURE 2 | Grand average ERPs for Experiment 1, recorded from channel FCz and P8 (see labels) and scalp distributions associated with the difference waves. The top row shows the "raw" ERPs for each of the frequency by reward conditions across tasks and electrodes. The middle row shows the dN2 and FRN difference waves across task and electrodes. The bottom row shows the scalp distributions of the dN2 and FRN across tasks. The scalp distributions reflect the base-to-peak measure of each of the dN2 and FRN. The black star on the scalp map denotes channel FCz, and the white star denotes P8. Note that negative is plotted up.

Apparatus and procedure

Stimuli and procedure were the same as in the Passive Experiment except where indicated. Each trial began with presentation of two tarot cards appearing on a computer display side-by-side (see **Figure 1**, Active Learning). Instead of passively counting their accumulated winnings as in the Passive Experiment, subjects were required to choose between the two tarot cards by pressing the appropriate key on the keyboard. The choice screen was displayed until the participant made their decision. When a selection was made the cards were replaced by a fixation cross for 600 ms and then the face-feedback stimulus was presented for 1200 ms. The feedback stimuli were presented and organized in the same manner as in the Passive Experiment.

Tarot cards were detailed images (six images in total) presented in random pairs. Subjects were instructed to try to learn which cards had a better chance of "paying off" in any given pairing, and to maximize their winnings by consistently making the best choice. In addition, subjects were told there would be "hard" blocks in which the pay-off chances for making the right choice were only 10 and 30%, and "easy" blocks in which the pay-off chances were 70 and 90%. Because of the length of the task, the number of trials was reduced from 600 in the Passive Experiment to 400 for the Active Experiment. The task consisted of eight blocks of 50 trials each and the conditions were counterbalanced across blocks as in the Passive Experiment. Additionally, we included only 8 (rather than 16) money count reports (one per block). As in the Passive Experiment, we assessed accuracy in reporting the money count for the Active Experiment by dividing the number of correct reports by the number total reports.

EEG data acquisition and analysis

The EEG data were acquired and analyzed and the dN2 and FRN were assessed in the same way as in the Passive Experiment.

RESULTS

Behavioral results

The mean accuracy was 82.5% (SD = 21.6%) for the attend-color condition and 86.2% (SD = 15.1%) for the attend-gender condition. This effect of task condition on accuracy was not significant ($p > 0.05$).

EEG results

The raw ERPs, difference waves and scalp maps are shown in **Figure 3**. Inspection of the scalp distributions suggests that the attend-color dN2 was mostly flat across the scalp but that it exhibited a maximum over lateral-occipital sites (PO7, −3.8 μV). This was also true for the attend-gender dN2 (PO7, −3.7 μV). A 2 × 2 ANOVA on dN2 amplitude with electrode (FCz vs. P8) and task (attend-color vs. attend-gender) as repeated factors yielded no significant effects (all *p*s > 0.05). The mean dN2 amplitudes were as follows: Attend-color: FCz, −3.1 μV, P8, −3.1 μV; attend-gender: FCz, −3.1 μV, P8, −3.1 μV.

Inspection of the scalp distributions of the FRN indicates the FRN was strongly frontal–central in both conditions (attend-color: FCz, −6.7 μV; attend-gender: Cz −5.2 μV followed by CP1, −5.1 μV, and FCz, −5.0 μV). A 2 × 2 ANOVA on FRN amplitude with electrode and task as repeated factors confirmed this impression, revealing an effect of electrode such that the FRN was larger at FCz than at P8 (−5.9 vs. −4.3 μV), $F(1, 19) = 14.3$, $p < 0.01$, $\eta^2 = 0.43$. There was also an effect of task such that the attend-color FRN was larger than the attend-gender FRN (−5.6 vs. −4.5 μV), $F(1, 19) = 5.9$, $p < 0.05$, $\eta^2 = 0.24$. The interaction of electrode and condition was not significant ($p > 0.05$). Further analysis revealed that in the attend-color condition the FRN was significantly larger at FCz than at P8 (−6.7 vs. −4.6 μV), $t(19) = -3.2$, $p < 0.01$, and in the attend-gender condition the FRN was also larger at FCz than at P8 (−5.0 vs. −4.0 μV), $t(19) = -2.2$, $p < 0.05$. An additional *t*-test revealed that the scalp distribution of the attend-gender FRN was not significantly larger at Cz than FCz ($p > 0.05$).

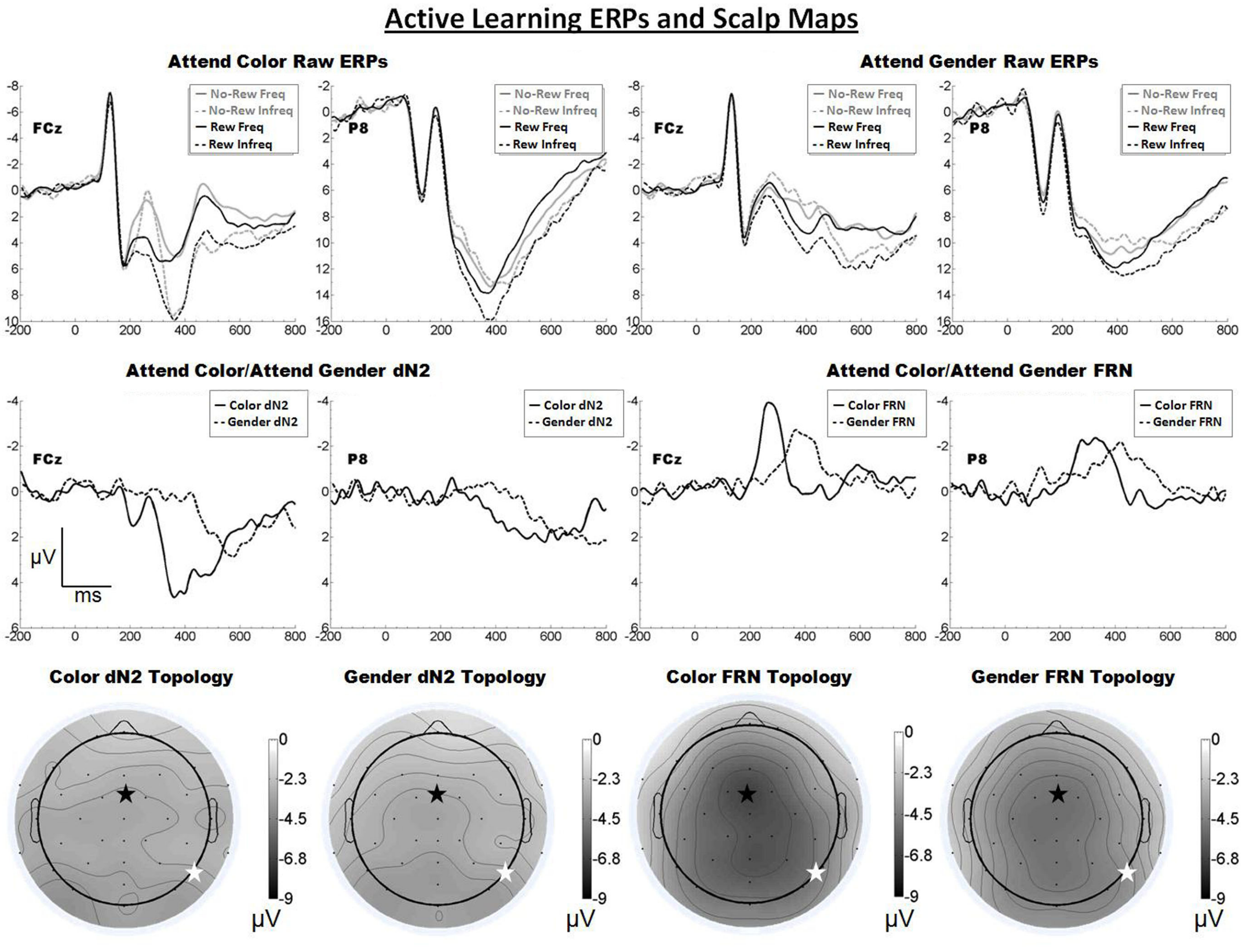

FIGURE 3 | Grand average ERPs for Experiment 2, recorded from channel FCz and P8 (see labels) and scalp distributions associated with the difference waves. The top row shows the "raw" ERPs for each of the frequency by reward conditions across tasks and electrodes. The middle row shows the dN2 and FRN difference waves across task and electrodes. The bottom row shows the scalp distributions of the dN2 and FRN across tasks. The scalp distributions reflect the base-to-peak measure of each of the dN2 and FRN. The black star on the scalp map denotes channel FCz, and the white star denotes P8. Note that negative is plotted up.

DISCUSSION

As predicted, increasing the complexity of the stimulus display resulted in a larger FRN for both the attend-color and attend-gender conditions, evidently because these task elements were better able to engage the system that produces the FRN. Further, the FRN appeared frontal central in both conditions, as predicted. By contrast, the dN2 was small and its topology was relatively flat in contrast to the results of the Passive Experiment and our previous work (Warren et al., 2011). We suggest that component overlap with the FRN reduced dN2 amplitude in this task in both the attend-color and attend-gender conditions, a question that we will return to in our across experiments analysis (see below).

EXPERIMENT 3: MODERATE LEARNING

The probability manipulation in the Passive Experiment elicited a strong dN2 but the passive nature of the task did not strongly engage the systems that produce the FRN. By contrast, the challenging learning task utilized in the Active Experiment produced a large FRN that strongly attenuated the dN2. In the Moderate Experiment, we sought to utilize a task that would produce both a dN2 and FRN to compare the two components within a single experiment. We therefore simplified the decision task in the Active Experiment such that it would engage (putatively) the DA system sufficiently to produce a FRN, but not so strongly that the FRN would obscure the dN2. We predicted that in this task the dN2 would exhibit a variable scalp distribution across the attend-color and attend-gender conditions, whereas the FRN would not.

METHOD

Participants

Twenty-two people (five males) participated in this study.

Apparatus and procedure

Stimuli and procedure were the same as in the Passive Experiment and the Active Experiment except where indicated. Instead of passively watching faces or choosing between two tarot cards, on each trial participants made a choice between a left or right key press. The decision screen consisted only of the words "left or right?" (see **Figure 1**, Moderate Learning). Participants chose between a left or right key press and were subsequently presented with the face-feedback stimulus. Subjects were told that for a random number of consecutive trials, each key had a set probability of "paying off," and the underlying probabilities would change randomly approximately every 20 trials. Subjects were instructed to try to maximize their winnings by finding and choosing the "better" key during any given set of trials, and to switch their choice whenever they suspected the underlying probabilities had changed. Subjects were told there would be easy blocks of trials with high probabilities of pay-off, and hard blocks of trials with low probabilities of pay-off, just as in the Active Experiment. The decision screen was presented until subjects made a choice whereupon a fixation cross was presented for 500 ms, followed by the face feedback for 1000 ms. Trial numbers were increased to 100 trials per block over eight blocks, counterbalanced across blocks in the same manner as in the Passive Experiment.

Subjects were required to report their exact reward earnings count for each set of trials (starting at zero from the last accuracy test), twice per block, for a total of 16 reports. Responses within \$0.25 of the correct count were coded as correct; total accuracy was defined as the number of correct reports divided by the number of total reports (16).

EEG data acquisition and analysis

The EEG data were acquired and analyzed, and the dN2 and FRN were assessed as in the Passive and Active experiments.

RESULTS

Behavioral results

Mean accuracy was 90.3% (SD = 11.5%) in the attend-color condition and 84.7% (SD = 18.5%) in the attend-gender condition. We eliminated the data from three subjects for having either attend-color or attend-gender accuracy scores more than 2 SD below the mean. With these subjects eliminated, attend-color accuracy was 92.8% (SD = 7.6%) and attend-gender accuracy was 90.8% (SD = 8.2%). This difference in accuracy was not significant ($p > 0.05$).

EEG results

The raw ERPs, difference waves and scalp maps are shown in **Figure 4**. Inspection of the scalp distributions suggest the attend-color dN2 was mostly frontal central (FCz, 4.5 μV) but with a left-lateral-occipital maximum (PO7, −4.6 μV). A two-tailed t-test indicated these channels were not significantly different ($p > 0.05$). The attend-gender dN2 was maximal at PO8 (−3.2 μV). The impression of a mostly frontal–central attend-color dN2 was supported by the results of 2 × 2 ANOVA on dN2 amplitude with electrode and task as repeated factors. There was an effect of task such that the attend-color dN2 was larger than the attend-gender dN2 (−4.1 vs. −2.5 μV), $F(1, 18) = 13.9$, $p < 0.01$, $\eta^2 = 0.44$, and there was an interaction of task and electrode such that the attend-color dN2 was larger at FCz than P8 (−4.5 vs. −3.7 μV), whereas the attend-gender dN2 was larger at P8 than FCz (−2.9 vs. −2.1 μV), $F(1, 18) = 10.0$, $p < 0.01$, $\eta^2 = 0.36$. One-tailed paired t-tests indicated these differences were significant, attend-color: $t(18) = -1.9$, $p < 0.05$; attend-gender: $t(18) = 2.7$, $p < 0.01$.

By contrast, inspection of the scalp maps in **Figure 4** suggests that the attend-color FRN was relatively shallow and maximal at central channels (CPz, −4.6 μV, followed by Pz, −4.5 μV, Cz, −4.5 μV, CP1, −4.5 μV, and FCz, −4.4 μV). The attend-gender FRN was maximal at CPz (−4.2), followed by Cz (−4.0 μV); FCz was the seventh most negative channel (−3.6 μV). Two-tailed t-tests indicated in the attend-color condition the amplitude of the FRN at CPz (where it was maximal) and FCz did not differ significantly ($p > 0.05$), but in the attend-gender condition the amplitude of the FRN was larger at CPz than FCz, $t(18) = 2.6$, $p < 0.05$. A 2 × 2 ANOVA on FRN amplitude revealed an effect of electrode such that the FRN was larger at FCz than at P8 (−4.0 vs. −2.7 μV), $F(1, 18) = 10.4$, $p < 0.01$, $\eta^2 = 0.37$. The effect of task was also significant such that the attend-color task yielded a larger FRN than the attend-gender task (−3.7 vs. −3.0 μV), $F(1, 18) = 5.8$ $p < 0.05$, $\eta^2 = 0.24$. The interaction of electrode and task was not significant ($p > 0.05$). As in Experiments 1 and 2, we used one-tailed paired samples t-tests comparing FRN amplitude at FCz and P8 in the attend-color and attend-gender conditions. In the attend-color condition, the FRN was significantly larger at

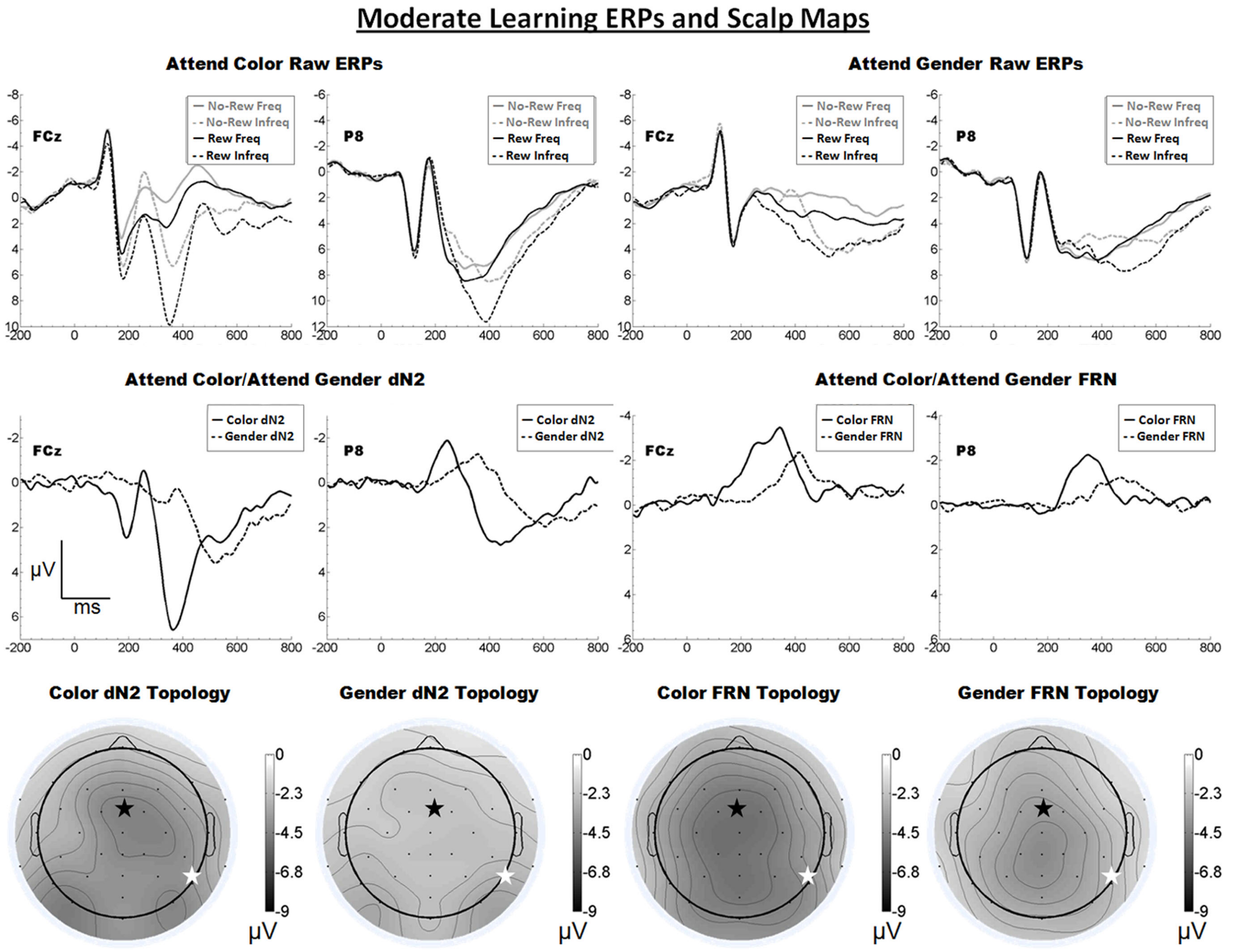

FIGURE 4 | Grand average ERPs for Experiment 3, recorded from channel FCz and P8 (see labels) and scalp distributions associated with the difference waves. The top row shows the "raw" ERPs for each of the frequency by reward conditions across tasks and electrodes. The middle row shows the dN2 and FRN difference waves across task and electrodes. The bottom row shows the scalp distributions of the dN2 and FRN across tasks. The scalp distributions reflect the base-to-peak measure of each of the dN2 and FRN. The black star on the scalp map denotes channel FCz, and the white star denotes P8. Note that negative is plotted up.

FCz than at P8 (-4.4 vs. $-2.9\ \mu V$), $t(18) = -2.9$, $p < 0.01$. In the attend-gender condition, the FRN was also larger at FCz (-3.6 vs. $-2.5\ \mu V$), $t(18) = -2.7$, $p < 0.01$.

DISCUSSION

As predicted, we found that in a task designed to engage the learning system only moderately, a FRN was elicited over central scalp sites irrespective of whether participants attended to the faces or tint of the feedback stimuli. However, the scalp distribution of FRN in the attend-gender distribution was somewhat more parietal than in the attend-color condition, which is indicative of component overlap with the P3; we suggest that the P3 on reward trials was exposed by the reduced FRN in this condition. Also as predicted, the scalp distribution of the dN2 varied between frontal–central and (right) lateral-occipital locations depending on which stimulus attribute participants attended. However, in the attend-color condition the amplitude of the dN2 at left-lateral-occipital location PO7 was comparable to that of FCz. This unexpected anomaly was addressed with the following experiment.

EXPERIMENT 4: CONTROL TASK

As a control, we ran an additional experiment that followed a more standard approach for eliciting the dN2 and FRN. Namely, we dissociated face processing from color processing entirely by employing the same task as in the Moderate Experiment, but in one condition the stimuli consisted only of yellow and blue colors (without faces), and in a second condition the stimuli consisted of male and female faces (without colors; see **Figure 1**, Control). In principle, in the previous experiments the mere presence of the information on the unattended dimension could have influenced processing along the attended dimension, thereby disrupting the dN2 or FRN. Thus the control experiment allowed for a pure assessment of these ERP components in a relatively standard oddball task. The Control Experiment was identical to the Moderate Experiment except for this change.

METHOD

Participants

Nineteen people (five males) participated in this study.

Apparatus and procedure

Stimuli and procedure were exactly the same as in the Moderate Experiment except that in the attend-gender task, monochromatic faces were presented as feedback, and in the attend-color task, blue and yellow rectangles (exact same size as the face stimuli) were presented as feedback (**Figure 1**, Control).

EEG data acquisition and analysis

The EEG data were acquired and analyzed, and the dN2 and FRN were assessed as in the Passive, Active, and Moderate Experiments.

RESULTS

Behavioral results

Mean accuracy was 94.1% (SD = 9.7%) in the attend-color condition and 88.2% (SD = 16.9%) in the attend-gender condition. We eliminated the data from one subject whose accuracy scores on both the attend-gender and attend-color trials was more than 2 SD below the mean. For the remaining subjects, attend-color accuracy was 95.8% (SD = 6.1%) and attend-gender accuracy was 91.0% (SD = 12.0%). This difference was not significant ($p > 0.05$).

EEG results

The raw ERPs, difference waves and scalp maps are shown in **Figure 5**. Inspection of the scalp maps suggests the attend-color dN2 was maximal at frontal–central sites (FCz, −4.8 μV) and the attend-gender dN2 was maximal lateral-occipital sites (PO8, −3.0 μV). This impression was confirmed by a 2 × 2 ANOVA on dN2 amplitude with electrode and task as repeated factors, indicating an effect of task such that the attend-color dN2 was larger than the attend-gender dN2 (−4.3 vs. −2.5 μV), $F(1, 17) = 34.0$, $p < 0.001$, $\eta^2 = 0.67$, and an interaction of task and electrode such that the attend-color dN2 was larger at FCz than P8 (−4.8 vs. −3.8 μV), whereas the attend-gender dN2 was larger at P8 than FCz (−3.0 vs. −2.0 μV), $F(1, 17) = 18.0$, $p < 0.01$, $\eta^2 = 0.51$. One-tailed paired t-tests indicated that these differences were significant, attend-color: $t(17) = -2.5$, $p < 0.05$; attend-gender: $t(17) = 3.0$, $p < 0.01$.

By contrast, inspection of the scalp maps in **Figure 5** suggests that the attend-color FRN was shallowly distributed over central channels (CPz, −6.5 μV; FCz was the fifth most negative electrode, −6.3 μV). A paired t-test indicated no significant difference between these channels ($p > 0.05$). The attend-gender FRN also appeared shallowly distributed over central channels (FCz, −4.3 μV, followed by CPz, −4.3 μV). Another paired t-test indicated no significant difference between these channels ($p > 0.05$). A 2 × 2 ANOVA on FRN amplitude revealed an effect of electrode such that the FRN was larger at FCz than at P8 (−5.3 vs. −3.5 μV), $F(1, 17) = 12.8$, $p < 0.01$, $\eta^2 = 0.43$. The effect of task was also significant (−5.2 vs. −3.6 μV), $F(1, 17) = 15.3$, $p < 0.01$, $\eta^2 = 0.47$, and there was no interaction of electrode and task ($p > 0.05$). One-tailed paired samples t-tests indicated that the FRN was significantly larger at FCz than P8 in both the attend-color and attend-gender conditions, attend-color: −6.3 vs. −4.1 μV, $t(17) = -3.3$, $p < 0.01$; attend-gender:. −4.3 vs. −2.8 μV, $t(17) = -3.0$, $p < 0.01$.

DISCUSSION

The Control Experiment confirmed that the scalp distribution of the dN2, but not that of the FRN, is sensitive to the dimension of the eliciting stimulus attended to by the participant. Further, this experiment accounted for the potentially confounding influence of stimulus information along the unattended dimension. The left-lateral-occipital maximum observed in the Moderate Experiment was not reproduced in the Control Experiment, suggesting that inadvertent processing of the irrelevant dimension may have exercised the FFA in the attend-color condition of that experiment. Of course, it is also possible that the left-posterior maximum observed in that condition was simply a statistical fluke.

BETWEEN SUBJECTS ANALYSIS (ACROSS EXPERIMENTS)

Experiments 1–4 confirmed our prediction that the scalp distribution of the FRN would remain frontal central whereas that of the dN2 would change according to task demands. Further, we found that the FRN interfered with the dN2 in conditions where the FRN was large. However, the specific nature of the interference remains to be investigated. To do so, we compared how these components varied across (rather than within) experiments to examine systematically the effects of increasing FRN amplitude on the dN2. For this purpose we focused on the attend-color condition where the effects of the interaction were greatest (because both components in this condition are frontal–central). Furthermore, we compared the results of the Passive, Active, and Moderate Learning Experiments, but not the Control Experiment, as the stimuli in the last experiment deviated from the first three and thus are not fully comparable. Finally, to investigate the specific mechanism driving changes in the FRN and dN2 across experiments, we assessed the base-to-peak amplitude of "raw" N2 in each of the four conditions separately: Frequent reward, frequent no-reward, infrequent reward, and infrequent no-reward. We predicted that, all other things being equal, the raw N2 would be larger to infrequent relative to frequent events (due to NE activity), but that this increase would be attenuated in the case of infrequent rewards (due to overlap with the DA-driven reward positivity).

METHOD

We began with an across-experiment comparison of dN2 and FRN amplitudes. (It should be noted that these experiments were performed sequentially, rather than treated as three counterbalanced conditions within a single experiment). To analyze the raw N2s for each of the four reward by frequency conditions for each experiment, we quantified the size of the raw-N2 base-to-peak as the change in voltage between the peak of the raw P2 and the peak of the raw N2. The N2 peak was assessed as the maximum negative amplitude in the ERP between 200 and 300 ms after onset of the feedback stimulus, and the raw P2 peak was assessed as the maximum positive voltage between 100 ms after onset of the feedback stimulus and the latency of the N2 peak for each subject and condition.

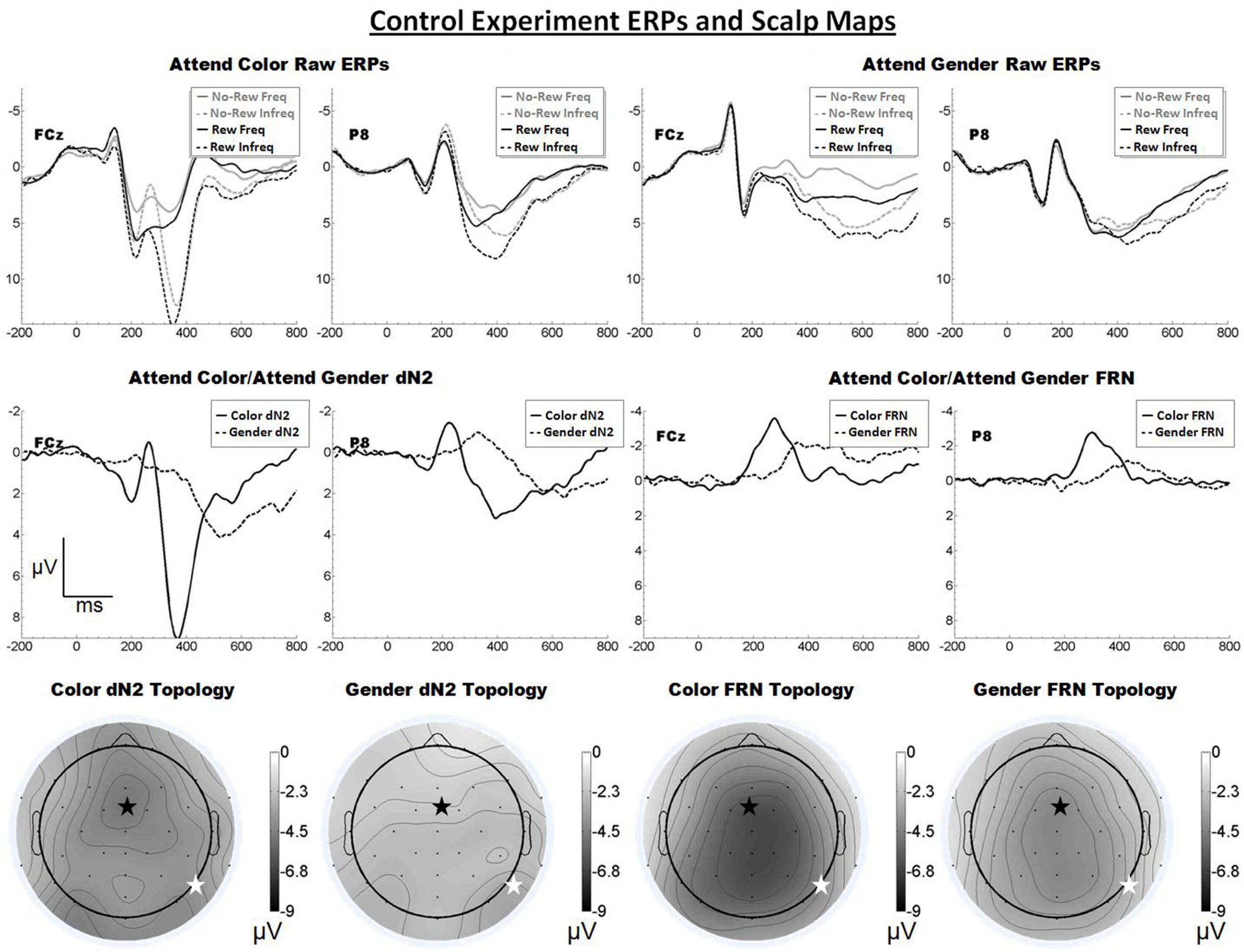

FIGURE 5 | Grand average ERPs for Experiment 4, recorded from channel FCz and P8 (see labels) and scalp distributions associated with the difference waves. The top row shows the "raw" ERPs for each of the frequency by reward conditions across tasks and electrodes. The middle row shows the dN2 and FRN difference waves across task and electrodes. The bottom row shows the scalp distributions of the dN2 and FRN across tasks. The scalp distributions reflect the base-to-peak measure of each of the dN2 and FRN. The black star on the scalp map denotes channel FCz, and the white star denotes P8. Note that negative is plotted up.

Lastly, we normalized N2 amplitude across subjects to assess within-subject variance in raw-N2 amplitude across conditions. To do so, we converted the raw-N2 values to z-scores as follows: For each subject, we determined the mean and SD of the raw-N2 values across the infrequent no-reward, infrequent reward, frequent no-reward, and frequent reward conditions. We then divided the difference between each raw-N2 value and the mean raw-N2 value by the SD of the raw-N2 values [see **Figure 7** for raw (top) and normalized (bottom) means].

RESULTS

A 3×2 mixed ANOVA with component (dN2 vs. FRN) as a repeated factor and Experiment (1–3) as a between subjects factor revealed a significant main effect of component such that the FRN was larger than the dN2 (-5.1 vs. $-4.0\,\mu$V), $F(1, 56) = 6.4$, $p < 0.05$, $\eta^2 = 0.10$. There was also an interaction of experiment and component indicating that the FRN and dN2 changed in different ways across experiments, $F(3, 56) = 10.2$, $p < 0.001$, $\eta^2 = 0.27$ (**Figure 6**). The between subjects effect of experiment was not significant ($p > 0.05$).

We decomposed the interaction of component and experiment with a set of three two-tailed independent samples t-tests (exp. 1 vs. exp. 2, exp. 1 vs. exp. 3, exp. 2 vs. exp. 3) for each component. The dN2 was larger in the Passive Experiment than in the Active Experiment (-4.5 vs. $-3.1\,\mu$V), $t(38) = 2.0$, $p = 0.05$. The dN2 in the Moderate Experiment ($-4.5\,\mu$V) was not significantly different than in the Passive Experiment ($p > 0.05$). The dN2 in the Moderate Experiment trended toward being significantly larger than the dN2 in Active Experiment, $t(37) = 1.9$, $p < 0.10$. By contrast, the FRN exhibited a different pattern across experiments. The FRN in the Active Experiment was significantly larger than in the Passive Experiment (-6.7 vs. $-4.1\,\mu$V), $t(38) = 3.0$, $p < 0.01$, and also significantly larger than the FRN in the Moderate Experiment ($-4.4\,\mu$V), $t(37) = -2.5$, $p < 0.05$, whereas the FRN between the

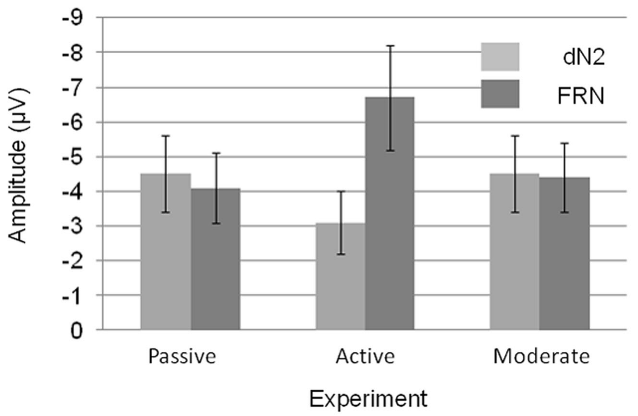

FIGURE 6 | Mean dN2 and FRN base-to-peak amplitudes across experiments. Note that negative is plotted up. Error bars represent 95% within subjects confidence intervals.

Passive and Moderate Experiments did not differ significantly ($p > 0.05$). Levene's test for equality of variances was significant for the FRN comparison between the Passive and Active, and Active and Moderate Experiments, but the difference remained significant when the correction was applied ($p < 0.01$, $p < 0.05$, respectively). These results suggest that the Active Experiment was the critical experiment for demonstrating a change in the dN2 and FRN across experiments: The dN2 was smallest in the Active Experiment and similar between the Passive and Moderate Experiments, whereas the FRN was largest in Active Experiment and similar between the Passive and Moderate Experiments.

To investigate what caused the changes in the dN2 and FRN amplitudes across experiments, we examined the normalized "raw" N2 values (see Methods). We subjected raw-N2 z-scores (**Figure 7**, bottom) to a $2 \times 2 \times 3$ mixed ANOVA with reward condition (reward vs. no-reward), frequency condition (infrequent vs. frequent) as repeated factors, and Experiment (1–3) as a between subjects factor. This analysis revealed a main effect of reward condition such that rewards produced a less negative raw N2 than no-rewards, $F(1, 56) = 19.5$, $p < 0.001$, $\eta^2 = 0.26$, and a main effect of frequency condition such that the infrequent raw N2 was more negative than the frequent raw N2, $F(1, 56) = 27.3$, $p < 0.001$, $\eta^2 = 0.33$. There was also an interaction of reward condition and frequency condition such that the effect of reward was larger in the infrequent condition than in the frequent condition, $F(1, 56) = 6.1$, $p < 0.05$, $\eta^2 = 0.10$. In addition, experiment interacted with both reward condition, $F(2, 56) = 3.6$, $p < 0.05$, $\eta^2 = 0.11$, and frequency condition, $F(2, 56) = 4.7$, $p < 0.05$, $\eta^2 = 0.14$, such that the difference between frequent and infrequent normalized raw N2s was smallest, and the difference between reward and no-reward normalized raw N2s was largest in the Active Experiment.

We used independent samples t-tests on normalized raw-N2 values to uncover which of the four normalized raw N2s (infrequent no-reward, infrequent reward, frequent no-reward, and frequent reward) best accounted for the change in the FRN and dN2 across experiments (**Figure 7**, bottom). The infrequent, no-reward raw N2 was similar across experiments (all ps > 0.05), as was the frequent, reward raw N2 (all ps > 0.05). The frequent, no-reward raw N2 was significantly larger in the Active Experiment than in the Passive Experiment, $t(38) = -3.0$, $p < 0.01$, whereas the infrequent, reward raw N2 was significantly smaller in the Active Learning than Passive Experiment, $t(38) = -3.1$, $p < 0.005$. Results were the same in comparing the Active Experiment with the Moderate Experiment: The frequent, no-reward raw N2 was larger in the Active Experiment, $t(37) = -3.1$, $p < 0.005$, whereas the infrequent reward raw N2 was smaller in Active Experiment, $t(37) = 2.9$, $p < 0.01$. There were no significant differences between the Passive Learning and Moderate Experiments (all ps > 0.05). These results suggest that the apparent need for greater deliberative strategy in the Active Experiment produced a larger negativity to frequent no-reward trials, and a greater attenuation of the raw N2 on infrequent reward trials.

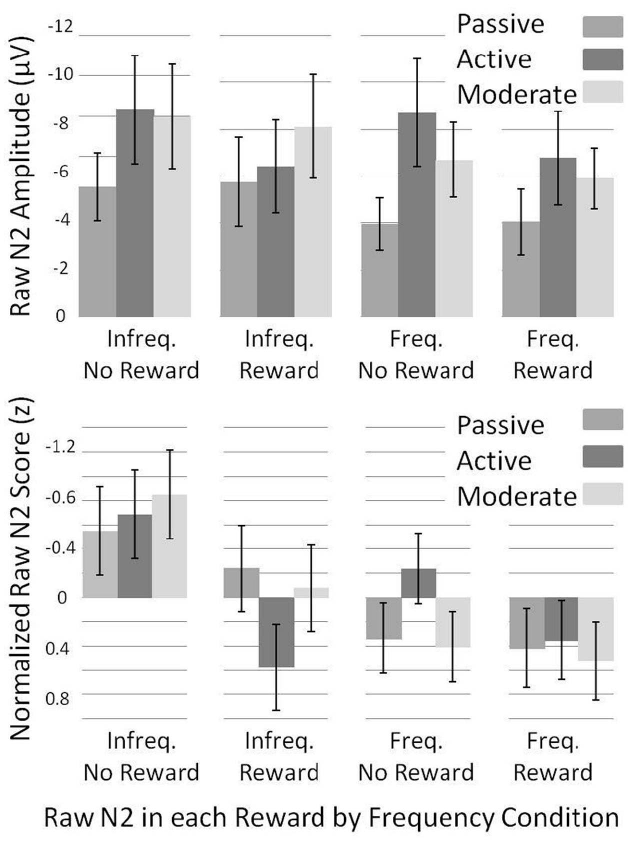

FIGURE 7 | Normalized (bottom) and un-normalized (top) raw-N2 *z*-scores and amplitudes across experiments for each of the frequency by reward conditions. Note that negative is plotted up. Error bars represent 95% confidence intervals for the mean of each condition by experiment.

DISCUSSION

We examined how challenging subjects with an involving learning and decision-making task impacted dN2 and FRN amplitude across experiments. We demonstrated that across three experiments, the task that most engaged a deliberative learning strategy enhanced the FRN and simultaneously attenuated the dN2, albeit the latter finding only trended toward statistical significance for the comparison between the Active vs. Moderate Experiments. We also examined the raw N2s that underlie the dN2 and FRN as a function of frequency, reward, and learning engagement. We converted the raw-N2 values to z-scores to control for between subjects variability in the overall size of the raw N2, and then analyzed how the normalized N2s for each of the frequent reward, frequent no-reward, infrequent reward, and infrequent no-reward conditions changed across experiments according to task demands. Independent samples t-tests on raw-N2 z-scores indicated that the larger FRN and smaller dN2 in the Active Learning experiment were driven both by a larger raw N2 to frequent no-rewards and greater attenuation of the raw N2 to infrequent rewards compared to the Passive Learning and Moderate Experiments. These contrasting changes worked synergistically to increase the amplitude of the FRN but against each other to decrease the amplitude of the dN2.

GENERAL DISCUSSION

The modified LC–P3 theory holds that the dN2 is produced by the impact of a brief, cortex-wide increase in cortical NE due to phasic LC firing in response to infrequent, task-relevant events. In support of this, we demonstrated that the dN2 exhibits a scalp distribution that changes according to task specifics in a manner consistent with a noradrenergic origin. Furthermore, the modified LC–P3 theory and the reinforcement learning theory of the FRN together hold that the dN2 and FRN are driven independently by modulation of the raw N2 at frontal–central channels by both the NE system and the DA system. We suggest that whereas NE amplifies the raw N2, DA depresses it, such that these influences interfere with one another in producing scalp potentials over anterior regions of the scalp. We demonstrated that factors which exercise learning and decision-making systems enhance the FRN but attenuate the dN2. Furthermore, we provided evidence that these changes in the FRN and dN2 are driven most strongly by an enhanced negativity to frequent no-rewards and an attenuated positivity to infrequent rewards.

As the name indicates, our account of the relationship between NE system activity and the dN2 is a modification of the original LC–P3 theory (Nieuwenhuis et al., 2005a). Below we review the LC–P3 theory in detail and provide the motivation for our modification to it.

THE ORIGINAL LC–P3 THEORY

The P3 is a positive deflection in the ERP typically peaking ∼300–500 ms after the eliciting stimulus. It has a broad, parietal scalp distribution that is thought to represent the summation of activity in multiple, dispersed neural generators (e.g., Johnson, 1993). Nieuwenhuis et al. (2005a) characterize four main categories of conditions that influence P3 amplitude: Subjective probability (unexpected events elicit a larger P3 than expected events), motivational salience (targets elicit a larger P3 than distracters), applied attention (attended stimuli elicit a larger P3 than ignored stimuli, and targets elicit a larger P3 under conditions that demand full attention compared to dual-task conditions), and attention-capturing stimuli (task-irrelevant stimuli that are highly deviant from the stimulus context elicit a larger P3 than less deviant stimuli).

The LC–P3 theory (Nieuwenhuis et al., 2005a) proposes that the P3 is an electrophysiological manifestation of cortex-wide noradrenergic modulation through the LC efferent projection system. In support of the LC–P3 theory, Nieuwenhuis and colleagues presented a comprehensive review of the literature, marshaling abundant evidence that conditions antecedent to phasic LC firing are the same as those conditions that exercise the P3. Additionally, Nieuwenhuis et al. (2005a) refer to psychopharmacological and animal lesion studies for support for the link between the P3 and noradrenergic modulation. By and large, noradrenergic agonists such as clonidine and direct lesions of the LC have been reported to reduce the amplitude of a P3-like potential observed in monkeys (e.g., Pineda et al., 1989; Pineda and Westerfield, 1993; Swick et al., 1994), and Halliday et al. (1994) found that clonidine reduced the amplitude of the P3 in human subjects.

ISSUES WITH THE ORIGINAL LC–P3 THEORY

The LC–P3 theory possesses considerable explanatory power and accounts for a wide range of existing data. However, two issues warrant further examination. First, neurophysiological evidence indicates that the NE phasic burst arrives in cortex too early to produce the P3 directly. Aston-Jones and Cohen (2005) suggest NE should reach the cortex within approximately 170 ms of target onset, but the P3 typically does not begin for another 50 ms until about 220 ms following target onset (and reaches maximum amplitude from about 300 to 600 ms post-stimulus). Thus there is greater than a 50-ms discrepancy between the time of NE arrival in cortex and the onset of the P3. Although this estimate of the timing of NE arrival is based on single-cell recordings in monkeys, Aston-Jones et al. (1985) demonstrated that conduction speeds in NE-releasing neurons vary across species such that the actual timing of NE arrival in cortex is relatively preserved despite varying axonal distances. Further, P3 onset sometimes occurs after motor response initiation suggesting that the underlying mechanism does not directly implement the stimulus–response mapping (as would be expected if it reflected a signal detection process mediated by the LC) but rather is involved in a subsequent, related process (Ritter et al., 1979; Duncan-Johnson and Donchin, 1982; Krigolson et al., 2008). For example, Krigolson et al. (2008) found that when a target changed location in a continuous tracking task, participants adjusted their motor behavior accordingly even before the change in target location elicited the P3. In contrast, studies in monkeys indicate that (unlike the P3) phasic LC activity consistently precedes behavioral responding and has been strongly associated with processes that lead to the response (e.g., Clayton et al., 2004; Rajkowski et al., 2004).

A second issue with the original LC–P3 theory is related to the “attentional blink,” a deficit in stimulus processing attributed to the LC refractory period (e.g., Usher et al., 1999; Nieuwenhuis et al., 2005a,b; Warren et al., 2009). When two targets are embedded within a rapid serial visual presentation task, the first target can be reported with high accuracy but the second target is reported with significantly worse accuracy if it is presented within a window 200–600 ms after onset of the first target (Raymond et al., 1992); spared accuracy for the second target when it appears within 200 ms of onset of the first is termed “lag-1 sparing.” Nieuwenhuis et al. (2005a,b) argued that the properties of the NE system could account for the attentional blink: They proposed that the onset of the first-target elicits NE system phasic response, with the subsequent flood of NE to the cortex benefiting processing of the first target, and also the second target if the second target is presented within ∼100 ms of the first – thus accounting for lag-1 sparing. After this initial period of effective target processing (∼200 ms from onset of the first target to offset of a second-target presented 100 ms later), the LC is inhibited and cortical levels of NE are not sufficient to process effectively any targets presented 200–600 ms after onset of the first target – accounting for the attentional blink. Consistent with this proposal, McArthur et al. (1999) showed a significant negative correlation between the amplitude of the first-target P3 and second-target accuracy, such that the size and temporal profile of any subject's attentional blink mirrored the size and temporal profile of that subject's first-target P3; according to the LC–P3/LC-AB theories, larger bursts of NE to the first target result in larger P3s, followed by a relatively deep or extended refractory periods that produces a larger attentional blink.

Nevertheless, this proposal raises the question: If the P3 reflects the NE burst, which should facilitate stimulus processing, then why does the P3 peak during the period of the attentional blink (between 300 and 500 ms after the first target), which by definition is a period of impaired stimulus processing? Instead, one might predict that the electrophysiological manifestation of NE activity would precede the attentional blink, during the time of effective of stimulus processing associated with lag-1 sparing.

THE MODIFIED LC–P3 THEORY

Nieuwenhuis and colleagues provide alternative explanations for these apparent discrepancies within the LC–P3 account (see Nieuwenhuis et al., 2005b; Nieuwenhuis and Jepma, 2010). However, the assumption that the dN2 (rather than the P3) reflects the LC-induced enhancement of cortical processing eliminates these issues outright. This modification accounts for the two issues above as follows. First, it aligns the timing of the putative ERP response to NE activity (the dN2, occurring at about 200 ms post-stimulus, as opposed to the P3, which occurs about 300–600 ms post-stimulus) with the actual timing of the phasic NE signal (about 170 ms post-stimulus). Furthermore, unlike P3 onset, the onset of the N2 consistently precedes the overt behavior (e.g., Krigolson et al., 2008); in fact, detailed analyses of RT data to compatible stimuli in a speeded response compatibility task suggests that stimulus information begins to impact the response selection mechanism at about 170 ms post-stimulus (during N2 onset) and exerts the maximal impact on the response selection process about 250 ms post-stimulus (during N2 maximum; Holroyd et al., 2005). Second, the modified theory associates the P3 with the period of impaired cortical processing due to NE depletion (rather than abundance), which corresponds to the time profile of the attentional blink. Additionally, the modified theory provides an ERP correlate of both NE abundance (the dN2) *and* NE depletion (the P3) in the cortex and naturally accounts for the evidently close relationship between the two ERP components, because the duration of the refractory period of the LC (P3) is directly related to the size of the initial NE burst (N2).

Critically, the evidence reviewed by Nieuwenhuis et al. (2005a) as support for the original LC–P3 theory applies equally well to the modified LC theory. For example, the amplitudes of both the P3 and the N2 are sensitive to the same factors: The P3 is typically preceded by the N2, and in early studies of the impact of stimulus probability on the ERP, these two ERP components were collectively termed the N2/P3 complex because of their tendency to co-vary in amplitude and latency (e.g., Duncan-Johnson and Donchin, 1977; see also Ritter et al., 1979). In fact, all of the antecedent conditions noted by Nieuwenhuis and colleagues to apply to both P3 amplitude and LC phasic activity also apply to N2 amplitude. Thus, both N2 amplitude and P3 amplitude increase with increasing unexpectedness of a task-relevant event, and both are larger to targets than non-targets (e.g., Courchesne et al., 1975; Squires et al., 1975, 1976; Simson et al., 1976; Duncan-Johnson and Donchin, 1977; Ritter et al., 1979; Nieuwenhuis et al., 2003). Both also scale to the amount of attention paid to a stimulus, with a larger N2 and larger P3 to attended vs. unattended stimuli, and to attention-capturing/highly deviant stimuli vs. less deviant stimuli (Hillyard et al., 1971; Courchesne et al., 1975; Squires et al., 1975, 1977; Ford et al., 1976; Daffner et al., 2000a,b; Folstein et al., 2008).

INTERACTION OF THE NE AND DA SYSTEMS

The reinforcement learning theory of the FRN holds that DA dips and bursts modulate ongoing activity in the ACC. Specifically, reward feedback elicits a phasic burst of DA that produces a positivity in the ERP typically between 200 and 300 ms of the eliciting stimulus (Holroyd et al., 2008), whereas no-reward feedback elicits a dip in DA that produces a negative deflection in the same time range (Holroyd and Coles, 2002). Furthermore, the theory holds that DA signals scale according to the degree of expectedness of the feedback, such that infrequent rewards elicit a larger DA burst and reward positivity than frequent rewards, and infrequent no-rewards elicit larger DA dips and negative deflections than frequent no-rewards. Critically, the theory proposes that the FRN reflects DA-dependent modulation of ACC activity but does not specify exactly what neural process is being modulated. However, empirical evidence suggests that the ACC produces a negative deflection (the N2) that perhaps reflects response conflict or a related stimulus/response decision-making process (e.g., Botvinick et al., 2001). Thus it has been argued that the reward positivity elicited by phasic DA activity attenuates the N2 produced in the ACC (Holroyd, 2004; Holroyd et al., 2008). The proposal that dopamine dips increase N2 amplitude by disinhibiting ACC activity has remained unconfirmed (Holroyd and Coles, 2002), perhaps because phasic decreases from baseline DA activity are relatively shallow when compared to the relatively large increases in DA activity associated with phasic bursts.

According to the modified LC–P3 theory, infrequent events elicit a phasic release of NE that enhances cortical processing and produces an amplified negative deflection in the ERP between about 200 and 300 ms after onset of the eliciting stimulus. Critically, NE modifies activity in the same time range as the putative DA signals, including ACC activity when it is present. According to this position, increased NE gives rise to a larger N2 produced in the ACC. Thus, the two factors push and pull the frontal–central N2 associated with ACC activity up and down.

Here we examined the interaction of the NE and DA systems by including both a frequency and reward manipulation within the same experiment. We hold that frequency insofar as it relates to the expectedness of reward or no-reward has an effect on the DA system independent of its effect on the NE system. For the NE system, infrequent events consistently increase NE release and the associated negativity, whereas for the DA system infrequent rewards produce a relatively large burst in DA and associated positivity and infrequent no-rewards elicit a relatively large dip in DA and an associated negativity. Consistent with this, we observed a significant interaction of frequency and reward such that the difference in N2 amplitude between reward and no-reward was larger when rewards and no-rewards were infrequent relative to when they were frequent. This replicates previous work on the effect of reward-expectedness on the FRN (Holroyd et al., 2003, 2009; Hajcak et al., 2007; Baker and Holroyd, 2009).

We further examined the interaction of the NE and DA systems by systematically manipulating the degree of participant engagement in reward tasks – and by extension putatively the degree of DA system engagement – across three experiments. In keeping with the reinforcement learning theory of the FRN, we predicted that the enhanced FRN in the Active Experiment would be driven by both a greater attenuation of the raw N2 to reward feedback and by a greater enhancement of the raw N2 on no-reward trials. Consistent with this, independent samples *t*-tests on normalized raw-N2 amplitude indicated that in the Active Experiment, the raw N2 to infrequent reward feedback was significantly smaller than the raw N2 to infrequent reward feedback in both the Passive and Moderate Experiments, suggesting that greater DA system engagement resulted in a larger DA-associated positivity that attenuated the raw N2. Similarly, the raw N2 to frequent no-reward feedback was significantly larger in the Active experiment than in the Passive and Moderate Experiments, suggesting a larger DA dip enhanced the raw N2 in the Active Experiment. These differences cannot be attributed to greater engagement of the NE system in the Active Experiment (rather than greater DA system engagement) because greater NE release would have produced a *larger* negativity to infrequent reward feedback.

The finding of a decrease in the amplitude of the raw-N2 to infrequent reward feedback in the Active Experiment relative to the other experiments is expected in light of previous work associating reward processing with a positive deflection in the ERP that attenuates the N2 (e.g., Holroyd et al., 2008; Baker and Holroyd, 2011). However, the finding of an increased raw N2 to frequent no-reward feedback in the Active Experiment relative to the other experiments to our knowledge constitutes the first evidence of an increased negative deflection elicited by no-reward feedback. Although the reinforcement learning theory of the FRN holds that brief decreases in DA activity in response to unexpected no-reward feedback increase the amplitude of a negative deflection in the ERP (Holroyd and Coles, 2002), the FRN difference-wave approach cannot determine whether the difference between the ERPs is due to a positivity to rewards, a negativity to no-rewards, or both (Holroyd et al., 2008). Our results indicate that the raw N2 is increased to no-reward feedback as predicted by the reinforcement learning theory of the FRN (Holroyd and Coles, 2002), especially under conditions that demand high task engagement.

The raw N2s to infrequent no-rewards and frequent rewards were not statistically different between the Active Experiment and either of the Passive or Moderate Experiments. This raises the question: Why are frequent no-rewards and infrequent rewards particularly sensitive to changes in deliberative strategy, whereas infrequent no-rewards and frequent rewards are relatively insensitive? The answer may have to do with the fact that both the infrequent no-reward feedback and the frequent reward feedback always occurred in the same blocks of trials. In this context rewards accumulated frequently (and therefore no-rewards were infrequent). Perhaps this condition of the Active Experiment is much like the Passive and Moderate experiments, in the sense that subjects could disengage from the task because it was apparently easy. By contrast, subjects would have remained engaged in the blocks where rewards were infrequent and no-rewards frequent. Hence with increasing engagement of learning and decision systems across experiments, subjects may have been similarly unmoved to rewards and no-rewards in easy blocks but differentially reactive to rewards and no-rewards in difficult blocks.

OTHER ISSUES

These experiments were intended to exercise the system that produces the FRN differentially – most in the Active Experiment, least in the Passive Experiment, and to an intermediate degree in the Moderate Experiment[2]. Note that the Active Experiment was characterized by 15 potentially learnable relationships whereas the Moderate Experiment was characterized by only two such relationships (left button vs. right button). Thus although the degree of engagement in the Moderate Experiment was likely larger than in the Passive Experiment, this difference may have been small relative to the Active Experiment.

A second notable issue is the fact that the base-to-peak measure of the raw N2s can fail to capture some variability in the ERP due specifically to the reward positivity. That is, the base-to-peak method is insensitive to positive deflections that go beyond attenuating the N2 to create a positive deflection in the same time range: The most positive value for the raw N2 that can be assessed is 0 μV, because the algorithm finds the most negative value in the N2 time window and subtracts from that the most positive value preceding it. Despite this limitation, the method nevertheless yielded significant differences in the raw N2 across experiments that confirmed our hypotheses.

Finally, we observed a main effect of task such that the attend-color dN2 was larger than the attend-gender dN2, and the attend-color FRN was larger than the attend-gender FRN. This is a replication of our previous dN2 results (Warren et al., 2011). We interpret this effect as being due to both increased latency jitter in the attend-gender condition because of longer categorization latency, and also lower accuracy and confidence in the attend-gender condition, a factor known to attenuate the dN2 (Hillyard et al., 1971).

CONCLUSION

Both the NE system and the DA system modulate processing in the ACC. However, whereas the NE system includes the ACC among many cortical targets, innervation by the DA system of frontal midline cortex is especially great. Consistent with this distinction, we demonstrated that the dN2, an ERP component that we propose reflects noradrenergic modulation of cortical activity, exhibits a scalp distribution that is maximal at varying locations dependent on the relative engagement of specific cortical areas. By contrast, the FRN, which has been associated with DA system activity, is consistently maximal at scalp locations over the ACC. Furthermore, we demonstrated that under conditions in

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[2] In fact, a linear regression analysis not reported here demonstrated FRN amplitude was significantly predicted by task engagement across experiments, while the dN2 exhibited a trend toward the inverse relationship.

which the DA system should be highly engaged – specifically, in an apparently complex learning and decision-making task – the neural processes underlying the FRN and dN2 appeared to interfere with one another such that the FRN was enhanced and the dN2 was attenuated. Finally, we demonstrated that negative feedback stimuli (i.e., feedback associated with the absence of a potential reward) were associated with a negative deflection in the ERP that was larger than the raw-N2 typically elicited by motivationally salient events. Taken together, these results paint a picture of two neuromodulatory systems that have relatively independent effects on the ERP despite considerable overlap in the space and time domains as well as shared antecedent conditions. The ACC seems to be at the center of this overlap: recruiting the NE system, which in turn facilitates processing by the ACC and other brain areas, and utilizing DA bursts and dips for the purpose of adaptive decision making. These considerations suggest the ACC plays a crucial role in both fast and efficient processing of task-relevant events and adaptive decision making based on a reinforcement history implemented by the DA system.

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Experience and abstract reasoning in learning backward induction

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Backward induction is a benchmark of game theoretic rationality, yet surprisingly little is known as to how humans discover and initially learn to apply this abstract solution concept in experimental settings. We use behavioral and functional magnetic resonance imaging (fMRI) data to study the way in which subjects playing in a sequential game of perfect information learn the optimal backward induction strategy for the game. Experimental data from our two studies support two main findings: First, subjects converge to a common process of recursive inference similar to the backward induction procedure for solving the game. The process is recursive because earlier insights and conclusions are used as inputs in later steps of the inference. This process is matched by a similar pattern in brain activation, which also proceeds backward, following the prediction error: brain activity initially codes the responses to losses in final positions; in later trials this activity shifts to the starting position. Second, the learning process is not exclusively cognitive, but instead combines experience-based learning and abstract reasoning. Critical experiences leading to the adoption of an improved solution strategy appear to be stimulated by brain activity in the reward system. This indicates that the negative affect induced by initial failures facilitates the switch to a different method of solving the problem. Abstract reasoning is combined with this response, and is expressed by activation in the ventrolateral prefrontal cortex. Differences in brain activation match differences in performance between subjects who show different learning speeds.

Keywords: neuroeconomics, game theory, backward induction, learning, deductive reasoning

1. INTRODUCTION

Backward induction (BI) is a recursive algorithm, wherein inferences regarding a decision problem made at an earlier stage are applied to the process of deriving yet further inferences on the problem. As a mathematical construction, backward induction constitutes a benchmark of game theoretic rationality that prescribes the behavior of rational players in finite sequential games of perfect information. In game theory, the concept is at the basis of abstract theorems; most notably Zermelo's (1908,1912) theorem on the existence of equilibria in pure strategies for those games, or Selten's (1965) and Selten and Stoecker's (1986) theorem characterizing Sub-game perfect equilibria.

In contrast to its applicability in mathematical proofs, backward induction has at times been considered inapposite as a descriptive account of the cognitive processes operating in human subjects during the sort of strategic interactions that game theorists would conceptually represent as sequential games (e.g., Fey et al., 1996; Aymard and Serra, 2001; Johnson et al., 2002). In part, backward inductive reasoning has been considered an unlikely description of the human thought process during such game situations, because it requires the cognitive enactment of a solution concept that is considerably complex and ostensibly unnatural. However, we find evidence that subjects playing the sequential game of perfect information in our experiment have a common pattern of learning the optimal solution, and that although individuals may differ in their speeds for producing this pattern, this path is common and reproduces the steps of the backward induction algorithm.

To argue effectively this conclusion, we first review what the backward induction algorithm prescribes. We illustrate backward induction in finite sequential games of perfect information. These are games in which players alternate in actions, know, and remember precisely the choices made by other players in previous stages of the game, and know exactly the payoff structure for all players involved. A strategy for a player is a rule assigning a move at every decision point. For these games, backward induction prescribes the following procedure to construct a strategy for every player: At the very last stage of the sequential game, when the final player makes the last choice of the game, she should move to maximize her payoff from the choice made at this stage. We can call this step the last stage. Since the game ends at the last stage, and because payoffs are known, rationality prescribes the outcome of the last player's choice. In other words, all players, including the last player herself, can unambiguously determine what would constitute the payoff maximizing choice given the options available at the last stage. The second to last player should anticipate the unambiguous criteria according to which the last player will choose, and conclude that his second to last choice will ultimately yield the payoffs induced by the optimal move of the last player. After this has been established, the original game is effectively replaced by a game with shorter length where the last move is eliminated and the payoff at the last stage is defined to be the payoff following the optimal choice of the last player. Iterating this process until the initial decision point is reached produces a strategy for every player.

Backward inductive reasoning relies in an essential way on the human ability for recursive thought, which itself has been posited as a prerequisite for quintessential human achievements such as language acquisition and basic numeracy (Hauser et al., 2002). Hence, to the extent that this innate human ability to think recursively manifests itself in strategic games, there may indeed exist a link between fundamental cognitive processes in humans and the abstract game theoretic concept of backward induction. Following this conjecture, we conduct two studies of a particular strategic social interaction that facilitates recursive learning. These studies were designed to address two fundamental questions: First, what are the neural correlates of recursive learning in the strategic environment, and second, how do the cognitive processes involved in recursive learning connect to abstract backward inductive reasoning.

2. EXPERIMENTAL PARADIGM

2.1. HIT-N GAME

The finite sequential game which subjects play in our experiment is played by two parties on a virtual playing board, and is the same as used in Gneezy et al. (2010), Bouton (1901–1902), and Dufwenberg et al. (2009). The board used to display the game in the imaging study is presented in **Figure 1**.

For the basic variant of the Hit-N game used in this experiment, the first player to move is allowed to move a single common playing piece on the board, and she is allowed to move it only forward, by 1, 2, or 3 positions; no more or no less. The move then goes to the second player, who is allowed the same action of moving the figure 1, 2, or 3 positions forward. From thereon the opportunity to move according to the 1-2-or-3-only rule alternates between the two players. The player who reaches the final position (15 in experiment 1) first wins that game. We refer to this game as $G(15, 3)$. A second game in our experiment involves the game $G(17, 4)$ which is played on a virtual playing board of length 17, and allows players to move 1, 2, 3, or 4 positions forward.

We apply backward induction reasoning to this game to derive the optimal strategy: Players moving in position 12, 13, or 14 can win by reaching position 15 immediately. It follows that players moving at 11 have lost, since they can only move to 12, 13, or 14, where the opponent, as we have just seen, wins. Players can now replace the original game with the shorter game where the first player to reach position 11 wins: a move is optimal in the original game if and only if it is optimal in the reduced game. The same argument, repeated, shows that the player who first gets to position 7 wins; after which it can be concluded that the first to reach 3 wins. In summary, all positions different from 3, 7, and 11 are winning positions, because from there the player who is moving can reach either position 3, 7, or 11, and win: she just has to be sure to move there. On the other hand, positions 3, 7, and 11 are losing positions, and there is not much that the player moving there can do but hope for an error of the opponent. The argument we have just presented is the BI solution to $G(15, 3)$. A similar argument shows that the losing positions in $G(17, 4)$ are $\{2\}$,$\{7\}$, $\{12\}$, and the groups of winning positions are $\{1\}$, $\{3, 4, 5, 6\}$, $\{8, 9, 10, 11\}$, $\{13, 14, 15, 16\}$.

2.1.1. *The behavioral study*

We use data from (Gneezy et al., 2010) as a behavioral sample, and focus here on error rate, response time, and their relation. A total of 72 subjects competed in 20 trials of $G(15, 3)$, and 52 out of the 72 subjects played an additional 10 trials of $G(17,4)$.The incentive structure for $G(15, 3)$ promised \$5 for winning more than 5 trials over the 20 game period, and \$20 for winning more than 11 trials. For $G(17, 4)$ subjects were promised \$10 for winning more than 5 games.

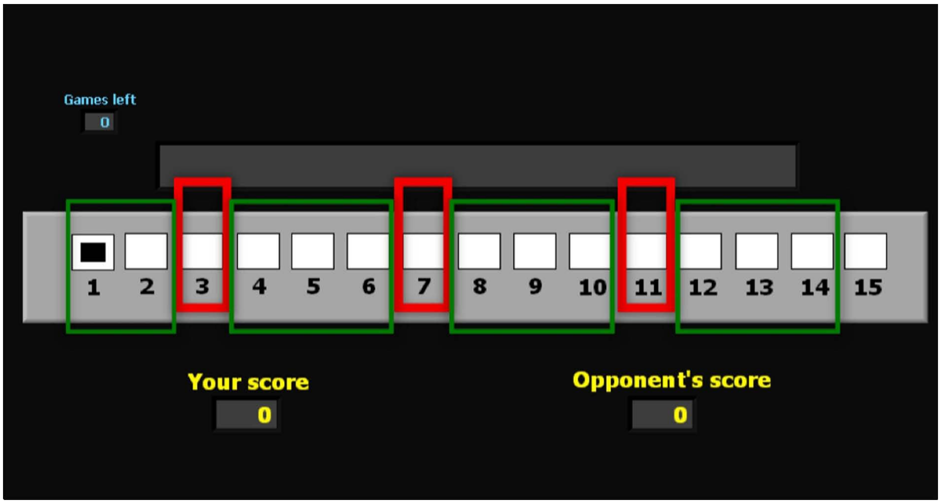

FIGURE 1 | Board of positions for the game *G*(15, 3). This is the board of positions used in the imaging experiment. The superimposed red rectangles indicate the losing positions 3, 7, and 11. The green rectangles indicate the winning positions. In the lower section of the **Figure 2** displays indicate the current score of the subject and the (computer) opponent.

2.2. THE fMRI STUDY

A total of 12 subjects participated in the MRI study. They played first 20 trials of $G(15, 3)$, then 20 trials of $G(17, 4)$ against a computer. The game, incentives, and instructions include three modifications to those used in the behavioral study. First, subjects are informed that they are playing a computer, programmed to win and subject to small errors. Also subjects play 20 trials of $G(17, 4)$ (compared to 10 trials in study 1). Finally subjects were allowed 10 s to make a choice on each of their turns.

Data were collected at the Center for Magnetic Resonance Research (CMRR) at University of Minnesota using a 3-T Siemens Trio scanner. Both studies were approved by the Institutional Review Board (IRB) at the University of Minnesota. Subjects in both studies signed an informed consent form after they were given the instructions.

3. MODEL

To motivate the need for a theoretical model and the structure we are going to use, we begin by considering the relation between two key observable variables, response time and error rate. The response time is the length of the time interval between the moment in which the move of the opponent (another player or the computer) is observed and the moment in which the subject makes his next move. To define the error rate, we focus on $G(15, 3)$ and note that at every winning position one, and only one, of the possible moves is correct, and the other two are incorrect. An error is the choice of the wrong move, and the error rate is the frequency of this event, conditional on the position being a winning position for the subject (these are the only positions at which an error is possible). The correct response rate is the difference from 1 of the error rate.

How are these two variables related? It may be reasonable to assume that, everything else being equal, a longer response time is associated with a higher correct response rate. This for example would be the case if the response time were varied exogenously, since by thinking about the problem for a longer time the subject would be more likely to achieve a richer understanding of what constitutes a good move. We point out that the condition of everything else being equal is crucial for this assertion. Considering now, that the length of the response time is not exogenous, but is decided upon by the subject who is reasoning about the decision, the relationship between response time and error rate may be different; indeed reversed: Since the reasoning activity can be assumed – in some measure – costly, a decision maker may compare and trade-off the estimated returns and costs from the reasoning activity. If the returns are estimated to be low, he may prefer to discontinue the process. If they are high, he might continue. Consider also, ability as an individual characteristic: An individual with lower cognitive skills may find the returns to his reasoning unsatisfactory, stop early, and be more likely to make the wrong choice. Similarly, a subject who has not acquired a basic familiarity with the game may conclude very little from his examination, stop cognitively engaging, and commit errors at a high rate. Both cognitive ability and problem familiarity are subsumed under the concept of ability. Considering response time as a choice variable together with differences in ability, the average relation at the individual level between response time and correct response rate may therefore be negative. In our data we find this to be the case. **Figure 2** illustrates this point.

The simple regression in **Table 1** of the correct response rate on the individual average response time confirms the negative relation, again in both games.

Given the observed relation it appears particularly useful to consider a model in which response time is endogenously determined, and that reflects the notion that subjects choose to think about a problem, decide whether to stop thinking, and only then select a move.

3.1. OPTIMAL INFORMATION PROCESSING

In our experiment, at each turn, a player observes the position in the game, considers a set of potential cues and insights, and tries to identify the best move at the current position. At any point in time before choosing a move, he can terminate the process and then make a move determined by the conclusions reached up to this point. If he does not terminate the process, he has to decide the intensity of the effort devoted to the decision. The quality of his decision will then depend on his ability to reason about the game as well as his effort in doing so. We consider ability as an individual characteristic of the player, and this may describe both a player's natural, general skills, as well as her acquired understanding of the game. We also consider effort as a choice variable. Ultimately, both effort and ability contribute positively to the agent's problem solving success.

We model the above process as an optimal information acquisition problem to be solved in the time interval before the move. In the model, the subject has to choose an action, and has beliefs over which of the feasible actions [for example, the set $\{1, 2, 3\}$ in $G(15, 3)$] in currently the best. In every instant during this process the agent can observe an informative signal on what the best action is, update her belief, and decide whether to continue the information acquisition process or to stop and choose what, given the current belief, is the optimal action. The model outlined above constitutes a general inter-temporal decision problem which can be formulated as a dynamic programming problem with an action set that consists of the agent's effort and the decision to continue or stop processing information about the game. The state space of the problem is the set of beliefs over the action set, assigning to each action the probability that it is the best action. Information acquired in every instant is a partially informative signal on the true state; that is, on which among the feasible actions is the optimal one.

3.2. MODEL PREDICTIONS

It is clear that if ability is so low that any processed signal is entirely non-informative, the optimal time spent should be zero, and that correct response rates in this case will consequently be low. This is likely to occur in the early stages of the game, when subjects are just beginning to familiarize with the task, and lack even the basic insights to make even minor headway into the problem. At this stage we should observe a short response time and a high error rate. The effect should also be more pronounced at the difficult positions, those further from the end: this is because reasoning about the best move can only produce useful insights when the individual has some idea of what happens in later stages of the

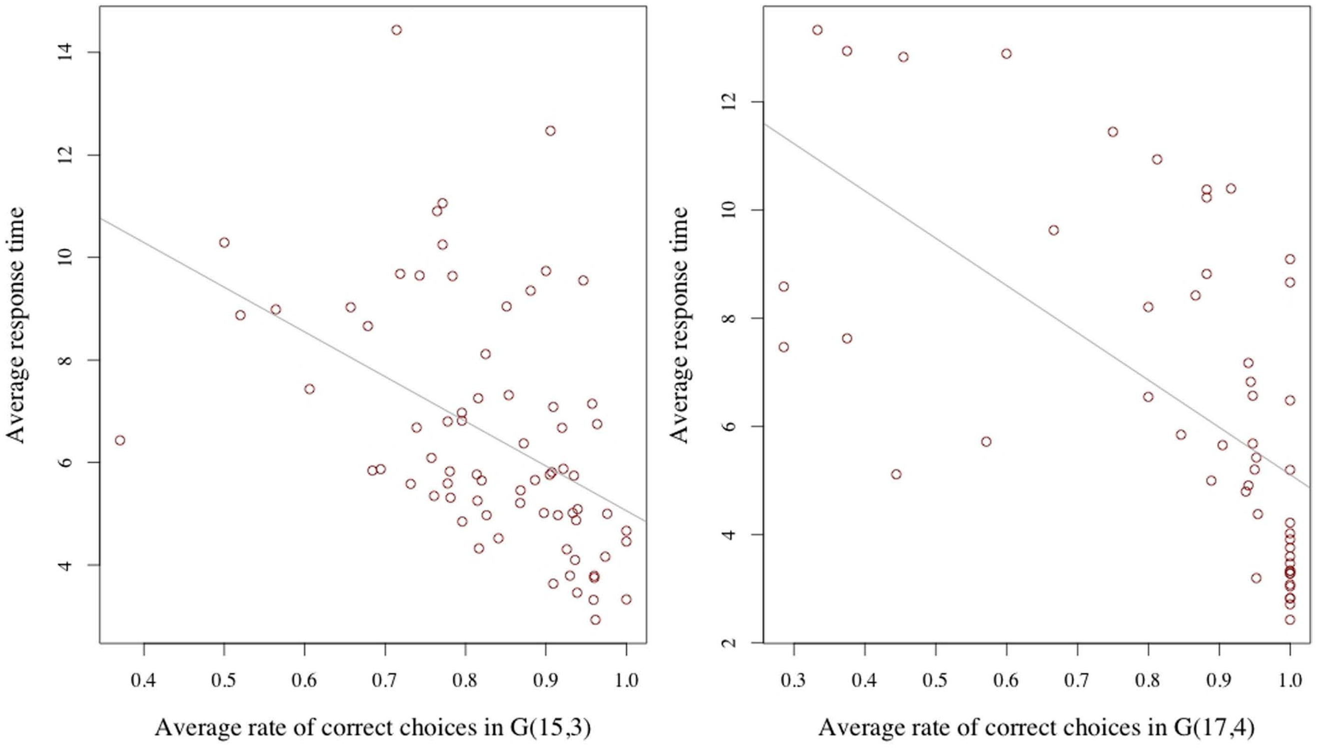

FIGURE 2 | Average response time and average correct rate. The averages are computed for each subject over the trials for the $G(15, 3)$ (on the left) and $G(17, 4)$ on the right.

Table 1 | Average response time and average correct rate OLS for both games.

	RT 15 (b/se)	RT 17 (b/se)
Avg. correct G(15, 3)	−8.581*** (1.766)	
Avg. correct G(17, 4)		−8.633*** (1.797)
Constant	10.993*** (0.952)	11.010*** (1.017)
r^2	0.252	0.316
N	72	52

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

game, at positions closer to the end. In the initial rounds this understanding of the game at later stages is lacking, and the subject may prefer to discontinue the reasoning soon because it is not producing any useful insights.

At the opposite extreme, if ability is so large that the signal is completely informative, only a short time will be necessary while still leading to a high correct response rate. This is likely to occur of course at the late stages of the game, when a subject has an overall understanding of the optimal strategy. It is also likely to occur at the final positions, where very simple reasoning can provide the conclusion.

Between these two extremes, where signal is partly informative, the optimal policy will prescribe a positive response time. Overall the relation between ability and response time is non-monotonic: likely to be increasing for low values of ability, and decreasing for higher values.

A specific conclusion of the model is that the response time at a position is not necessarily monotonically increasing or decreasing with experience, but might instead be first increasing and then decreasing. At the early stages, low experience, which corresponds to low ability, induces an early stopping of the reasoning process (the information acquisition in our model), a short response time and a high error rate. At intermediate stages, as the subject acquires some basic understanding of the game, reasoning becomes more informative, hence stopping is postponed. Finally, in later periods the response time declines as subjects simply implement a solution algorithm which they now understand.

We will see that subjects' behavior broadly matches these predictions, and provide the conceptual framework for the analysis of the imaging data.

4. RESULTS

4.1. BEHAVIORAL RESULTS

We review the basic behavioral results presented in Gneezy et al. (2010) to prepare for the analysis of the imaging data. To analyze error rate, we define a subject's error j as a subject's failure to move the marker to j, whenever this is possible and moving to j is part of the winning strategy. In $G(15, 3)$ the possible errors of interest are failures to move the marker to any of the positions 3, 7, 11, or 15 whenever this would be possible. The error rate at j, e_j, is the fraction of times the error is made over the times the subject could avoid the error. For example e_3 is calculated as the number of times the subject had the opportunity of moving her opponent to position 3, yet failed to do so, divided by the times the subject held the move at position 1 or 2 in the game. The average error rate is the number of errors made at a winning position divided by the number of times the subject was in a winning position.

Response times for subjects show a marked decline across trials (see **Figure 3**), with subjects requiring more than 8 s on average to make a choice during the first three periods of the game, but not even half of that during the last 3 periods.

There is a substantial difference in the evolution of the response time in the two games. Consider first the game $G(15, 3)$: Note that the first trial has a very special role, since it is the one where subjects get acquainted with the task, and the rules of the game. If we ignore the first trial we see that the response time increases from the second to the fourth trial, and then declines, as the model predicts.

For the first trial of $G(15, 3)$ the error rate is 0.38, which is significantly lower than the average error rate that would be expected if choices were made randomly. Across 20 trials of study 1, the error rate steadily declines until it almost reaches zero: see **Figure 4**.

The four possible errors in $G(15, 3)$ occur at significantly different rates. No subject deviates from the winning strategy choice at the final 3 positions ($e_{15} = 0$). Error rates and average period marking the last occurrence of a particular error are lower for positions closer to the game's end ($e_3 \geq e_7 \geq e_{11}$): see **Figure 5**.

Each of the differences between e_3, e_7, and e_{11} is statistically significant ($p < 0.01$), and the pattern suggests that subjects indeed learn to identify losing positions in a sequential manner that begins from the game's final positions. These observations indicate that subjects progress through a sequence of minor realizations toward becoming proficient in the Hit game. The above trends for $G(15, 3)$ replicate in $G(17, 4)$. For both games we observe lower error rates at later positions, and an overall decrease of error rates over repeated trials. Average response times decline across trials in both games.

Subjects make significantly fewer mistakes in $G(17, 4)$ than in $G(15, 3)$ indicating that subjects transfer some of their acquired skill to the new game. Observing however, that only 20 out of 72 subjects manage to commit zero errors in $G(17, 4)$, it is likely, that most subjects have not fully developed the explicit BI solution to the sequential game after 20 trials of $G(15, 3)$.

Figure 6 illustrates the average response time in the losing positions, for each of the periods.

For position 11, the losing position which is closest to the end, the highest response time occurs in the first period, and declines in the periods thereafter. The peak for position 7 is reached at period

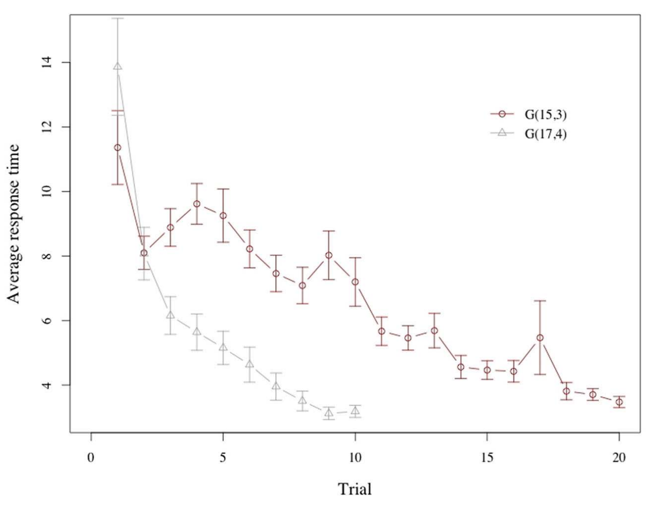

FIGURE 3 | Response time. Average response time across trials in $G(15, 3)$ and $G(17, 4)$. The plot shows an unexpectedly long response time for the very first trial, which is driven by subjects' response time at the initial onset of the game (see also **Figure 7**). At the onset of the game subjects appear to require additional time to familiarize themselves with the game environment. Removing the initial position of the initial round produces an increase in response time for $G(15, 3)$ in line with model predictions.

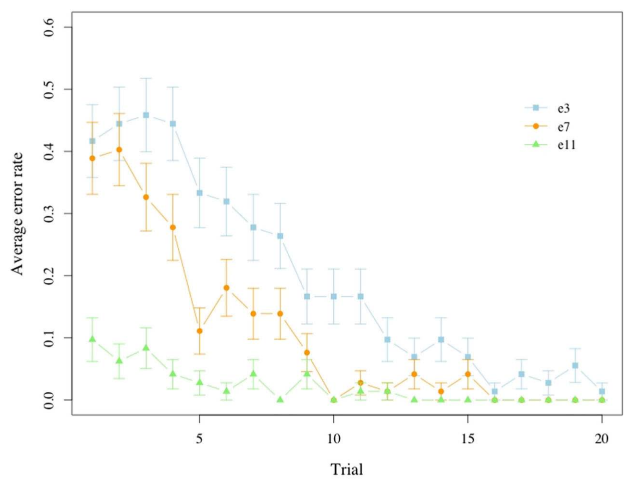

FIGURE 4 | Error rate by period. Average error by type for $G(15, 3)$.

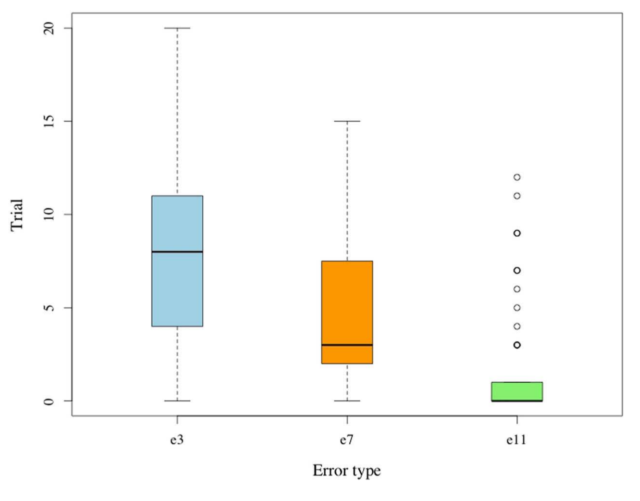

FIGURE 5 | Last trial for error. Whisker plot of trial during which the last error occurred; separated by type.

4, and that for position 3 is reached at period 5. As the model predicts, the response time is non-monotonic over the periods. For example the response time in period 7 is low at the initial stages, when subjects typically have a limited understanding of the game, but increases as the insight that the position 11 is a losing position is acquired and becomes available in the analysis of what to do at position 7. In later periods the response time at position 7 declines.

A similar relation can be seen in **Figure 7**, which illustrates the average response time at winning positions for $G(15, 3)$.

In this case too, the peak for the middle positions (winning positions {4, 5, 6} and {8, 9, 10}) is reached after an initial low value. The peak is reached at period 4 for {4, 5, 6} and at period 3 for {8, 8, 10}. The response time at the very first positions {1, 2} increases slowly; the maximum is reached at period 8, after an initial spike in period 1 which is likely to be due to the fact that the very first instance of position 1 is also the subjects' very first encounter with the game. The response time at the easy positions {12, 13, 14} monotonically declines after the initial period.

The figures we have seen present instructive average values over individuals' response times. A more accurate description is provided by the panel data regressions in **Table 2** for $G(15, 3)$ game and **Table 3** $G(17, 4)$ for which the dependent variable is the response time and the time variable for the panel is the index of the period. The independent variables are dummy variables corresponding to the groups of positions. They are indexed in increasing order according to their position on the board, left to right. For example, the first group of winning positions (*Win Pos 1*) in game $G(15, 3)$ indicates the set of positions {1, 2}. The second group of losing positions for $G(17, 4)$ indicates the position 7. In both regressions the variable dropped is the final group of winning positions, that is {10, 11, 12} for $G(15, 3)$ and {13, 14, 15, 16} for $G(17, 4)$.

The constant value is similar in both games, and around 4 s. The main effect of learning the game is estimated by the variables period and period square , indicating a significant and fast

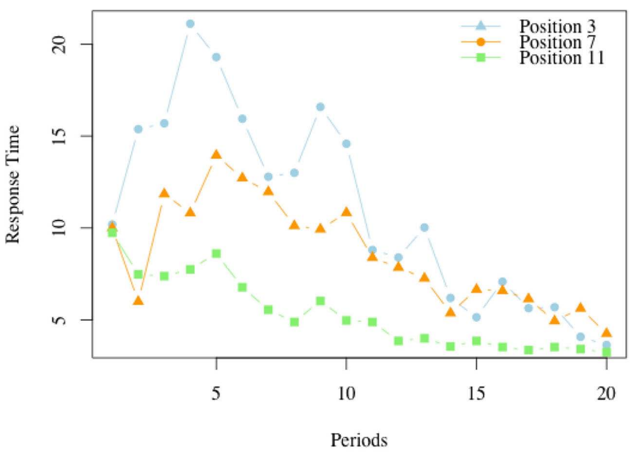

FIGURE 6 | Response times in losing positions, *G*(15, 3). For each of the 20 periods in which the game $G(15, 3)$ was played we report the average response time at each of the losing positions, 3, 7, and 11.

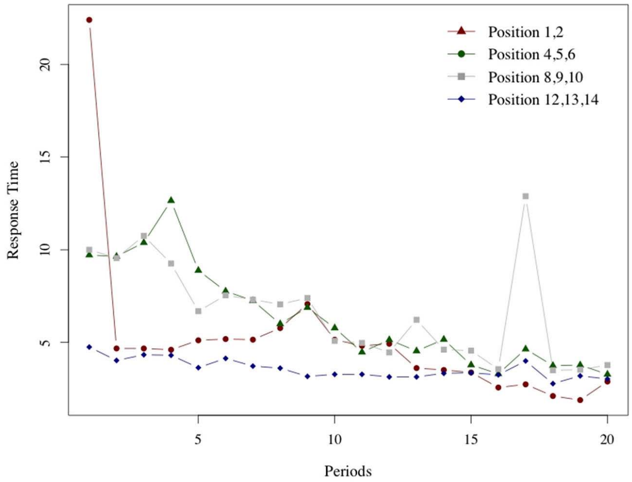

FIGURE 7 | Response times in winning positions. As in the previous **Figure 6** we report for each of the 20 periods in which the game $G(15, 3)$ was played the average response time at each of the four winning positions groups.

Table 2 | Response time in G(15, 3): panel data analysis.

	RT151(b/se)	RT152 (b/se)	RT153 (b/se)
Win pos 1	1.472*** (0.447)	1.293*** (0.432)	1.299*** (0.432)
Win pos 2	2.979*** (0.446)	2.690*** (0.432)	2.679*** (0.432)
Win pos 3	3.095*** (0.456)	3.009*** (0.442)	3.005*** (0.442)
Losing pos 1	4.223*** (0.499)	4.820*** (0.484)	4.849*** (0.484)
Losing pos 2	6.726*** (0.474)	6.946*** (0.459)	6.969*** (0.459)
Losing pos 3	1.280*** (0.466)	1.299*** (0.451)	1.306*** (0.451)
Period		−0.381*** (0.021)	−0.561*** (0.088)
Period square			0.009** (0.004)
Constant	3.800*** (0.396)	7.801*** (0.447)	8.460*** (0.544)
r^2			
N	5044	5044	5044

$*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

Table 3 | Response time in G(17, 4): panel data analysis.

	RT171 (b/se)	RT172 (b/se)	RT173 (b/se)
Win pos 1	2.972*** (0.920)	2.957*** (0.886)	2.958*** (0.874)
Win pos 2	3.307*** (0.904)	3.140*** (0.870)	3.066*** (0.859)
Win pos 3	2.711*** (0.913)	2.653*** (0.879)	2.637*** (0.868)
Losing pos 1	2.866*** (0.984)	3.327*** (0.948)	3.420*** (0.936)
Losing pos 2	4.078*** (0.943)	4.205*** (0.908)	4.262*** (0.896)
Losing pos 3	0.802 (0.926)	0.773 (0.891)	0.774 (0.880)
Period		−0.964*** (0.091)	−3.110*** (0.359)
Period square			0.204*** (0.033)
Constant	3.866*** (0.694)	8.429*** (0.797)	12.565*** (1.033)
r^2			
N	1442	1442	1442

$*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

[particularly in the game $G(17, 4)$] decline over time. The other variables confirm what we have seen in the aggregate analysis of the figures. Most notably, the increase in response time at losing positions is significantly higher than the one induced by winning positions; making more likely the conjecture that subjects carry over into the analysis of positions further from the end, insights they have obtained from the losing position 11, and possibly search for equivalent insight among positions earlier in the game.

4.2. THE fMRI DATA

4.2.1. Expected activation patterns and regions of interest

On the basis of the model and the analysis of the behavioral data we can formulate hypotheses to be tested in the study of the imaging data.

Learning of the method of backward induction should begin with the negative affective response experienced with moving at position 11, and realizing that the game is lost at that point. This experience should involve the reward system, particularly the Striatum (Schultz et al., 1997). We explore this hypothesis in section 4.3.

The predicted striatal response should be stronger, and occur earlier with subjects for whom behavioral evidence indicates that they posses a better understanding of the optimal strategy. We explore this hypothesis in section 4.4.

Further, the analysis of behavioral data has shown longer response times at the losing positions of game $G(15, 3)$. The brain activation at these three positions should be similar, but should occur at different points in time during the experimental session. Brain activation should involve both areas associated with reward system and areas involved in abstract reasoning. We test this hypothesis in section 5 (see in particular in **Figure 11**).

One of our main assertions is, that the affective response induced by the understanding that the game is lost at position 11 should occur together with activation of frontal areas involved in planning, particularly VLPFC (Crescentini et al., 2011). This hypothesis is also examined in section 4.5.

In what follows we present results obtained from an event-related random effects general linear model (rfxGLM) with 16 predictors. Predictors are dummy variables indicating the 7 sets of positions for $G(15, 3)$ over the first 10 trials (Early) and the last 10 trials (Late). A dummy variable indicating the computer's turn, and a constant term complete the model. The omitted variable corresponds to a resting period between trials. Unless explicitly stated, all results reported here are significant at an uncorrected threshold of $p \leq 0.005$; $t(11) \geq 3.59$ for the full sample, or with $t(5) \geq 4.77$ when split into Fast and Slow Learners. Fast Learners are defined as the 6 subjects with the lowest average error rate over both games. These are incidentally also the 6 subjects with the most wins in $G(15, 3)$. Correspondingly, Slow Learners are the 6 subjects with the highest average error rates.

The model and observed behavior suggests that subjects become proficient at the Hit-15 game via a sequence of insights pertaining to their experience at losing positions; the generic manifestation of which is the avoidance of the losing position at 11, followed by avoidance of position 7, and for some subjects avoidance of position 3. These adaptations, which are likely accompanied by (conscious) realization of these positions as losing positions happen at dramatically varying rates between subjects, and have critical relation to models of prediction error processing and temporal difference learning (see e.g., Schultz et al., 1997, or Daw et al., 2010). According to models of prediction error-based learning, unexpected occurrences of losing positions should be accompanied by corresponding BOLD signal change in areas involved with prediction error (PE) tracking, such as the Striatum (Schultz et al., 1997) and Insula (Preuschoff et al., 2008). We expect to see these PE responses whenever subjects first realize that a given position is a losing position, and also when subjects are unexpectedly placed onto an already identified losing position; both of which necessitate a yet incomplete understanding of the game, when played against a reasonably proficient opponent such as the computer program used for this study. This expectation follows, because prediction error responses should become less pronounced as subjects gain greater insight into the game as a consequence of their increased ability to accurately predict the games outcome. Hence, once the game's losing positions have been identified, finding oneself at a subsequent losing position becomes almost perfectly predictable at earlier stages, wherefore prediction errors should eventually approach zero.

4.3. PREDICTION ERROR RESPONSE IN THE STRIATUM AND INSULA

All subjects in the fMRI sample learn to identify position 11 as a losing position at some point during the game. In agreement with the idea that the identification of position 11 as a losing position induces an activation in the reward system, we find significant differences in striatal activation for subjects considering a move at losing position 11 compared to when considering a move at winning position {1, 2}. The difference in activation is in the direction of a negative prediction error, and an illustration is provided in **Figure 8**. (See also Appendix for time course graphs of BOLD activation).

Figure 8 also shows significant positive activation of the left and right Insula at coordinates (41, 19, 3), as subjects perceive the near inevitability of losing the game at position 11. This activation is consistent with the Insula's involvement in processing negative affect, and it's role in signaling negative prediction errors (Seymour et al., 2004)

4.4. PREDICTION ERROR RESPONSE FOR FAST LEARNERS

Given our main interest in the neural signature of the sequential, recursive way in which subjects learn the solution to the Hit-N game, we concentrate in **Figure 9** on the Fast Learners; those subjects who actually manage to quickly reduce the amount of errors they make in the game.

The left panel of **Figure 9** contrasts activation at position 11 to activation at position {1, 2} for Fast Learners. Consistent with the role of the Striatum in signaling prediction errors, we find that subjects show a strong initial negative response in the Striatum at losing position 11 during the first 10 rounds, which diminishes or disappears during the last 10 rounds. **Figure 10C** shows that this change of Striatal activity for Fast Learners is statistically significant at an uncorrected threshold of $p \leq 0.005$, [$t(5) \geq 4.77$]. At the same threshold, we observe significant activity in the Insula during both time periods.

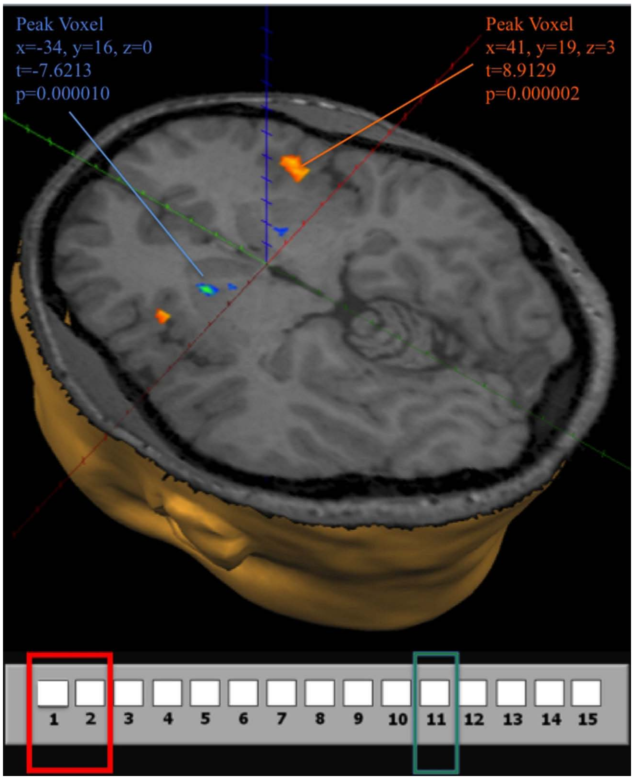

FIGURE 8 | Brain activity at the losing position 11 in *G*(15, 3). Contrast obtained from a GLM with 16 predictors on all 12 subjects. In the GLM we use the same 7 groupings for positions in the game, and differentiate between positions during the first (early) and last (late) 10 trials, for a total of 14 predictors. An additional predictor for computer choices and a constant term describe the full model. The contrast used in the figure shows activation when the current position is 11 during both early and late trials compared to activation at positions {1, 2} during early and late trials. The map shows activation at a false discovery rate $q < 0.05$.

Our analysis also shows strong activity in the Insula at position 7 compared to {1, 2} during early trials, and eventually activity in the Striatum at position 7 during late trials; indicating a shift of the prediction error from position 11 to position 7; the sequence – as we have already shown – in which subjects learn the losing positions.

Figure 10 provides support to the above observations by overlaying the contrasts of early and late activity at position 11 (compared to {1, 2}) for both Fast and Slow learners. Slow learners exhibit detectable striatal activation in direction of a prediction error only during the last 10 trials; consistent with the observation that these subjects learn the game according to the same general pattern, but at a slower pace, than subjects classified as Fast Learners. However, the direct test of the effects of Early/Late periods, Fast/Slow learners, and the interaction term of these classifications, shown in **Table 4**, did not identify a statistically significant effect for the interaction ($p = 0.158$).

4.5. EXPERIENCE-BASED LEARNING AND ABSTRACT REASONING

The center image of **Figure 10C** identifies a cluster of voxels in the ventrolateral prefrontal cortex (VLPFC; 47, 40, 3) with strong positive activation during the early losing position for Fast Learners. We are left to investigate the activity in this area when subjects are in losing positions for the game $G(15, 3)$.

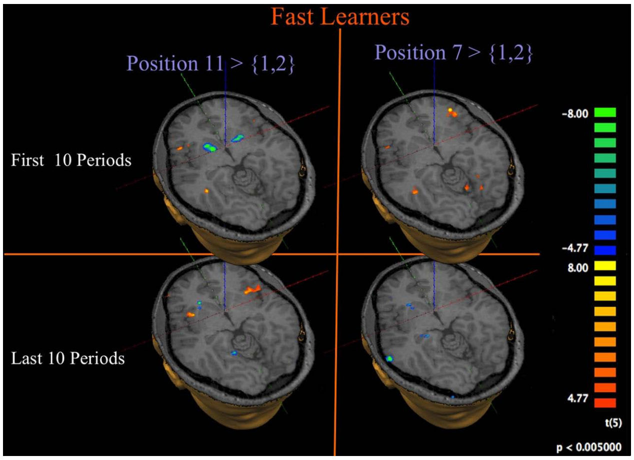

FIGURE 9 | Progression of activation at losing position 11 for fast learners. GLM and contrasts as for **Figure 8**, but limited to Fast Learners.

Our analysis of losing positions, illustrated in **Figure 11**, shows statistically significant increases of activation in the VLPFC at all of the losing positions during $G(15, 3)$. Given this region's association with tasks requiring spatial imagery in deductive reasoning (see Knauff et al., 2002 or Crescentini et al., 2011) the observation of higher activity during losing positions is of particular interest, as it indicates the special contribution that the experience of a losing position seems to make toward subject's progress in learning the game.

Figure 11 shows overlapping regions of activation for all losing positions experienced by Fast Learners that is most pronounced at position 11, and least pronounced at position 3; once again highlighting the critical nature of the initial losing position 11 for subject's learning experience with the game.

5. CONCLUSION

We have explored how subjects learn to play the Hit-N game, and how this process converges for all subjects to learning the optimal strategy with the method of backward induction. We found strong evidence for a sequential learning process in which subjects learn the losing positions at the game's end first. We showed that the behavioral characteristics (in error rate and response time) of this sequential learning process are consistent with a basic search model in which subjects choose an optimal search effort conditional on their ability and associated search costs.

We have also shown a neural pattern of activation in the brain's reward system, including the Insula and Striatum, that mirrors the behaviorally implied pattern of subjects learning to identify losing positions from the game's end. In particular, we find that the rate at which subjects learn to identify losing positions is also reflected by a differential onset of prediction error response between Fast and Slow Learners. A critical finding of our study is the implication of the prefrontal cortex in subject's progression toward finding the solution to the Hit-N game. Here we find

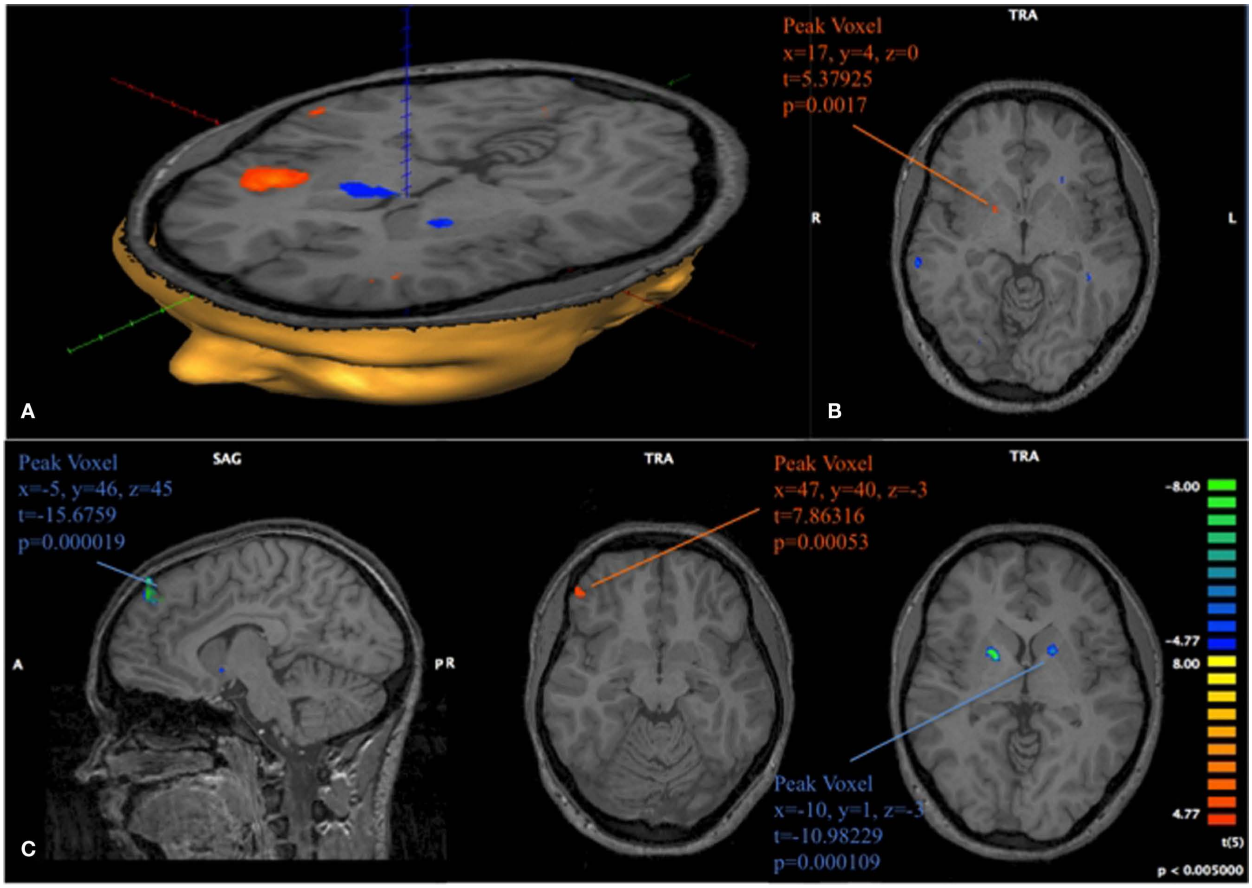

FIGURE 10 | Progression of activation in fast and slow learners. **(A)** Contrast obtained from a GLM with 16 predictors on 6 subjects classified as Slow Learners. The depicted contrast shows activation at position 11 compared to activation at position 1, 2 during late trials. $p < 0.005$ uncorrected, $t > 4.77$. **(B)** Same model as **(A)**. The depicted image subtracts the contrast obtained for positions 11 vs {1, 2} in late periods from the contrast obtained for those positions during early periods. Positive identification of Striatum in this contrast, is driven by a more strongly negative activation at position 11 in late periods for Slow learning subject. **(C)** 12 predictor GLM for 6 subjects classified as Fast Learners. As in **(B)**, we show the subtraction of the contrast (11 early-1, 2 early)–(11 late-1, 2). We find activation in Medial Prefrontal Gyrus (MPFG), VLPFC, and Striatum. Negative identification in Striatum is driven by a more strongly negative response at position 11 during early trials for Fast Learners. $p < 0.005$ uncorrected for all images depicted here.

Table 4 | Interaction between fast/slow learner, and early/late trial on BOLD signal contrast position 11 – position {1, 2} in Striatum.

	Perc. BOLD (b/se)
Dummy for fast learners	−0.09366 (0.08354)
Dummy for first 10 periods	0.15197 (0.32534)
Interaction term	0.17345 (0.11814)
Constant	1.02843*** (0.23005)
r^2	0.2144
N	24

$*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

that activity in VLPFC is higher at losing positions than at corresponding winning positions. Taken together, these findings point toward a cognitive process in which the affective experience of a losing position feeds critically into the subject's abstract cognitive engagement with the task.

While most of our discussion concentrated on subject's success in recursively learning to identify losing positions in the Hit-N game, it is clear that such a process – although enabling subjects to master any length Hit-N game – is not equivalent to an abstract, explicit understanding of the BI solution to the game; one which could be transferred instantaneously to other similar games, such as $G(17, 4)$. We see then, in both of our studies, that most subjects, despite quickly becoming highly proficient in $G(15, 3)$, fail to instantaneously achieve proficiency in $G(17, 4)$. Instead, subjects require an abbreviated learning period also for the second game.

What seems remarkable about the transition of behavior from G(15, 3) to $G(17, 4)$ is that subjects, even without ostensibly having explicit knowledge of the BI solution at the time they begin $G(17, 4)$, nonetheless commit fewer errors, and require a shorter learning phase for the theoretically more difficult second game. This observation provides strong indication that the recursive learning algorithm that enables learning of $G(15, 3)$ is also a contributor to the development of a precursory understanding of

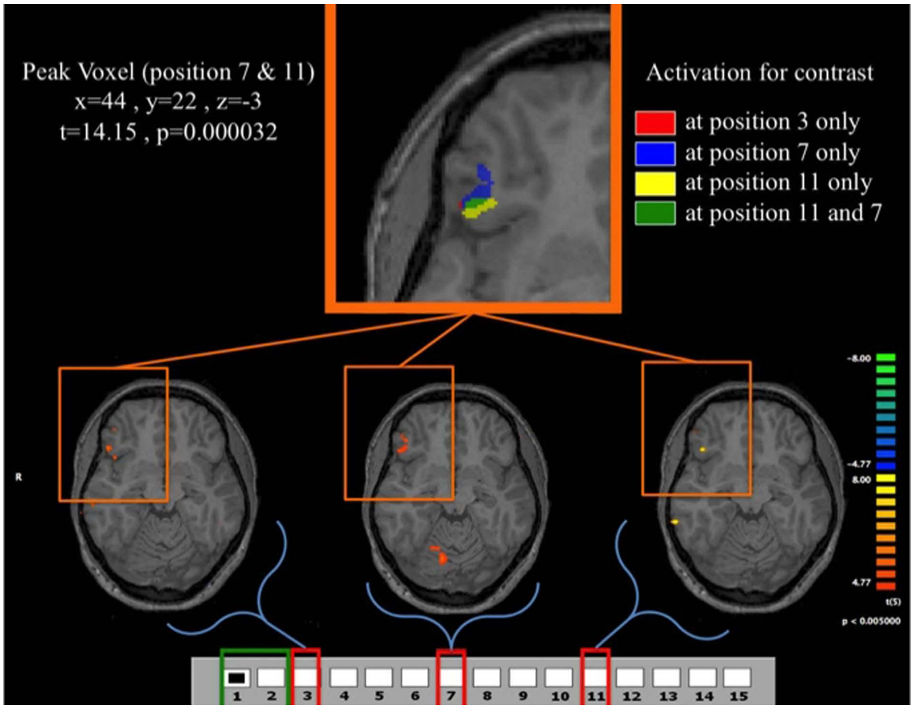

FIGURE 11 | Fast learners at the losing positions. Contrast for Fast Learners during first 10 periods at $p < 0.005$. The contrasts used are for each of the three losing position, compared to the predictor given by the game being in position {1, 2}. For example the contrast for the position 3 indicates the comparison between position 3 and position {1, 2}. The top panel shows the clusters in VLPFC activated for the different contrasts. The lower panel shows the activation for the contrasts (3,{1, 2}), (7,{1, 2}), and (11,{1, 2}). Activation in VLPFC is not found in Fast Learners during the last 10 rounds, and Slow Learners show it only during the last 10 rounds for 11-{1, 2}. As shown in **Figure 5**, Fast Learners do not make mistakes past round 10, while Slow Learners commit mistakes even at position e11 past round 10. It should be also noted here that a direct test of the interaction between subjects' categorization as Fast/Slow Learner and a dummy variable indicating Early/Late trials did not yield a statistically significant effect ($p = 0.158$ two-sided, see **Table 4**). We believe that the failure to identify such an effect at conventional significance level in our data may be due to small sample size, and an insufficiently precise measure of when subjects learn the game.

the game's abstract solution. One implication of this finding is that complex cognitive insights, such as understanding that backward inductive reasoning provides a solution to the general Hit-N game, can arise from the interaction of experience-based reward system responses and abstract reasoning within a relatively simple model. The fact that an experience-based understanding derived from playing $G(15, 3)$ is effective in improving subject's performance in $G(17, 4)$ suggests that at least some higher-order cognition and insights might be motivated and prepared by joint activity in the brain's reward system and prefrontal cortex.

6. MATERIALS AND METHODS

6.1. MRI DATA ACQUISITION

High resolution anatomical images were acquired first, using a Siemens $t1$-weighted 3D flash 1 mm sequence. Then, functional images were acquired using echo planar imaging with Repetition Time (TR) 2000 ms, Echo Time (TE) 23 ms, flip angle 90°, 64×64 matrix, 38 slices per scan, axial slices 3 mm thick with no gap. The voxel size was $3\,\text{mm} \times 3\,\text{mm} \times 3\,\text{mm}$.

The data were then preprocessed and analyzed using Brain Voyager QX 2.1. The anatomical images were transformed into Talairach space in 2 steps: first the cerebrum was rotated into anterior commissure – posterior commissure (AC-PC) plane using trilinear transformation, second we identified 8 reference points (AC, PC, and 6 boundary points) to fit the cerebrum into the Talairach template using trilinear transformation. We preprocessed functional data by performing slice scan time correction, 3D movement correction relative to the first volume using trilinear estimation and interpolation, removal of linear trend together with low frequency non-linear trends using a high-pass filter. Next, we co-registered functional with anatomical data to obtain Talairach referenced voxel time courses, to which we applied spatial smoothing using a Gaussian filter of 7 mm.

GLM MODELS

fMRI analysis was performed in Brain Voyager QX version 2.1. Contrasts obtained for $G(15, 3)$ are based on the results of an event-related general linear model with random effects using 16 predictors. Seven predictors signify the period in which a subject contemplates any of the positions {1, 2}, {3}, {4, 5, 6}, {7}, {8, 9, 10}, {11}, {12, 13, 14} during the first 10 trials of $G(15, 3)$. Another 7 predictors signify the same position during the last 10 trials. An additional predictor for times in which the computer is moving and an intercept term describe the model. Contrasts obtained for $G(17, 4)$ are based on the results of an event-related general linear model with random effects using 16 predictors. Seven predictors signify the period in which a subject contemplates any of the positions {1}, {2}, {3, 4, 5, 6}, {7}, {9, 10, 11}, {12}, {13, 14, 15, 16} during the first 10 trials of $G(17, 4)$. Another 7 predictors signify the same position during the last 10 trials. An additional predictor for times in which the computer is moving and an intercept term describe the model.

6.3. FAST AND SLOW LEARNERS

The fMRI study consists of 12 subjects. For analysis comparing Fast and Slow Learners in $G(15, 3)$, subjects were split into groups according to their overall error rate (a subject is slow if the error rate is larger than 40%), which also constitutes a splitting according to Wins in $G(15, 3)$ (a subject is slow if the number of wins in that game is less than five). Both are median values, but they are also values at which there is a large change of performance.

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APPENDIX

The following figures show time series plots of percentage BOLD signal change in the game G(15, 3) for clusters defined by the contrast of positions 11-{1, 2}, using t = 4.5, cs = 100. The x-axis represents positions in G(15, 3).

In graphs comparing early (first 10) and late (last 10) trials, error bars are for the mean condition over all 20 trials.

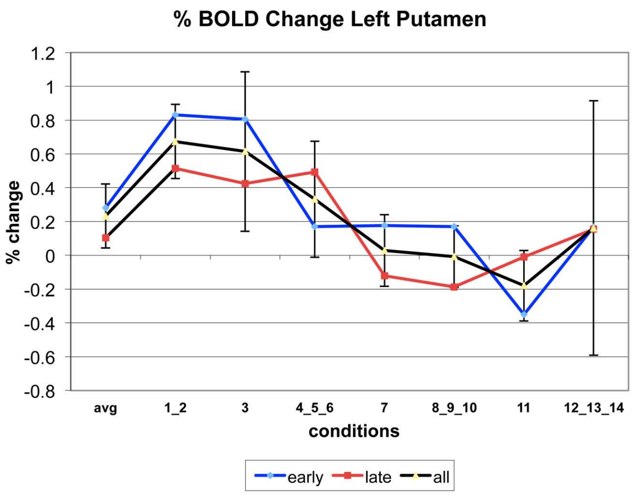

FIGURE A1 | Time series of percentage BOLD change for G(15,3).

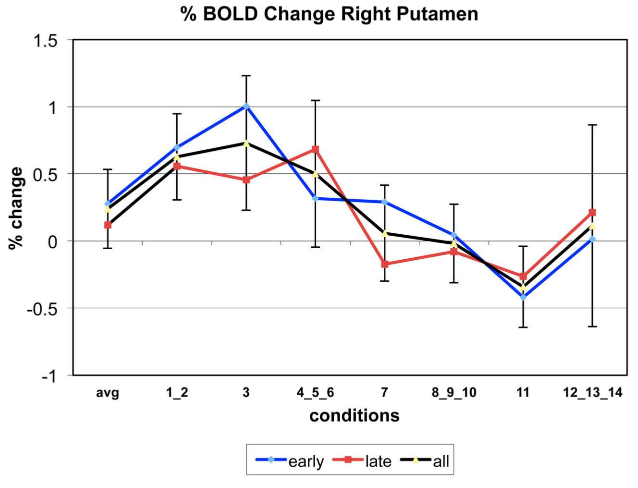

FIGURE A2 | Time series of percentage BOLD change for G(15,3).

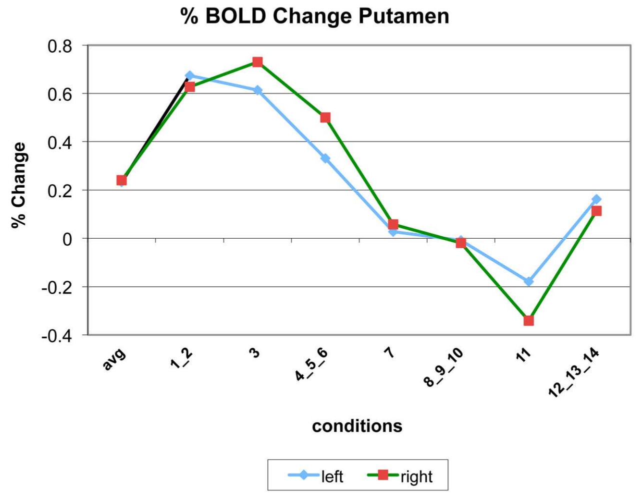

FIGURE A3 | Time series of percentage BOLD change for G(15,3).

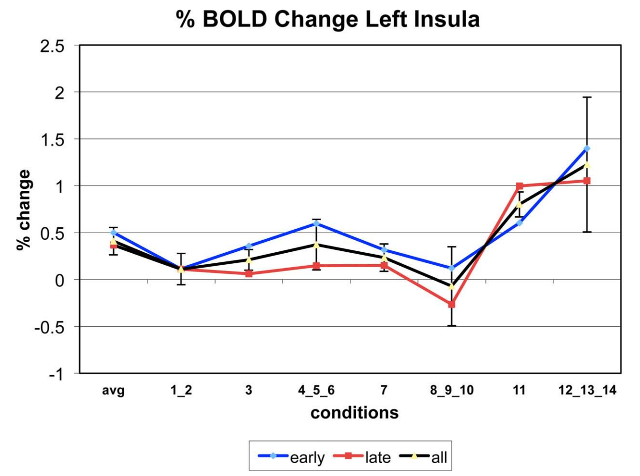

FIGURE A4 | Time series of percentage BOLD change for G(15,3).

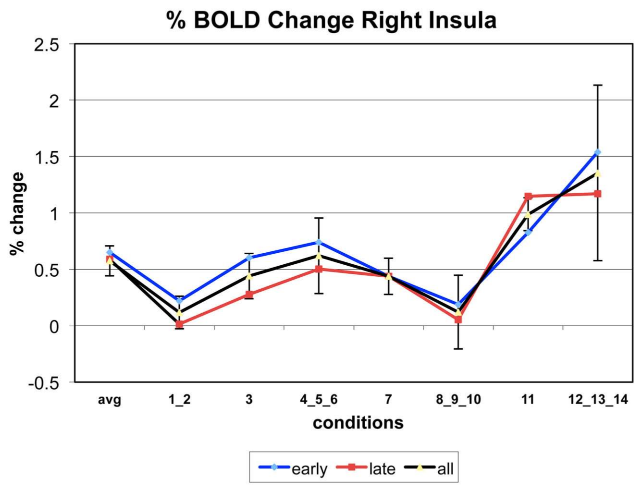

FIGURE A5 | Time series of percentage BOLD change for G(15,3).

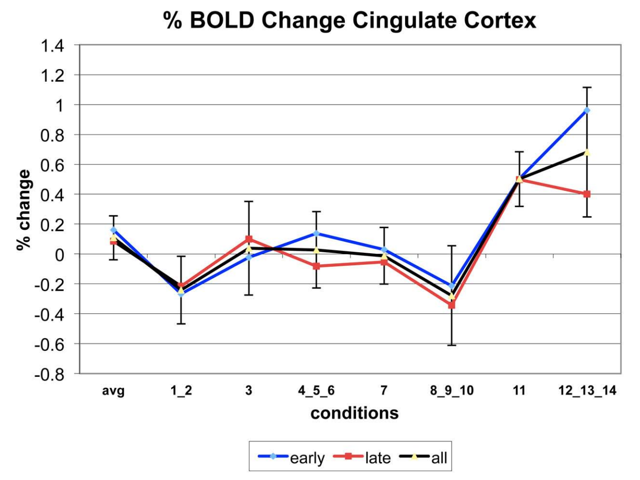

FIGURE A7 | Time series of percentage BOLD change for G(15,3).

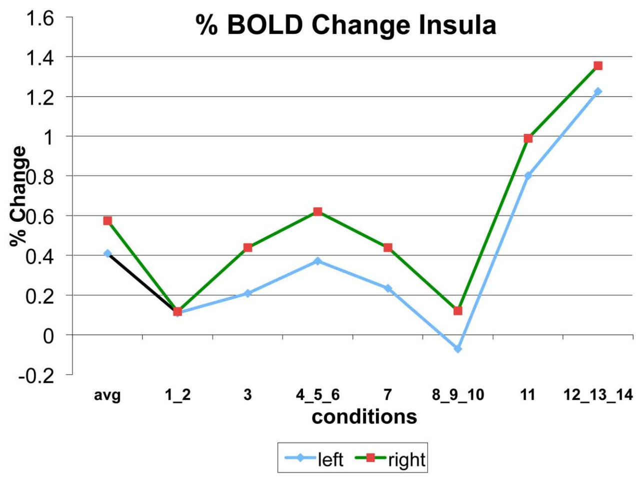

FIGURE A6 | Time series of percentage BOLD change for G(15,3).

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Transcranial alternating current stimulation increases risk-taking behavior in the Balloon Analog Risk Task

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The process of evaluating risks and benefits involves a complex neural network that includes the dorsolateral prefrontal cortex (DLPFC). It has been proposed that in conflict and reward situations, theta-band (4–8 Hz) oscillatory activity in the frontal cortex may reflect an electrophysiological mechanism for coordinating neural networks monitoring behavior, as well as facilitating task-specific adaptive changes. The goal of the present study was to investigate the hypothesis that theta-band oscillatory balance between right and left frontal and prefrontal regions, with a predominance role to the right hemisphere (RH), is crucial for regulatory control during decision-making under risk. In order to explore this hypothesis, we used transcranial alternating current stimulation, a novel technique that provides the opportunity to explore the functional role of neuronal oscillatory activities and to establish a causal link between specific oscillations and functional lateralization in risky decision-making situations. For this aim, healthy participants were randomly allocated to one of three stimulation groups (LH stimulation/RH stimulation/Sham stimulation), with active AC stimulation delivered in a frequency-dependent manner (at 6.5 Hz; 1 mA peak-to-peak). During the AC stimulation, participants performed the Balloon Analog Risk Task. This experiment revealed that participants receiving LH stimulation displayed riskier decision-making style compared to sham and RH stimulation groups. However, there was no difference in decision-making behaviors between sham and RH stimulation groups. The current study extends the notion that DLPFC activity is critical for adaptive decision-making in the context of risk-taking and emphasis the role of theta-band oscillatory activity during risky decision-making situations.

Keywords: DLPFC, BART, risk-taking, theta-band oscillations, lateralization

INTRODUCTION

When facing risky situations humans have to weigh up the consequences of failure against the rewards for success. Assessing risk inevitably involves a conflict between the desire to win and the fear of penalty. In such situations, the ability to identify and weight risks and benefits is highly important in order to make proper predictions concerning potential outcomes that will best serve individual survival and future goals. In this regard, the cognitive architecture, neural, and electrophysiological basis of decision-making processes in the context of risk-taking has gained a lot of attention in the last two decades. Studies of patients with focal brain lesion (e.g., Bechara et al., 1994, 1996; Tranel et al., 2002), alongside numerous neuroimaging and electroencephalogram (EEG) studies (e.g., Rogers et al., 1999; Paulus et al., 2001; Sanfey et al., 2003a,b; Ernst and Paulus, 2005; Trepel et al., 2005; Krain et al., 2006; Rao et al., 2008; Gianotti et al., 2009; Hare et al., 2009; Mohr et al., 2010) suggest that decision-making processes involve a distributed subcortical–cortical network that includes multiple prefrontal, parietal, limbic, and subcortical regions.

Within this network, prefrontal cortex (PFC) involvement appears to be vital in decision-making under risk. Based on traumatic brain injuries or other pathologies affecting the PFC (Bechara et al., 1996; Rahman et al., 2001) it seems that PFC dysfunction typically manifests in a tendency for riskier decision-making behavior and an apparent disregard for negative consequences of actions during risky decision-making. In particular, the dorsolateral prefrontal cortex (DLPFC) has been considered to play an important role in decision-making under risk, probably due to its function in executive control, goal maintenance, and inhibitory control (Miller and Cohen, 2001; Knoch et al., 2006; Rao et al., 2008; Hare et al., 2009), as well as decision implementation (Mohr et al., 2010). This hypothesis seems particularly plausible for right hemisphere (RH) role in risky decision-making under risk ("RH hypothesis"), and mostly pronounced in right PFC/DLPFC function as found in patients with right-sided lesions (Tranel et al., 2002; Clark et al., 2003), and is supported by several neuroimaging, EEG, and brain stimulation studies (e.g., van't Wout et al., 2005; Knoch et al., 2006; Fecteau et al., 2007a; Gianotti et al., 2009), and by a recent meta-analysis (Mohr et al., 2010). For instance, a repetitive transcranial magnetic stimulation (rTMS) study showed that individuals displayed riskier decision-making in a standard gambling paradigm after disruption of the right, but not the left, DLPFC (Knoch et al., 2006). Mohr et al. (2010) found that the right DLPFC (in conjunction with parietal cortex) has a role in risk processing during decision-making, particularly in the implementation of the risk decision, and the integration of the risk information with other aspects that may be relevant.

However, several findings call in to question the RH hypothesis role in risky decision-making under risk. For instance, a transcranial direct current stimulation (tDCS) study showed that after bilateral DC stimulation individuals displayed a conservative, risk-averse response style in a standard gambling paradigm (Fecteau et al., 2007b). In this study, unilateral DC stimulation to left or right DLPFC did not affect decision-making style at all, whereas both kinds of bilateral DC stimulations, regardless of electrodes polarity, produced the same behavioral outcome. Furthermore, in another tDCS study it has been found that DC modulation of the DLPFC influenced driving behavior, with anodal excitation of both the left and the right DLPFC leads to a more careful driving behavior (Beeli et al., 2008). Similar to Fecteau et al. (2007b), Beeli et al. (2008) did not find any clear functional lateralization patterns. These findings add to previous studies and suggestions such as Clark et al. (2003) report that patients with left-sided prefrontal lesions also displayed abnormal risk-taking behaviors, and to a meta-analysis of different neuroimaging studies which revealed that risky and ambiguous decision-making elicited activity bilaterally in the PFC (mainly orbitofrontal and DLPFC; Krain et al., 2006). This variety of evidence suggests that functional DLPFC lateralization in risk-taking behavior is still an unsolved issue that calls for further examination. Moreover, past studies, mostly studies that utilized brain stimulation techniques such as TMS and tDCS are restricted in the way they can uncover what is the electrophysiological mechanism that underlies the cognitive process in question.

Regional patterns of oscillatory activities can take place according to the behavioral tasks on which the brain is currently engaged (Thut and Miniussi, 2009). Studies into the role of brain oscillations in conflict and reward situations have demonstrated the relevance of oscillations in the theta-band (4–8 Hz). In particular, theta-band oscillatory activity over the medial frontal cortex has been proposed to reflect an electrophysiological mechanism for coordinating neural networks involved in monitoring behavior and the environment as well as facilitating task-specific adaptive changes in performance in conjunction with lateral PFC and sensory–motor areas. Different studies have identified that an induced oscillatory response in the theta-band during feedback processing is greater in power and phase coherence following negative feedback or errors relative to positive feedback or wins (e.g., Luu and Tucker, 2001; Luu et al., 2003, 2004; Cohen et al., 2007, 2008; Marco-Pallares et al., 2008; Cavanagh et al., 2009, 2010; Christie and Tata, 2009; van de Vijver et al., 2011). Furthermore, when an action or outcome is suboptimal and medial frontal cortex signals a need for adjustment, this also appears to lead to an increase in cognitive control, possibly via the additional recruitment of lateral PFC (Kerns et al., 2004; Ridderinkhof et al., 2004). Lateral PFC is assumed to adjust higher-level decision-making strategies to changing contexts and demands and to integrate information over time (McClure et al., 2004; Lee and Seo, 2007).

There is some evidence for the lateralization of the electrophysiological mechanism involved in risk-taking behavior. Gianotti et al. (2009) reported that individual's tonic cortical lateral PFC asymmetry in theta and delta bands predicted their behavior in a standard gambling paradigm. In other words, the extent to which baseline slow-wave oscillations in theta and delta bands was greater in the RH than in the left hemisphere, was positively associated with level of risk taken in Slovic's (1966) risk task. Specifically, using a source localization technique, they found that the baseline cortical activity in the right PFC predicts individual risk-taking behavior. A recent study by Christie and Tata (2009) showed that feedback-induced theta during the Iowa gambling task (IGT) was substantially right lateralized. Christie and Tata's (2009) finding adds to previous suggestions (Gehring and Willoughby, 2004; Marco-Pallares et al., 2008), which promote the hypothesis that medial frontal theta and the recruitment of right lateral PFC reward-related theta-band oscillatory activity may be regarded as the electrophysiological mechanism which mediates decision-making processes during risk-taking situations. In the current study, we aim to investigate this hypothesis and specifically the notion that theta-band oscillatory balance between right and left regions, with a predominance role to the RH, is crucial for regulatory control during decision-making under risk. To the best of our knowledge, no past study has reported a direct causal link between oscillations and lateralization patterns to risky decision-making behaviors. In order to investigate this hypothesis, we used a novel stimulation technique called transcranial alternating current stimulation (tACS).

Transcranial alternating current stimulation provides a powerful approach to establish the functional role of neuronal oscillatory activities in the human brain and to explore the functional role of neural oscillations in cognitive tasks by stimulating the brain with biophysically relevant frequencies during task performance. tACS is supposed to induce regional brain oscillations in a frequency-dependent manner, thereby interacting with specific functions of the stimulated region (Kanai et al., 2008, 2010; Pogosyan et al., 2009; Thut and Miniussi, 2009; Zaehle et al., 2010; Paulus, 2011). This technique is still largely unexplored and volume conduction effects are not wholly understood (Kanai et al., 2010; Zaghi et al., 2010; Feurra et al., 2011; Schutter and Hortensius, 2011). Nevertheless, recent studies have demonstrated tACS efficiency in different domains. For instance, Kanai et al. (2010) showed that cortical excitability of the visual cortex as measured by the thresholds for TMS evoked phosphenes, exhibits frequency dependency whereby 20 Hz tACS over the visual cortex enhances the sensitivity of the visual cortex. A recent study by Zaehle et al. (2010) provided direct physiological evidence of interaction between tACS and ongoing alpha oscillation in the occipital region. When tACS was delivered at the alpha-frequency, entrainment of the EEG amplitude in this frequency was observed. A recent study demonstrated that stimulation in alpha and gamma bands over the associative sensory cortex induced positive sensory sensations (Feurra et al., 2011). It has also been demonstrated that tACS at prefrontal sites during sleep improved procedural memory consolidation (Marshall et al., 2006).

Transcranial alternating current stimulation differ from other stimulation techniques that modulate brain frequencies, most notably rTMS. In general, low-frequency rTMS (<1 Hz) is often used to decrease excitability in an off-line mode (e.g., the task is administrated after the stimulation). In contrast, AC stimulation can possibly lead to one of two outputs: by inducing synchronous changes in brain activity, the AC stimulation can enhance ongoing oscillations and to increase/enhance cortical excitability, or AC stimulation can interrupt with ongoing cortical activity by introducing cortical noise, thus disrupt cortical excitability. This technique therefore allows us to exploit both properties of "enhancement" and "interference" in an on-line paradigm.

In the current study, we investigated whether on-line tACS can modulate the neural excitability of left and right PFC in a frequency-dependent manner. We aimed to examine whether risk-taking strategies can be modified in healthy individuals and to provide direct evidence for the causal role of lateralized hemispheric control, frequency-dependent, of risk-taking during a gambling game. Specifically, we focused on the theta-band (4–8 Hz) as the main oscillatory frequency and the DLPFC as the main structure of interest. In the current experiment, participants were randomly allocated to one out of three stimulation conditions that included right or left AC stimulation, or a sham stimulation, and performed the Balloon Analog Risk Task (BART; Lejuez et al., 2002) during the AC stimulation.

The BART is a task which involves learning from experience (i.e., experience-based decision), that was originally developed to be used as a behavioral measure of risk-taking tendencies. The task has been found to have a convergent validity with real-world risk-related situations, and provides an ecologically valid model to assess human risk-taking propensity and behavior (Lejuez et al., 2002; Schonberg et al., 2011). The average number of adjusted pumps a person tolerates in the task was found to correlate with self-reported drinking, smoking, risky sexual behaviors, and substance use in healthy adults and adolescents (Lejuez et al., 2002, 2003a,b, 2004, 2005; Aklin et al., 2005; Hunt et al., 2005).

We predicted that AC stimulation over the right DLPFC would increase RH theta-band power; consequently, participants would display a more conservative, risk-averse response style (i.e., smaller number of average adjusted pumps during the BART compare to sham). On the other hand, AC stimulation over left DLPFC was predicted to increase LH theta-band power, thus violate the hemispherical balance, and to disrupt decision-making processing; thus, we expected that participants would display riskier decision-making style (i.e., larger number of average adjusted pumps during the BART compare to sham). Finally, we investigated whether individual differences such as gender and trait motivation characteristics may moderate tACS effectiveness on performance, since both factors have been suggested to moderate decision-making processes to some extent (Tranel et al., 2005; Demaree et al., 2008).

MATERIALS AND METHODS

PARTICIPANTS

Participants in the experiment were 27 healthy college students (mean age = 23.89 SD = 2.45; range 18–30 years, 13 male, 14 female), each participant received 40 Shekel (equivalent to ∼10$) for participating in the experiment. All participants gave informed consent in accordance with the Declaration of Helsinki and the procedures had the approval of the local ethics committee. Participants had no metallic implants, previous history of any neurological disorders, medication, or substance abuse. All participants were right-handed as assessed by the Edinburgh Handedness Inventory (handedness score ≥90; Oldfield, 1971). The participants were randomly allocated to one of three stimulation groups [LH stimulation ($N = 9$)/RH stimulation ($N = 8$)/Sham stimulation ($N = 10$)].

BALLOON ANALOG RISK TASK

In the BART (Lejuez et al., 2002; Hunt et al., 2005), participants have to make a choice in a context of increasing risk. Participants inflated a computerized balloon by pushing a "pump" button. The balloon can explode at any moment. Participants have to decide after each pump whether to keep pumping and risk explosion, or to stop. In our modified version of the BART, participants accumulated points in a temporary bank with each pump (10 points). When the participant decided to stop pumping, the accumulated points transferred to a permanent bank. However, if the balloon explodes, all of the points accumulated in the temporary bank were lost. The probability that a balloon would explode was fixed at 1/128 for the first pump. If the balloon did not explode after the first pump, the probability that the balloon would explode was 1/127 on the second pump, 1/126 on the third pump, and so on until the 128th pump the probability of an explosion was 1/1 or a certainty. According to this algorithm, the average breakpoint was 64 pumps. Detailed instructions provided to the participants were based on those provided by Lejuez et al. (2002). Following instructions and a short guided practice, the task was administered until 30 balloons (i.e., trials) were completed. Note that participants did not actually receive the final sum of points stored in the permanent bank. Instead, they were informed at the beginning of the session that they are part of a tournament in which they play against other participants, for the prize of 250 Shekel (equivalent to ∼70$), and their objective was to obtain the largest amount of points possible in order to win the prize.

Similar to previous studies that used the BART (e.g., Lejuez et al., 2002), the main outcome measure of the current examination was the adjusted number of pumps. In addition, total number of balloon explosions on the BART was calculated. Adjusted values were calculated based on the average number of balloon pumps on those balloons that did not explode. Adjusted values are preferable, because including balloon pumps from all trials (including those in which balloons exploded) result in the inclusion of trials in which the participants were forced to stop pumping because of the explosion (Lejuez et al., 2002; Aklin et al., 2005). Because the adjusted value consisted only of no-explosion trials, it considers being an index of a more adaptive (non-punitive) form of risk-taking behavior (Hunt et al., 2005). In contrast, evaluating the frequency of balloon explosions provided an index of a more maladaptive form of risk-taking whereby risk exceeded an acceptable level and ultimately was punished (via explosion and loss of money; Hunt et al., 2005). Furthermore, because the BART was performed during the whole stimulation duration, we calculated the time course of this measures (adjusted number of pumps and frequency of balloon explosions for three blocks, each block contain 10 balloons).

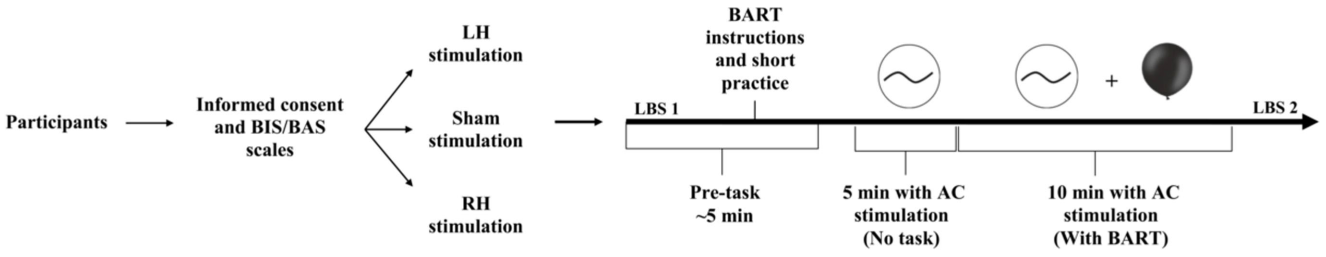

FIGURE 1 | Overview of the study design. Participants arrived at the lab, answered the BIS/BAS scales (Carver and White, 1994), and were randomly assigned into one of three stimulation conditions: left, right, or sham stimulation. After a short practice, sham or AC stimulation administered and lasted a total of 15 min, with 6.5 Hz, 1 mA peak-to-peak intensity in the active stimulation conditions. The stimulation started 5 min before the task began and was delivered during the entire course of the BART, which lasted <10 min. Before and after stimulation and the BART participants performed the line-bisection task.

In addition, a recent advance in modeling methods of the BART task, originally introduced by Wallsten et al. (2005), validated recently by Bishara et al. (2009), and further developed by van Ravenzwaaij et al. (2011) propose a model where BART performance is governed by different component processes such as risk-taking (involving the tradeoff between reward and penalties) and general sensitivity to payoff which affects task performance. Whereas adjusted values and frequency of balloon explosions are usually considered to tap the construct of risk-taking, payoff sensitivity can be measured with the evaluation of participants' deviation from the optimal expected-value strategy. We report these measures in the Results section.

tACS AND GENERAL PROCEDURE

A double blind, randomized and sham-controlled trial was used in a between participants design (see **Figure 1**). The experiment included three types of stimulation, two active stimulation conditions and one sham condition. We used the international EEG 10/20 system to determine stimulation sites. To stimulate the LH, one electrode was placed over the left DLPFC (F3) and the reference electrode was placed over the left temporal (CP5). To stimulate the RH, one electrode was placed over the right DLPFC (F4) and the reference electrode was placed over the right temporal (CP6). For sham stimulation, the electrodes were placed in the same positions as for active conditions (half of the participants with LH montage and the other half with RH montage).

The stimulation started 5 min before the task began and was delivered during the entire course of the BART, which lasted <10 min. tACS was induced by two 5 cm × 5 cm saline-soaked synthetic sponge electrodes and delivered by a battery-driven, constant-current stimulator (Magstim Ltd., Wales). The waveform of the stimulation was sinusoidal and there was no DC offset. AC was delivered at a frequency of 6.5 Hz and the intensity was 1 mA (peak-to-peak). For active stimulation conditions the AC stimulation was delivered for 15 min. For sham stimulation, stimulation was delivered for 30 s and then turned off. Thus, participants felt the initial itching sensation associated with brain stimulation but received no active current for the rest of the stimulation period. This method of sham stimulation has been shown to be reliable with respect to DC stimulation (Gandiga et al., 2006). In the present study participants were kept blinded with regard to the type of the stimulation; the AC procedure used, with AC delivered at a frequency of 6.5 Hz, did not induce any flickering sensation or any other side effects, as verified by questioning participants after the stimulation.

ASSESSMENT OF MOTIVATION

At the start of the session, participants completed the BIS/BAS scales (Carver and White, 1994) in order to evaluate trait motivational characteristics. The BIS/BAS scales (Carver and White, 1994) measures two independent based dimensions of motivation (Gray, 1987; Pickering and Gray, 1999; Gray and McNaughton, 2000): the BAS, which regulates responses to rewarding stimuli, and the BIS, which regulates inhibitory processes to aversive stimuli. All items were judged on a four-point scale ranging from 1 ("I strongly agree") to 4 ("I strongly disagree"). The BIS/BAS scales assess one behavioral inhibition measure (BIS; e.g., "I worry about making mistakes") and three personality measures related behavioral approach (BAS): (1) The positive anticipation of rewarding events (BAS Reward Responsiveness – BAS RR; e.g., "When I see an opportunity for something I like I get excited right away"); (2) Items tapping strong pursuit rewards (BAS Drive – BAS D; e.g., "I go out of my way to get things I want"); (3) The tendency to seek out new rewarding situations (BAS Fun Seeking – BAS F; e.g., "I am always willing to try something new if I think it will be fun").

LINE-BISECTION

Before and immediately after BART performance and AC stimulation, participants performed two line-bisection trials as a simple and non-invasive behavioral measure of a hemispheric bias. On each trial, participants were asked to mark the exact center of a 180-mm black line printed horizontally on a white sheet of paper. The line was printed at mid height of the page and was closer to the right border on one trial and closer to the left border on the other. Participants used a fine-point pen to bisect the line as accurately as they could. Scores reflected the percent of deviation from the center of the line: positive scores reflect a bias to the right side (stronger LH activation), and negative scores reflect a bias to the left side (stronger RH activation; Goldstein et al., 2010; Nash et al., 2010).

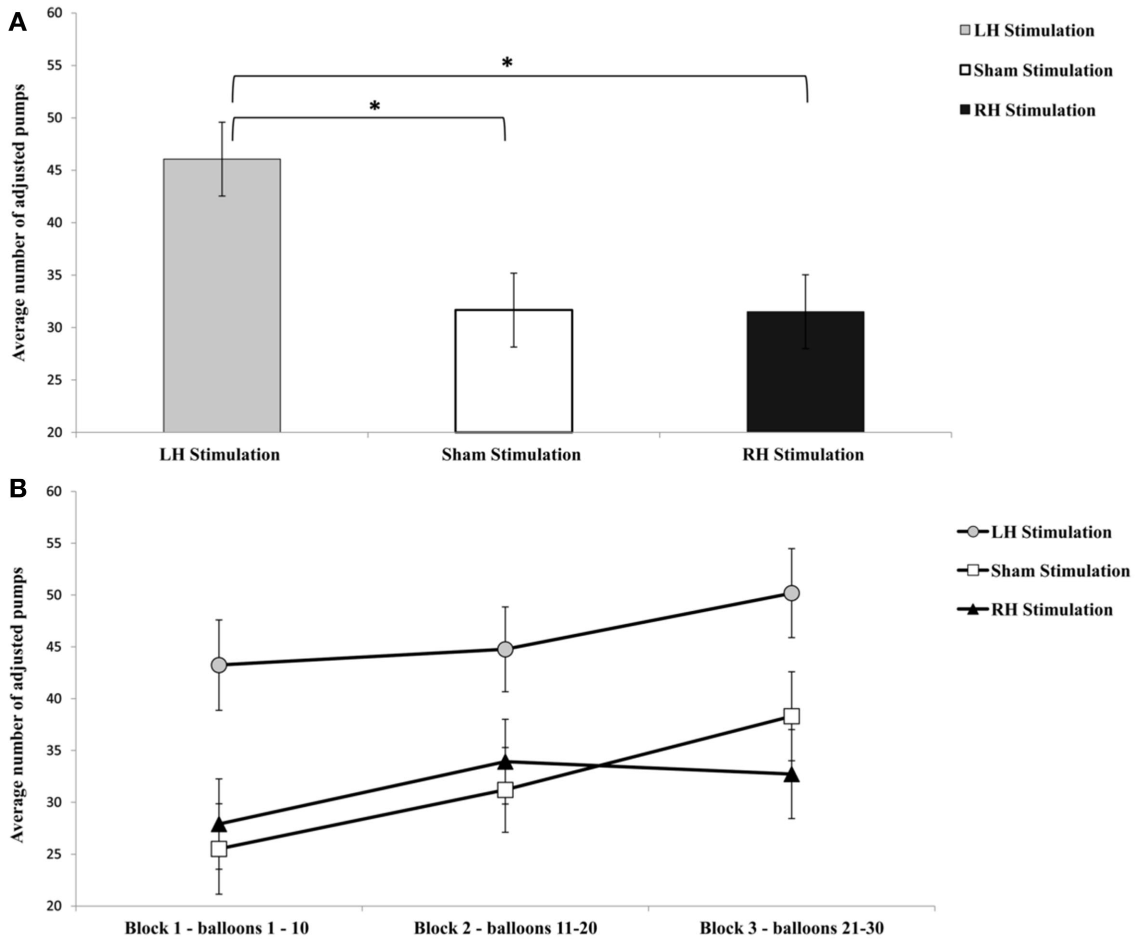

FIGURE 2 | Graphic display of the average number of adjusted pumps (the total pumps of the balloon that did not explode) for each stimulation group (A) and the average number of adjusted pumps for each group and time period (B). Error bars indicate SEM. $^{*}p < 0.05$.

RESULTS

BART PERFORMANCE

The data from the BART task was analyzed with a mixed AVOVA model that included one between-subject factor and one within-subject factors. The between-subject factor was Stimulation Group (LH stimulation/RH stimulation/sham stimulation) and the within-subject factor was Time (first block/second block/third block). Average number of adjusted pumps and total number of balloon explosions served as the dependent variables. When relevant, *post hoc* analyses were performed using a Bonferroni correction for multiple comparisons. Three participants (two in the sham group and one in the LH stimulation group) were excluded from all analyses as outliers (2 SD above or below the mean of the group for the adjusted number of pumps).

The analysis of average number of adjusted pumps revealed a main effect for Stimulation Group [$F_{(2,21)} = 5.63$, $p < 0.05$; $\eta_p^2 = 0.35$; see **Figure 2**]. *Post hoc* tests revealed an effect and show that the LH stimulation group differed significantly from both the sham stimulation ($p < 0.05$) and RH stimulation ($p < 0.05$) groups. In addition, the analysis revealed a main effect for Time [$F_{(2,42)} = 5.93$, $p < 0.05$; $\eta_p^2 = 0.22$]. A trend analysis showed a linear trend across blocks one to three [$F_{(1,21)} = 7.60$, $p < 0.05$; $\eta_p^2 = 0.26$]. *Post hoc* tests reinforced this linear trend, and revealed that the first and the last blocks differed significantly ($p < 0.05$). However, the analysis did not reveal any significant interaction between the two factors ($F < 1$).

The analysis of total number of balloon explosions also revealed a main effect for Stimulation Group [$F_{(2,21)} = 6.63$, $p < 0.01$; $\eta_p^2 = 0.39$; see **Figure 3A**]. *Post hoc* tests revealed that the LH stimulation group differed significantly from sham stimulation group ($p < 0.01$), and marginally differed from RH stimulation group ($p = 0.056$). In addition, the analysis revealed a marginal effect for Time [$F_{(2,42)} = 2.96$, $p = 0.06$; $\eta_p^2 = 0.12$]. *Post hoc* tests revealed that there was no significance different between the first block ($M = 3$; $SD = 1.56$) and the second block ($M = 2.75$; $SD = 1.32$). However, the second and the third block ($M = 3.54$; $SD = 1.31$) differed significantly ($p < 0.001$). The analysis did not reveal any significant interaction between the two factors ($F < 1$).

We further analyzed balloon explosions frequencies by defining for each participant whether a balloon explosion was a one-time explosion or a sequential explosion (a one-time explosion was defined as the number of total balloon explosions minus number

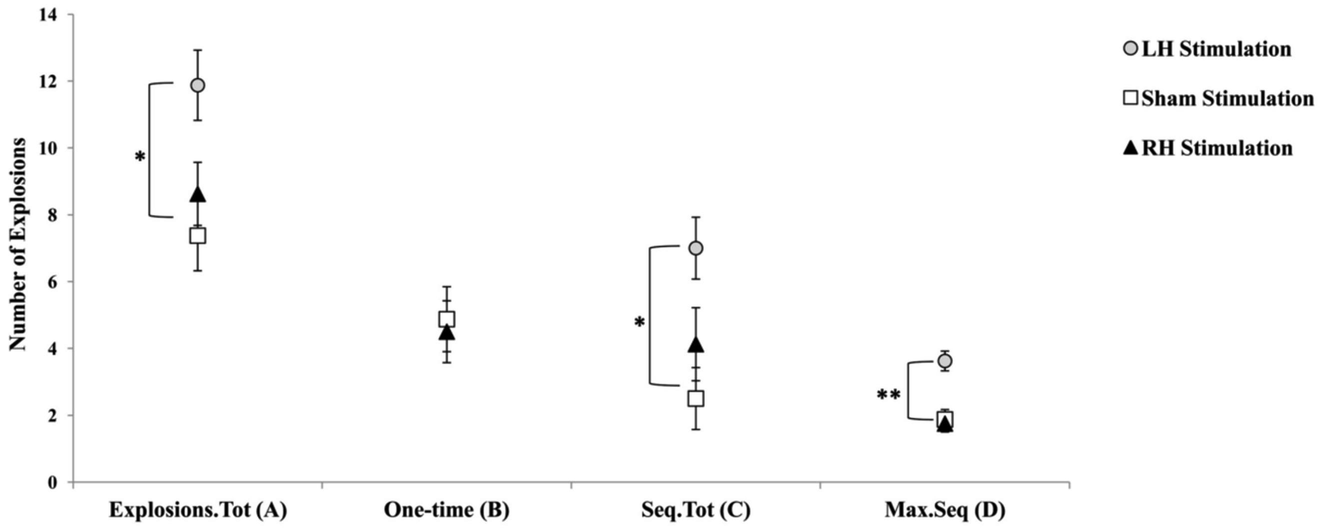

FIGURE 3 | Graphic display of the different balloon explosions frequencies dependent measures. (A) Explosions.Tot = total number of balloon explosions; **(B)** One-time = total number of one-time balloon explosions; **(C)** Seq.Tot = total number of sequential balloon explosion; **(D)** Max.Seq = maximum number of balloon explosions in a sequence. Error bars indicate SEM. $^*p < 0.05$. $^{**}p < 0.01$.

Table 1 | Pearson's correlations among different BART performance parameters.

	(1)	(2)	(3)	(4)	(5)	(6)
(1) One-time	–					
(2) Seq.Tot	−0.51**	–				
(3) Max.Seq	−0.22	0.76***	–			
(4) Pumps.Adj	0.28	0.56***	0.65***	–		
(5) Points.Tot	0.35*	0.35*	0.47**	0.94***	–	
(6) Explosions.Tot	0.22	0.74***	0.69***	0.85***	0.67***	–

One-time = total number of one-time balloon explosions; Seq.Tot = total number of sequential balloon explosion; Max.Seq = maximum number of balloon explosions in a sequence; Pumps.Adj = average adjusted number of pumps; Points.Tot = total points earned; Explosions.Tot = total number of balloon explosions.

**Correlation is significant at the 0.05 level (one-tailed).*

***Correlation is significant at the 0.05 level (two-tailed).*

****Correlation is significant at the 0.01 level (two-tailed).*

of explosions in trial *n* that were followed by no-explosion in trial $n+1$; sequential explosion was defined as the number of total balloon explosions minus total number of explosions in trial *n* that were followed by an explosion in trial $n+1$, $n+2$, etc.; the two measures are complementary). In addition, based on this simple calculation, we also defined another variable term "Maximum sequential explosions" that reflected the highest number of balloon explosions in a sequence for each participant. Consequently, each participant had three additional measures of the original balloon explosions frequency. The rationale to use these indices is based upon the idea that the use of a maladaptive index of risk-taking (e.g., number of balloon explosions) in a task with a random schedule of explosions may create an artifact with respect to the actual number of explosions that were a result of a risk behavior that exceeded an acceptable level and resulted in an explosion. Overall, the new indices were used in order to verify whether participants in the LH stimulation group indeed tend to pump the balloon more, a tendency that may be manifested not only in a higher overall number of explosions compare to the two other stimulation groups, but particularly in a higher number of non-random explosions. Pearson's correlations coefficients between the three newly defined measures and the other original BART parameters were calculated and presented in **Table 1**. The correlations of number of sequential explosions and maximum sequential explosions to the other BART known parameters suggest that these variables are reliably correlated, contrary to the number of one-time explosions.

Furthermore, based on these new measures, we conducted a MANOVA with Stimulation Group as between-subject factor and each of the newly defined measures as the dependent variables. We reveled a Stimulation Group effect [Wilks' Lambda = 0.45, $F_{(6,38)} = 3.13, p < 0.05; \eta_p^2 = 0.32$]. Follow-up testing showed that no stimulation group effect was found with respect to number of one-time explosion ($F < 1$; see **Figure 3B**). However, a Stimulation

Table 2 | Demographics and motivation information for the Sham, LH, and RH stimulation groups.

Variables and measures	Group		
	Sham stimulation ($N = 8$)	**LH stimulation ($N = 8$)**	**RH stimulation ($N = 8$)**
DEMOGRAPHICS			
Gender	5 Males/3 females	3 Males/5 females	4 Males/4 females
Age	25 (3.59)	22.87 (1.55)	23.62 (2.07)
Years of education	14.75 (1.08)	13.25 (0.88)	14 (1.07)
BIS/BAS SCORES			
BIS	13.50 (2.26)	13.12 (2.53)	14.50 (3.20)
BAS	22.75 (6.92)	21.62 (4.68)	23.87 (5.44)
BAS D	7.87 (2.23)	7.12 (2.85)	8.25 (1.91)
BAS FS	7.37 (3.45)	7.75 (1.90)	7.25 (2.12)
BAS RR	7.50 (2.45)	6.75 (1.83)	8.37 (2.13)

Values shown as mean (SD). BIS, behavioral inhibition system; BAS, behavioral approach system; BAS D, behavioral approach drive; BAS FS, behavioral approach fun seeking; BAR RR, behavioral approach reward responsiveness.

Group effect was found with respect to number of sequential explosions [$F_{(2,21)} = 4.34$, $p < 0.05$; $\eta_p^2 = 0.29$; see **Figure 3C**]. *Post hoc* tests revealed that the LH stimulation group differed significantly from the sham stimulation group ($p < 0.05$). A similar effect was reveled with respect to the maximum of sequential explosions [$F_{(2,21)} = 7.61$, $p < 0.01$; $\eta_p^2 = 0.42$; see **Figure 3D**]. *Post hoc* tests revealed robust effect and show that the LH stimulation group differed significantly from both the sham stimulation ($p < 0.01$) and RH stimulation ($p < 0.01$) groups. These analyses confirmed and elaborated on our previous mentioned results by demonstrating that participants who received the LH stimulation demonstrated a strategy of risky decision all along the BART, which systematically differed to the sham and RH stimulation groups. All the groups tolerated a similar number of one-time explosions, that resulted from the inherent nature of the task, but only participants receiving LH stimulation displayed a tolerance for losses, and in particular, sequential losses.

Lastly, we computed a behavioral index that taps participants' behavior in relation to optimal behavior in the BART task (e.g., payoff sensitivity). The optimal expected-value strategy was to pump 64 times and then stop. Explosion points were determined for each balloon in the manner described (i.e., each pump had an *a priori* probability of 1/128 of yielding an explosion) but with the constraint that explosions were scheduled to occur on average on Pump 64 over the entire 30 balloons and within each sub-block of 10. We calculated the mean squared distance (MSD) of each participant number of pumps at a given trial from the optimal number of pumps. MSD therefore reflects participants' sensitivity to payoffs, so that a closer score to zero represents an optimal strategy. Pearson's correlations coefficients between this measure and the two main BART outcome parameters reported earlier (e.g., average number of adjusted pumps and total number of balloon explosions) were performed, and showed a very high correlation ($r = -0.91$, $p < 0.000$; $r = -0.80$, $p < 0.000$; for adjusted pumps and balloon explosions, respectively). The fact that these parameters are highly correlated indicates that payoff sensitivity and risk-taking measures are confounded.

GENDER AND MOTIVATION BIAS

We investigated a possible moderation effect of individual differences such as gender and trait motivation characteristics (see **Table 2** for descriptive statistics) on performance. First, we separately entered gender as a covariate to the mixed AVOVA models reported earlier. There was no significant effect to gender or any significant interactions with other factors in any of the models. Second, in order to investigate the role of motivation bias on performance, we separately entered BAS, BIS, and BAS subscales scores as covariates to the mixed AVOVA models reported earlier. All models produced non-significant effects for motivation bias. The stimulation groups did not differ in any demographic variables or in any BIS/BAS parameter ($F < 1$).

LINE-BISECTION BIAS

In order to evaluate how BART performance and AC stimulation affected hemispheric bias as measured by the line-bisection, we analyzed line-bisection scores in a mixed ANOVA model that included Stimulation Group (LH stimulation/RH stimulation/sham stimulation) as the between-subject factor and Time (Before/After) as the within-subject factor. The analysis revealed a main effect for Time [$F_{(1,18)} = 23.70$, $p < 0.000$; $\eta_p^2 = 0.53$]. The line-bisection index was more negative after performing the BART task ($M = -0.16$, $\mathrm{SE} = 0.06$) compare to before ($M = 0.18$, $\mathrm{SE} = 0.07$), indicating that the BART had the expected hemispheric effect, i.e., RH engagement which lead to stronger RH activation. This asymmetry shift can be further emphasized – 18 out of 24 participants achieved a positive line-bisection score before the BART and AC manipulation (this was significantly higher than 50% by a binomial test, $p < 0.05$), but after task and stimulation, 18 out of 24 achieved a negative score (this was significantly higher than 50% by a binomial test, $p < 0.05$). We separately analyzed before and after line-bisection scores for the different AC groups using paired samples t-tests. Participants in the Sham [$t_{(7)} = 3.25$, $p < 0.05$] and RH stimulation [$t_{(7)} = 5.6$, $p < 0.001$] groups showed the asymmetry shift, however participants in the LH stimulation showed only a non-significant trend [$t_{(7)} = 1.47$, n.s]. This finding implies that the BART did not produce the expected asymmetry shift within the LH stimulation group.

DISCUSSION

The current study explored the cognitive architecture, neural, and electrophysiological basis of decision-making processes in the context of risk-taking. Overall, we report that participants receiving AC stimulation of 6.5 Hz to the LH, with one electrode located over the left DLPFC and the reference electrode located over left temporal cortex, displayed a risky response style, making more pumps on the BART, and tolerated a larger number of balloon explosions than those with sham stimulation and those with RH stimulation. This is the first study showing that neuromodulation in the theta-band can causally modulate decision-making style in healthy participants. In addition, this result supports previous evidence showing that the DLPFC is causally involved in modulating risky decision-making behaviors.

The current result supports, to some extent, the hypothesis that the theta-band oscillatory balance between right and left regions is crucial for regulatory control during decision-making under risk. As predicted, participants receiving AC stimulation to the LH displayed a risky response style. It has been proposed that in conflict and reward situations, theta-band oscillatory activity over the frontal medial cortex may reflect an electrophysiological mechanism for coordinating neural networks involved in monitoring behavior and the environment as well as facilitating task-specific adaptive changes. Furthermore, induced oscillatory response during feedback processing found to be greater in power and phase coherence following negative feedback or errors relative to positive feedback or wins (Luu and Tucker, 2001; Luu et al., 2003, 2004; Cohen et al., 2007, 2008; Marco-Pallares et al., 2008; Cavanagh et al., 2009, 2010; Christie and Tata, 2009; van de Vijver et al., 2011). We propose that AC stimulation at the theta-band to the LH, created continuous disruption to participants' ability to process and adjust their actions based on negative feedback or errors, as shown by their persistent tendency to tolerate losses, and in particular, sequential losses. We further claim that the balance between right and left regions, and in particular, the predominance of the RH, is needed in order to be able to adopt a conservative, risk-averse response style during the BART. Since we interfered with this balance and especially with RH dominance, participants lacked the ability to adjust their risk-taking behaviors and tend to display a risky response style.

Previous studies addressed the relative contribution of the right and the left prefrontal regions in risk-taking behaviors and particularly the role of the DLPFC in this kind of behavior. Various studies have provided clear evidence for the role of the right DLPFC in decision-making and risk-taking situations. Using low-frequency rTMS van't Wout et al. (2005) found a disruption to the right DLPFC resulted in accepting more frequently unfair offers and taking longer to refuse unfair offers. Knoch et al. (2006) reported that suppression of activity in the right but not the left DLPFC with low-frequency rTMS made participants choose high-risk prospects more often. Moreover, using a different brain stimulation methodology, i.e., tDCS, Fecteau et al. (2007b) showed that during right anodal/left cathodal stimulation over the DLPFC, participants chose more often the safe prospect compared with the sham and reversed polarization groups. However, other studies have not found clear lateralization effects (e.g., Fecteau et al., 2007b; Beeli et al., 2008). It has been suggested that divergent results from different brain stimulation studies might be due to differences in the risk-taking paradigm used and/or the method of stimulation involved (Fecteau et al., 2007b).

Our results are in line with the RH hypothesis in risk-taking behaviors, and address lateralization in terms of electrophysiological balance between left and right cortical regions in the theta bend. Previous suggestions (Gehring and Willoughby, 2004; Marco-Pallares et al., 2008; Christie and Tata, 2009) have already raised the hypothesis that right medial frontal/prefrontal theta may be regarded as the electrophysiological mechanism which mediates decision-making processes during risk-taking situations, and the present study adds a causal link between the electrophysiological mechanism and theta-band activity to actual behavior.

In addition, it is important to note that we address lateralization in terms of hemispheric shift. It has been recently reported that BART performance elicited greater activity in the right DLPFC (Rao et al., 2008) providing further support to previous studies of patients with right-sided lesions (Tranel et al., 2002; Clark et al., 2003) that reported on a dysfunction in risky decision-making behaviors. Apart from the main findings reported earlier, the simple asymmetry index (i.e., the line-bisection task) provided further support for this hypothesis, and showed that only in the sham and RH stimulation groups, but not LH stimulation group, line-bisection bias was more negative after performing the BART compare to baseline performance. This finding indicates that the BART had the expected hemispheric effect, i.e., a RH enduring engagement, which was reflected by a stronger RH activation in those groups only. Tendencies toward rightward versus leftward errors in estimating the actual midpoints are taken to reflect relative primacy of right versus left visual fields, respectively, and neural activity in the contralateral hemisphere (Kinsbourne, 1970; Milner et al., 1992; Goldstein et al., 2010). Even though previous research suggests line-bisection bias may be more a marker of parietal than prefrontal function (Vallar and Perani, 1986), the simple and non-invasive line-bisection task has been recently found to serve as a neural index of asymmetrical activity related to the DLPFC (Nash et al., 2010).

In the present study, we failed to find an effect for AC stimulation over the RH. We expected that following RH stimulation, participants would display a more conservative, risk-averse response style. The results suggest that participants who received this stimulation behave as participants in the sham stimulation. This null result can be marked as a "floor effect" and can be explained in terms of behavioral, methodological, and electrophysiological aspects. First, with respect to behavior, this "floor effect" probably represents a possible limitation of our ability to modulate risk-taking behavior in healthy participants, and to increase their risk-averse response style. It is possible that RH stimulation will be more affective with populations that show deficits in risk-taking tasks such as patients with lesions in the PFC and other clinical populations, such as drug abusers, alcoholics, and pathological gamblers (Bechara et al., 1996; Rahman et al., 2001). Second, this "floor effect" may be also a direct outcome of the task properties, in which it is easy to demonstrate what is considered to be a risky behavior (e.g., a large number of adjusted pumps and a large number of balloon explosions), but it may be harder to reveal an overcautious, conservative, risk-averse response style. Third, this "floor effect" can be referred as close to the idea of the so called "natural frequency" (Rosanova et al., 2009), by which different corticothalamic brain modules are tuned to oscillate at a topographically organized "natural frequency." It is possible that the AC stimulation to the RH interacted with the neuronal oscillatory activity that already evoked by the task, i.e., the "natural frequency" that characterizes the decision-making processes that usually take place during processing, thus did not modulate any cortical activity or risk-taking behavior.

Overall, our results suggest that during risk-taking situations, the hemispheric balance is important. This suggestion may account for previous conflicting results, mentioned earlier, regarding the relative contribution of the right and left PFC/DLPFC in risky decision-making behaviors. This balance can metaphorically be described as a seesaw between left and right frontal/prefrontal areas that is theta dependent. The right hemispheric shift is vital, and especially the recruitment of right lateral PFC, in order to promote a conservative, risk-averse response style. Hence, it is clear that right prefrontal regions must be functionally and anatomically intact in order to facilitate such an on-line shift. However, the LH is also crucial for this shift, and especially the balance between the two. Theta-band tonic activity balance between left and right prefrontal regions has been found to predict risk-taking behavior (Gianotti et al., 2009), showing the importance of the hemispheric balance right from a pre-stage of risk-taking situations. In addition, this hypothesis is similar to a novel framework of risk processing suggested by Mohr et al. (2010). Based on a meta-analysis on the neural basis of risky behavior, the authors proposed a potential mechanism of risky decision-making that involves two parallel and reciprocal risk processes; one is emotional and the other one is cognitive. These processes involve the anterior insula and the thalamus as the key regions which mediate emotional processing, whereas the dorsomedial PFC evaluates the risk of the stimulus on a cognitive level. According to their framework, both parts of risk processing (emotional and cognitive) inform the actual decision process performed in DLPFC and parietal cortex. It is possible that our hypothesis represents, to some extent, Mohr et al.'s (2010) framework, with the frontal/prefrontal hemispheric balance as the cognitive level of processing, and the mandatory recruitment of the right DLPFC as the exaction phase. This suggestion is reasonable given the findings that when the medial frontal cortex signals a need for adjustment, this also involves an additional recruitment of lateral PFC (Kerns et al., 2004; Ridderinkhof et al., 2004).

A final note, apart from matters of lateralization, the current study addressed the issue of cognitive processes that govern BART performance. Previous work highlighted the role of two key concepts, namely, risk-taking and payoff sensitivity (e.g., Bishara et al., 2009). However, in the current study, risk-taking and payoff sensitivity measures were highly correlated, and presumably are confounded, and means that in practice these definitions of performance are interchangeable, at least for the specific task paradigm used. Therefore, it is difficult to distinguish between these two-component processes and as a consequence to draw a firm conclusion to whether participants in the different stimulation groups were more risk-averse or risk seeking, since participants respond in a risk-aversive manner in general. This issue has been acknowledged previously (e.g., Freeman and Muraven, 2010). In the current experiment, average number of pumps per group was below the average explosion point across balloons (64, which is also the optimal number of pumps to maximize earnings), hence the group that pumped the balloon more earned more points. This finding is not unique to our experiment, as participants generally respond in a risk-aversive manner on the BART (see also Lejuez et al., 2002, 2003a; Bornovalova et al., 2009; Freeman and Muraven, 2010). Apparently, human subjects and also rats (see Jentsch et al., 2010) exhibit risk-averse profiles when performing the BART (or BART alike task in the case of rats), producing fewer than the optimal number of responses, and earning less than possible probably because of over-estimation of the risk associated with the task (Bornovalova et al., 2009; Jentsch et al., 2010).

Several limitations must be considered when interpreting the results. First, the present study used only one band of stimulation frequency, was restricted to specific locations, and measured behavioral effects of a particular risk-taking paradigm. Future research should elaborate the scope of reference and examine more bands, in various cortical locations using a verity of risk-taking paradigms. Second, no direct assessment of DLPFC activity was made by any imaging technique before and/or after tACS stimulation, so any attempt to bond between DLPFC activity, tACS effects, and risk-taking behaviors call for further examination. Future research should document neural baseline and changes accruing after AC stimulation in order to be able to infer about the neural circuitry and the mechanisms that are influenced by AC stimulation. Third, we stimulated all participants in the active conditions in our study with 6.5 Hz, thereby ignored possible inter individual variability that may be captured and elaborate our knowledge regarding the electrophysiological mechanism in question. For example, it is possible to stimulate each participant with her/his transition frequency (TF). TF shows a large inter individual variability ranging from about 4 to 7 Hz (Klimesch et al., 1996; Klimesch, 1999), so TF can be measured in order to create a tailored stimulation for each participant in future studies. Forth, in the present study we did not find that individual differences such as gender and/or trait motivation characteristics moderate tACS effectiveness on performance. Although we did not find a gender or motivation difference in the BART measures, additional studies should specifically explore whether there is a gender or motivational bias in decision-making in regards to brain stimulation. Finally, in the current study, we employed a procedure similar to the one used by Hunt et al. (2005), where participants did not actually receive money for their BART performance, rather they were competing for a monetary prize. It is possible that this kind of incentive procedure may have generated a competitive environment and may have bias choice behavior. Future research is needed to clarify this issue.

CONCLUSION

The current study report a novel finding demonstrating that neuromodulation in the theta bend can causally modulate decision-making style by increasing risk-taking behavior in healthy participants and provides further support to previous evidence by showing that the DLPFC is causally involved in modulating decision-making. This study may inspire the use of tACS to further examination of risky decision-making behaviors, and hopefully in the near future would be beneficial as a therapeutic tool for patients with different brain lesions and other clinical populations, such as drug abusers, alcoholics, and pathological gamblers who show deficits in this kind of behavior.

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Neural correlates of dynamically evolving interpersonal ties predict prosocial behavior

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There is a growing interest for the determinants of human choice behavior in social settings. Upon initial contact, investment choices in social settings can be inherently risky, as the degree to which the other person will reciprocate is unknown. Nevertheless, people have been shown to exhibit prosocial behavior even in one-shot laboratory settings where all interaction has been taken away. A logical step has been to link such behavior to trait empathy-related neurobiological networks. However, as a social interaction unfolds, the degree of uncertainty with respect to the expected payoff of choice behavior may change as a function of the interaction. Here we attempt to capture this factor. We show that the interpersonal tie one develops with another person during interaction – rather than trait empathy – motivates investment in a public good that is shared with an anonymous interaction partner. We examined how individual differences in trait empathy and interpersonal ties modulate neural responses to imposed monetary sharing. After, but not before interaction in a public good game, sharing prompted activation of neural systems associated with reward (striatum), empathy (anterior insular cortex and anterior cingulate cortex) as well as altruism, and social significance [posterior superior temporal sulcus (pSTS)]. Although these activations could be linked to both empathy and interpersonal ties, only tie-related pSTS activation predicted prosocial behavior during subsequent interaction, suggesting a neural substrate for keeping track of social relevance.

Keywords: interpersonal ties, social ties, empathy, social decision-making, public good game, pSTS, ACC, insula

INTRODUCTION

In experience-based decision-making, rather than being provided with a description of the probability distribution of outcomes associated with certain choices, subjects have incomplete information about choice outcomes and their respective probabilities. Information regarding choice–outcome is acquired and integrated through continuous or pre-choice sampling with feedback. Evidence seems to suggest that people have different choice–preferences in decisions-from-experience paradigms than during description-based choice paradigms, although the origins of this putative preference gap are still under investigation (Rakow and Newell, 2010). Given the naturalistic nature of experience-based decision-making, disentangling its underlying cognitive and neural mechanisms may be crucial to understanding human choice behavior. Economic trade for example, is an omnipresent real-world example of experience-based decision-making. The probability distribution of outcomes during economic interactions can often only be gauged through the interaction itself. Interestingly, intermediate outcomes of the interaction may impact the probability distribution of future outcomes, lessening the degree of uncertainty along the way. Hence, not only is the subject gauging the probability distribution of outcomes, he or she may actually modulate the probability distribution of outcomes as the interaction unfolds. It has been suggested that interaction partners keep track of this dynamic process internally by means of the interpersonal tie one develops with one's interaction partner (van Dijk et al., 2002; van Winden et al., 2008). Another suggested influence on human choice behavior in social settings has been the presence of empathy (e.g., Hein et al., 2010). Here, we attempt to establish how well a trait variable like empathy and a dynamic state variable such as the interpersonal tie are able to predict prosocial choices during interactive decision-making.

The willingness to share resources without guarantee of return-benefit is crucial to achieve cooperation. This is illustrated by the Public Good family of economic games, where free riding typically leads to a breakdown of cooperation (Isaac and Walker, 1988). Experimental evidence suggests that the willingness to invest in a public good (including the voluntary punishment of free riders) is motivated by social factors beyond immediate personal gain (Fehr and Gächter, 2002; Rilling et al., 2002). These factors are often captured using the term altruism, which is observed in humans as well as various other mammals (Fehr and Fischbacher, 2003; de Waal, 2008). Many have linked the proximate cause of altruism to empathy, referring to the capacity to experience and understand the affective state of another person (Batson, 1991; Eisenberg, 2000; de Waal, 2008; Singer and Lamm, 2009). Recently, neural evidence has been presented in support of this view, linking empathy-related activation in the insula (Hein et al., 2010; Masten et al., 2011) and medial prefrontal cortex (Mathur et al., 2010; Masten et al., 2011) to prosocial behavior. Empathy promotes social cohesion (Farrow et al., 2001), scales with feelings of group membership (Sturmer et al., 2006) and as such may be a key motive for the willingness to share.

Individual differences in the willingness to share are often described in terms of social value orientations (Van Lange, 1999), which can be estimated by having subjects make choices between different monetary distributions regarding themselves and an unspecified other (Liebrand, 1984; Haruno and Frith, 2010). Social value orientation, like empathy, is considered to be a trait-like, stable disposition (Van Lange, 1999). However, recent evidence suggests that social value orientation toward an interaction partner can change, depending on the success or failure of an intermediate interaction (van Dijk et al., 2002). A complementary influence on prosocial behavior might therefore be the development of interpersonal ties, or feelings of social connectedness with an interaction partner. Such ties are different from empathy in that they consist of the extent to which someone cares about another person (van Dijk et al., 2002), rather than one's ability to share someone's emotions (Eisenberg, 2000; de Waal, 2008; Singer and Lamm, 2009). The degree to which one is able to experience empathy seems to be a personality characteristic (Mehrabian, 1997; Singer et al., 2004b), while interpersonal ties are dynamic, resulting from interaction itself (van Dijk et al., 2002; van Winden et al., 2008). Positively developing ties may instill prosocial behavior, while negatively developing ties may be associated with antisocial behavior, such as a reduced willingness to invest further in the other's well-being, or even vengeful behavior, such as punishing the other at a cost to oneself (Fehr and Gächter, 2002).

Compared to empathy, the cognitive, affective, and neural mechanisms of interpersonal ties have remained relatively exempt of empirical scrutiny. Various studies have focused on normative aspects of social interactions, such as trust (King-Casas et al., 2005) and fairness (Singer et al., 2006). Other studies have focused on the neural basis of cooperation itself. For example, left orbitofrontal cortex (OFC) and medial parts of the frontal cortex have been associated with cooperative and competitive behavior respectively (Decety et al., 2004). Cooperative behavior in an iterated prisoner's dilemma game has also been found to elicit increased activity in reward-related areas such as the striatum (Moll et al., 2006; Haber and Knutson, 2010), as well as the ventromedial prefrontal cortex (VMPFC) and the OFC (Rilling et al., 2002). Increased (decreased) VMPFC activation has further been found when inferring generous (selfish) play in a public good game played by others (Cooper et al., 2010). Although these regions may be involved in the formation of interpersonal ties, it is unknown whether they are also involved in keeping track of such ties over longer periods of time. Studies on social cognition point to the relevance of the posterior superior temporal sulcus (pSTS) in representing the social significance of other agents. For example, gray matter density abnormalities in the STS have been associated with autism in children (Boddaert et al., 2004), stimuli that have acquired relevance during meaningful social interaction (e.g., faces of cooperative game partners) have been shown to activate the pSTS (Singer et al., 2004a); the (p)STS is important in keeping track of one's influence on other agent's intentions and strategies (Hampton et al., 2008; Haruno and Kawato, 2009); and activation of the pSTS during the perception of agency correlates with individuals' self-reported altruism (Tankersley et al., 2007).

To determine the influence of empathy and interpersonal ties in determining prosocial behavior, we first established the presence of neural responses related to empathy and interpersonal ties during computer controlled (imposed) sharing. In a second step, we determined how these neural responses related to previous cooperation success and whether they predicted subsequent prosocial behavior. To establish neural empathy and tie-related responses during computer-imposed sharing, we administered a distributional outcome test (DOT; Liebrand, 1984; Haruno and Frith, 2010), with monetary outcomes benefiting the other at the expense of oneself and vice versa (see **Table 1**), both before and after anonymous interaction in a public good game. In the DOT, subjects were repeatedly confronted with changing payoff distributions, of which the computer would choose one on each trial. We used functional magnetic resonance imaging (fMRI) to examine individual differences in the neural responses to DOT outcomes. Subtracting fMRI responses during the pre-interaction DOT from the responses during the post-interaction DOT, allowed us to isolate neural responses to sharing that could be related to the intermediate public good game interaction (see Materials and Methods). Choices between distributional outcomes were made by the computer, kept equal across participants, and kept equal between pre- and post-interaction DOTs, to ensure that neural responses could be compared across time and across participants.

MATERIALS AND METHODS

SUBJECTS

We collected data from 34 interaction pairs. Due to our complex experimental setup, five subjects had to be excluded from analysis because of computer or human error during data collection and transfer. Subjects were students from the University of Amsterdam or international exchange students enrolled in courses at the University of Amsterdam. All subjects gave written informed consent prior to the onset of the experiment. The 29 subjects in the scanner had an average age of 22.6 (SD ± 2.7), 14 were female. Their 29 interaction partners had an average age of 23.3 (SD ± 4.5), 11 were female. In 14 interaction pairs both partners had the same sex. In five pairs both partners were female. Chi-square and t-tests confirmed that the scanning group did not differ significantly from the group outside the scanner in age, sex, or any of the behavioral measures.

EXPERIMENTAL PROCEDURE

Subjects were tested in pairs. One subject was positioned in the scanner while the other was seated in a separate room behind a laptop. The procedure was fully anonymous, such that subjects would

Table 1 | Alternatives during the scanned pre- and post-interaction distributional outcome test (DOT).

Trial	Alternative A		Alternative B		Other gains at expense of self	Self gains at expense of other	Equality in one of the alternatives
	Self	Other	Self	Other			
1	500	0	498	44		x	
2	498	44	492	87		x	
3	492	87	483	129		x	
4	483	129	470	171		x	
5	470	171	354	354			x
6	354	354	171	470			x
7	498	44	500	0	x		
8	492	87	498	44	x		
9	483	129	492	87	x		
10	470	171	483	129	x		
11	354	354	470	171			x
12	171	470	354	354			x
13	−500	0	−498	−44	x		
14	−498	−44	−492	−87	x		
15	−492	−87	−483	−129	x		
16	−483	−129	−470	−171	x		
17	−470	−171	−354	−354			x
18	−354	−354	−171	−470			x
19	−498	−44	−500	0		x	
20	−492	−87	−498	−44		x	
21	−483	−129	−492	−87		x	
22	−470	−171	−483	−129		x	
23	−354	−354	−470	−171			x
24	−171	−470	−354	−354			x
Sum	0	0	0	0			

The temporal order in which the trials were presented was randomized for each subject. Whether an alternative would appear on the screen as (Alternative A) or (Alternative B) was randomized on every trial. The computer would always choose what is designated here as (Alternative A).

never see each other or get any information about the other subject other than through computer-interfaced interaction during the public good game. The study was divided into two main parts: (1) a scanning phase and (2) a post-scanning part in which subjects filled out exit questions and an empathy questionnaire. Afterward, subjects were paid out. Average earnings totaled to around 45 euros per subject.

The scanning phase consisted of three scanning blocks. In the first block, we administered a pre-interaction DOT to test neural responses to different monetary distributions. In the second block, the subject pair played a two-person public good game. In the third block subjects were administered a post-interaction DOT. Right after the post-interaction DOT, subjects played the final rounds of the public good game. After scanning, subjects completed a general exit questionnaire and the balanced emotional empathy scale (BEES; Mehrabian and Epstein, 1972; Mehrabian, 1997).

DISTRIBUTIONAL OUTCOME TEST

Before and after public good game interaction, the DOT was administered, containing 24 test items (see **Table 1**). These test items were chosen because behavioral pilot testing showed that they discriminated most strongly between subjects when given the ability to freely choose among them. In the DOT however, subjects would not make a choice between the two payoff combinations themselves, but the computer would "randomly" pick an alternative. Unbeknownst to subjects, computer choices were predetermined such that the chosen alternatives and the resulting payouts were the same between participants and between the pre- and post-interaction DOT. Also unbeknownst to subjects, both the sum of the chosen distributions and the sum of the alternative distributions was zero, both for allocations to self and allocations to other.

At the start of each trial, subjects were asked to carefully inspect the payoff combinations presented by the computer, and to assess which alternative they preferred. Upon pressing a button, the alternatives would start to alternately highlight at a decreasing rate, until settling down on one of them (the "computer choice"). No changes were made to the display during the ensuing 8 s, so that a clean measure of a subject's neural response to the "computer choice" could be taken. To keep subjects engaged in this otherwise passive task, they were asked to subsequently indicate whether they agreed or disagreed with the computer choice using a simple yes/no button press, after which the test would continue to the next trial.

Importantly, the pre- and post-interaction DOT were identical in all respects, except for one difference. In the pre-interaction DOT, subjects were informed that the "other" was a random subject from the experiment, while in the post-interaction DOT, subjects were informed that the "other" was one's (anonymous) interaction partner during the preceding public good game. Hence differences between neural responses to the post- and pre-interaction DOT acted as a post–pre-interaction contrast, isolating differential neural responses to sharing as a result of the intermediate public good game interaction. Subtracting the pre-interaction DOT from the post-interaction DOT removes effects that cannot be related to the intermediate public good game interaction.

Therefore, we subtracted the normalized pre-interaction DOT fMRI signal from the post-interaction DOT signal, to isolate the component of the DOT response that may have been impacted by the intermediate public good game interaction (see below for analysis details). This is a non-standard fMRI analysis step, but pertinent to the type of information we wanted to extract from our design. We were interested in isolating changes in neural components of sharing preference as a result of experience-induced change over time (i.e., as a result of public good game interaction). The difference signal of neural responses acquired at different moments in time – while keeping all other variables the same – provided this measure.

PUBLIC GOOD GAME

The intermediate public good game was a finite, non-linear, self-paced public good game described elsewhere (van Dijk et al., 2002). The game consisted of 29 rounds between two subjects. On every round, subjects were given 12 monetary units, which they could divide freely between their private account and a public account. The payoff consequences of contributions to the public account were made explicit by use of an on-screen payoff table (see **Table 2**). Payoffs in this table were given by $14^*(X+Y)+32^*(12-X)-(12-X)^2-160$, where X represents a subject's own contribution to the public account, while Y denotes the other subject's contribution to the public account. The Pareto-optimum was at 10 tokens in the public good, but players could decide to invest more than 10 tokens, increasing the other's payoff at one's own expense. Likewise, participants could invest less than the Nash-equilibrium (three tokens), resulting in a payoff below Nash for the other at one's own expense.

Prior to the public good game, extensive on-screen instructions were given, followed by nine multiple-choice questions to check understanding. At round 25, the public good game was unexpectedly interrupted for the post-interaction DOT. Right after the post-interaction DOT subjects finished the last four rounds of the public good game. At the end of the experiment, payoffs were converted to real currency and paid out along with the other payouts.

POST-SCAN QUESTIONNAIRES FOR EMPATHY AND INTERPERSONAL TIES

After scanning, subjects completed an exit questionnaire and an empathy scale questionnaire. Interpersonal ties were measured during the exit questionnaire. Subjects were asked to indicate the interpersonal tie they felt with the subject they had interacted with during the public good game. The question was:

Please indicate on the scale below how much you like or dislike the participant you were paired with in part 2 and 3 of the experiment. Circle the number of your choice, where 1 stands for "very unpleasant person" and 9 stands for "very nice person."

Below was a 9-point scale running from "very unpleasant person" to "very nice person." Note that a value below five signals a negative tie, whereas a value above five signals a positive tie. Ratings emanated from previous cooperation success, as there

Table 2 | Payoff table during the public good game.

			Other												
	Public	***Y***	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
	X	**Private**	**12**	**11**	**10**	**9**	**8**	**7**	**6**	**5**	**4**	**3**	**2**	**1**	**0**
You	**0**	**12**	**80**	94	108	122	136	150	164	178	192	206	220	234	248
	1	**11**	85	**99**	113	127	141	155	169	183	197	211	225	239	253
	2	**10**	88	102	**116**	130	144	158	172	186	200	214	228	242	256
	3	**9**	89	103	117	**131**	145	159	173	187	201	215	229	243	257
	4	**8**	88	102	116	130	**144**	158	172	186	200	214	228	242	256
	5	**7**	85	99	113	127	141	**155**	169	183	197	211	225	239	253
	6	**6**	80	94	108	122	136	150	**164**	178	192	206	220	234	248
	7	**5**	73	87	101	115	129	143	157	**171**	185	199	213	227	241
	8	**4**	64	78	92	106	120	134	148	162	**176**	190	204	218	232
	9	**3**	53	67	81	95	109	123	137	151	165	**179**	193	207	221
	10	**2**	40	54	68	82	96	110	124	138	152	166	**180**	194	208
	11	**1**	25	39	53	67	81	95	109	123	137	151	165	**179**	193
	12	**0**	8	22	36	50	64	78	92	106	120	134	148	162	**176**

X denotes a participant's own contribution to the public account, Y denotes the other's contribution to the public account. Private is what is left in a participant's private account given that contribution level. The cell where X and Y cross shows one's own payoff given those contribution levels.

were no encounters between partners other than during anonymous interaction in the public good game. In addition, the exit questionnaire contained some questions on interaction strategy and control questions to check whether there had indeed been no contact with the other subject other than through computer-mediated interaction. To assess trait empathy, subjects completed the BEES (Mehrabian and Epstein, 1972; Mehrabian, 1997) after they had completed the exit questionnaire.

PAST COOPERATION SUCCESS AND FUTURE INVESTMENT BEHAVIOR

As a measure of previous cooperation success, we calculated the other's average contribution to the public good in the last five rounds prior to the second DOT (round 21–25; van Dijk et al., 2002). Future investment behavior was defined as a player's own average contribution to the public good in the rounds following the second DOT (round 26–28). The final round (round 29) was not included in the average because of the well-known "end" effect (Ledyard, 1995). A t-test confirmed that contribution in round 29 differed significantly from contribution in round 28 [$t(28) = 2.22$, $p = 0.03$], while this was not the case between round 28 and 27 [$t(28) = 0.81, p = 0.42$] or between round 27 and 26 [$t(28) = 0.85$, $p = 0.40$]. There was also no change between round 25 and round 26, either in one's own contribution [$t(28) = 0.57$, $p = 0.57$] or in the other's contribution to the public good [$t(28) = 1.22$, $p = 0.23$], showing that the interruption by the second DOT did not significantly impact subsequent public good game behavior. Control analyses confirmed that changing the size of the interval over which interaction success or future investment behavior was measured did not change the results.

IMAGE ACQUISITION AND PRE-PROCESSING

Images were acquired on a Philips 3 T Intera scanner. The functional recordings were acquired using a T2*-weighted sequence [40 coronal slices; flip angle (FA), 80°; echo time (TE), 30 ms; repetition time (TR), 2.3 s; slice thickness, 3 mm; field of view (FOV), 220 mm × 220 mm; in-plane voxel resolution, 2.3 mm × 2.3 mm]. Sessions ended with the acquisition of a high-resolution anatomical image using a T1 turbo field echo sequence [182 coronal slices; FA, 8°; TE, 4.6 ms; TR, 9.6 s; slice thickness, 1.2 mm, FOV, 256 mm × 256 mm; in-plane voxel resolution, 1 mm × 1 mm]. Pre-processing and data analysis was performed using the fMRI expert analysis tool (FEAT), v5.98 from the FMRIB's software library (FSL) package (http://www.fmrib.ox.ac.uk/fsl). fMRI images were motion corrected, slice-time aligned, aligned to the structural image of the subject, and spatially smoothed using a Gaussian kernel of 5 mm and high-pass temporally filtered using a Gaussian envelope of 50 s. Anatomical brains were extracted from the structural images, and transformed to the standard space of the Montreal Neurological Institute (MNI) using FMRIB's non-linear image registration tool (FNIRT). Finally, the functional data were co-registered to the MNI brain using non-linear parameters obtained from FNIRT.

DATA ANALYSIS

For each subject, general linear models (GLMs) were specified separately for the pre- and post-interaction DOT. A predictor was created for each trial, corresponding to the moment at which the "computer choice" (see **Table 1**) was presented to the subject. All predictors were convolved with a standard double gamma hemodynamic response function. The resulting GLMs were applied to the (pre-processed) fMRI signals that were acquired during the pre- and post-interaction DOT.

Next, the mean percent signal change on each trial of the pre- and post-interaction DOT was extracted for each subject and each region of interest (ROI). Trials were averaged depending on the sharing context (see **Table 1**): for each subject and each ROI, an average was created for trials in which the other obtained monetary gains at the expense of oneself ("Other gains at expense of Self"), and another average was created for trials in which oneself gained at the expense of the other ("Self gains at expense of Other"), separately for the pre- and post-interaction DOT. Subsequently, the resulting pre-interaction DOT averages were subtracted from the post-interaction DOT averages of corresponding sharing contexts, isolating the part of the neural response that was affected by the intermediate public good game experience, while subtracting out the bare neural responses to the monetary divisions in these sharing contexts (which were equal in both DOTs).

The post- minus pre-public good game interaction DOT difference signals from these sharing contexts ("Self gains at expense of Other" and "Other gains at expense of Self") for each of the ROIs were correlated against the empathy and interpersonal tie measures, as well as against the measures for past cooperation success and future investment behavior. Because we computed a lot of correlations, one needs to correct for multiple comparisons, as some correlations will turn up significant at the conventional 0.05 level by chance alone. We corrected for multiple comparisons by means of the false discovery rate (FDR) correction, which fixes the expected proportion of incorrectly rejected null hypotheses (type I errors) given the number of tests that were performed (Benjamini and Hochberg, 1995). All reported statistics in the experiment are two-tailed.

To summarize, the subtraction method and the FDR correction each correct for a potential source of spurious correlation: (1) The subtraction of the pre-interaction DOT from the post-interaction DOT isolates the part of the signal that can be related to the intermediate public good game. The subtraction method removes correlations between the DOT and our dependent measures that are not related to the intermediate public good game. Such correlations may be coincidental but "real" within the specific sample that we measured from, or they may even be real in the population at large. Regardless, the subtraction method removes them. (2) The FDR correction thresholds the resulting post- minus pre-interaction correlations such that they cannot be attributed to measurement errors (noise). The correlations that are identified using the combination of these two methods can therefore be attributed to the intermediate public good game, and cannot be attributed to chance.

To establish whether empathy and interpersonal ties might interact to predict behavior, we carried out a regression analysis. We used the BEES and liking ratings as measures for empathy and social ties respectively. An interaction term of the two was added. All terms were regressed onto the subject's future contributions in the three rounds following the second DOT.

SELECTION OF REGIONS OF INTEREST

For ROI selection, the results from the lower level DOT analysis were combined using a fixed effects higher-level analysis, in which corresponding trials from the pre- and post-interaction DOT were matched. Note that in this particular analysis, trials from the pre- and post-interaction DOT were combined (effectively averaged), rather than subtracted. Subsequently, the resulting individual subject statistics were analyzed at a group level using FMRIB's Local Analysis of Mixed Effects (FLAME1). At this stage, an F-test was performed over all 24 trials, allowing us to test in a non-directional way in what regions the combined pre- and post-interaction DOT contributed significantly to the fMRI signal at a group level. By using a non-directional F-test, the statistics were indifferent to the direction of hemodynamic changes between different types of trials within the DOT. Clusters with Z-values higher than 3.1 (uncorrected) were considered for inclusion as ROIs into the final analysis. From these clusters, ROIs were selected on anatomical grounds that are known to be involved in reward processing (striatum; Rilling et al., 2002; Moll et al., 2006; Haber and Knutson, 2010), empathy [anterior insular cortex (AIC) and anterior cingulate cortex (ACC)] (Wicker et al., 2003; Singer et al., 2004b; Singer and Lamm, 2009), social significance (pSTS; Singer et al., 2004a; Tankersley et al., 2007; Hampton et al., 2008), and social decision-making (VMPFC and OFC; Rilling et al., 2002; Decety et al., 2004). As striatal activity was part of a larger cluster, we extracted voxels from this cluster using the Harvard–Oxford Subcortical Structural Atlas included in the FSL package. Only voxels that had more than 50% probability of belonging to the nucleus accumbens (ventral striatum) or caudate (dorsal striatum) were included. No voxels exceeded the threshold in the putamen. See **Figure 1** for selected clusters. For the entire activation map of the F-test and the selection of ventral and dorsal striatum see **Figure 2**, for a list of all clusters see **Table 3**.

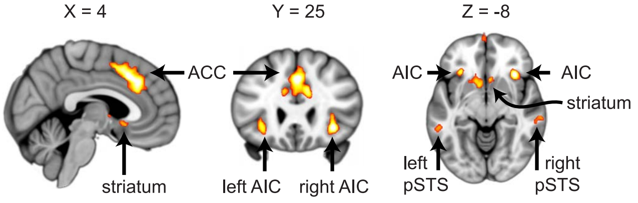

FIGURE 1 | Regions of interest involved in empathy (ACC, bilateral AIC), social significance (bilateral pSTS) and reward processing (striatum). Cross-sections of the brain are shown at MNI coordinates $X = 4$, $Y = 25$, and $Z = -8$. Voxels shown exceed an uncorrected threshold of $Z > 3.1$ ($p < 0.001$) on an F-test over the averaged pre- and post-interaction DOT trials (also see **Figure 2** and Materials and Methods).

Because the DOT data used for ROI selection were also used during hypothesis testing, a possible concern could be selection bias resulting from the non-independence error or "double dipping" (Kriegeskorte et al., 2009). However, the statistical tests used during hypothesis testing were not affected by circularity. For one, the result statistics used during ROI selection were different from those used during hypothesis testing. ROI selection was done on the averaged pre- and post-interaction DOT, while during hypothesis testing the pre- interaction DOT was subtracted from the post-interaction DOT. More to the point however, hypothesis testing was done by correlating this difference signal against measures of empathy, interpersonal ties, and interaction success, while none of these behavioral measures were used when generating the F-statistics used for ROI selection. Critically, this ensured that none of our results could be explained by double dipping.

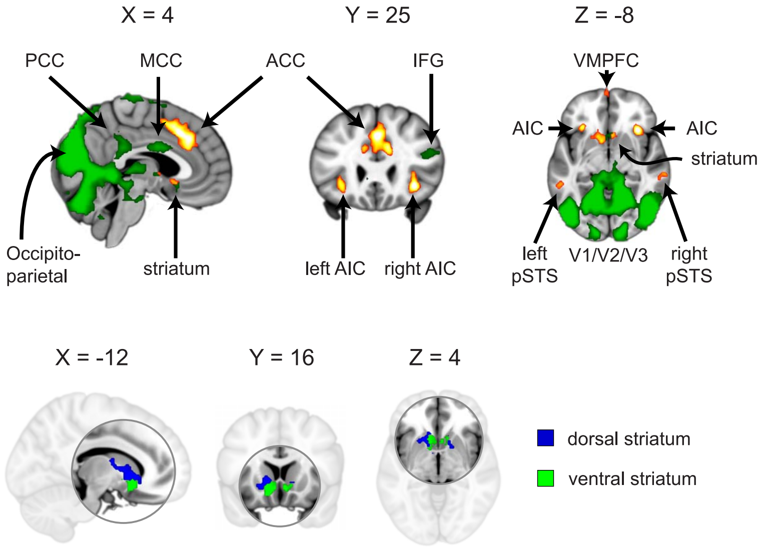

FIGURE 2 | Regions activated by an F-test over the 24 trials from the (averaged) pre- and post-interaction DOT. Voxels exceeding $Z = 3.1$ ($p < 0.001$, uncorrected) in clusters larger than 40 voxels are shown in green, with selected regions of interest (AIC, ACC, striatum, pSTS, VMPFC, and left OFC) shown in hot (yellow/orange; top). Ventral and dorsal striatum are depicted separately in blue/green (bottom). **Table 3** lists all clusters and MNI coordinates of cluster peak values.

Table 3 | Locus of peak activations in clusters resulting from an F-test over the 24 trials from the (averaged) pre- and post-interaction DOT ($Z > 3.1$, cluster size > 40).

Cluster index	Brain region	MNI coordinates of peak activation (mm)			Z score
		x	y	z	
1	Ventromedial prefrontal cortex (VMPFC)	−2	64	−10	4
2	Left posterior superior temporal sulcus	−56	−40	−6	4.43
3	Left orbitofrontal cortex (OFC)	−22	48	−26	5.32
4	Right posterior superior temporal sulcus	62	−26	−10	4.73
5	Near right lateral ventricle	26	−44	16	6.11
6	Left anterior insular cortex (AIC)	−30	26	−6	6.31
7	Left precuneus	−8	−52	28	4.42
8	Left central opercular cortex (middle part of the Sylvian fissure)	−66	−14	8	5
9	Left angular gyrus	−50	−72	30	4.26
10	Left parietal opercular cortex (posterior part of the Sylvian fissure)	−46	−36	16	6.37
11	Left postcentral gyrus	−38	−22	50	7.91
12	Right anterior insular cortex (AIC)	34	24	−6	8.21
13	Left superior temporal gyrus (posterior)	64	−30	14	7.05
14	Mid cingulate cortex (MCC)	4	0	28	6.62
15	Posterior cingulate cortex (PCC)	2	−34	26	6.88
16	Left early visual cortex (V1, V2, V3)	−16	−88	−20	8.21
17	Right early visual cortex (V1, V2, V3)	20	−90	−18	8.21
18	Left Precentral Gyrus	−44	−2	26	8.21
19	Anterior cingulate cortex (ACC)	2	24	38	8.21
20	Occipitoparietal cortex, extending into precentral gyrus and inferior frontal gyrus on the right, and into cerebellum, brain stem, thalamus, and striatum ventrally	0	−78	20	8.21

Regions of interest used in subsequent analyses are underlined.

RESULTS

ORTHOGONALITY OF TRAIT EMPATHY AND INTERPERSONAL TIES

Trait empathy was measured post-experimentally using the BEES (Mehrabian and Epstein, 1972; Mehrabian, 1997). Interpersonal ties were measured in an exit questionnaire in which subjects were asked to rate how much they liked or disliked their interaction partner. To assess whether these measures were somehow correlated, we calculated their correlation coefficient. This showed that our empathy and our interpersonal ties measure were unrelated ($r = -0.06$, $p = 0.76$).

NEURAL CORRELATES OF EMPATHY DURING IMPOSED SHARING

In order to assess the presence of neural correlates of trait empathy during imposed sharing, we correlated BEES scores with the post- minus pre-interaction neural DOT responses during the "Self gains at expense of Other" and "Other gains at expense of Self" sharing contexts, in all regions of interest (see **Table 4**). The FDR-corrected significance level at which these correlations were evaluated is 0.0043, as marked by three asterisks (see bottom of **Table 4** on the next page). After correction for multiple comparisons, the BEES scores showed correlations in AIC [$r = 0.61$, $p = 0.0004$] (**Figure 3**, top), ACC ($r = 0.64$, $p = 0.0002$; **Figure 3**, middle), and the striatum [$r = 0.53$, $p = 0.0043$] (**Figure 3**, bottom). This shows that responses in these areas were stronger for empathic subjects than for non-empathic subjects after, but not before interaction (**Figure 4**). Notably, empathy only correlated with neural responses to sharing when the other gained at one's own expense, and not the other way around (all $p > 0.3$).

NEURAL CORRELATES OF INTERPERSONAL TIES DURING IMPOSED SHARING

Similar to the empathy analyses, we correlated liking ratings with post- minus pre-interaction neural DOT responses in both sharing contexts for all regions of interest (see **Table 4**). After correction for multiple comparisons, only the pSTS correlated significantly with our interpersonal tie measure, and only when oneself gains at the expense of the other ($r = 0.58$, $p = 0.0011$), and not vice versa ($r = 0.32$, $p = 0.0928$; **Figure 5**, top). This suggests that gaining at another person's expense invokes activation in the pSTS, where the degree of activation correlates positively with the interpersonal tie one has developed with that person during previous interaction. Receiving reward at another's expense may invoke a tie-related response in the pSTS, where a strong response corresponds with a positive interpersonal tie with the other person, and a weak response corresponds with a negative tie. Again, the correlation is specific to the post- minus pre-interaction DOT, emphasizing the relevance of the intermediate interaction in driving the response (**Figure 6**).

Table 4 | Correlations for sharing with measures of empathy, social ties, past cooperation success, and future investment behavior.

Region of interest	Self gains at the expense of other		Other gains at the expense of self	
	Pearson	*p*-Value	Pearson	*p*-Value
CORRELATIONS WITH BALANCED EMOTIONAL EMPATHY SCALE (BEES)				
Anterior insular cortex (AIC)	0.03	0.8582	0.61	0.0004***
Left AIC	−0.06	0.7632	0.63	0.0003***
Right AIC	0.16	0.4079	0.46	0.0127*
Striatum	−0.18	0.3507	0.52	0.0043***
Dorsal striatum (caudate)	−0.10	0.5940	0.55	0.0020***
Left dorsal striatum	−0.17	0.3831	0.43	0.0203*
Right dorsal striatum	−0.01	0.9485	0.59	0.0008***
Ventral striatum (nucleus accumbens)	−0.23	0.2304	0.39	0.0344*
Left ventral striatum	0.00	0.9914	0.16	0.3941
Right ventral striatum	−0.37	0.0495*	0.48	0.0089**
Posterior superior temporal sulcus (pSTS)	−0.20	0.2999	0.28	0.1396
Left pSTS	−0.21	0.2639	0.27	0.1645
Right pSTS	−0.12	0.5230	0.19	0.3299
Anterior cingulate cortex (ACC)	0.14	0.4607	0.64	0.0002***
Left orbitofrontal cortex (OFC)	−0.14	0.4680	0.18	0.3472
Ventromedial prefrontal cortex (VMPFC)	−0.04	0.8170	0.38	0.0447*
CORRELATIONS WITH 9-POINT LIKE SCALE (INTERPERSONAL TIE)				
Anterior insular cortex (AIC)	0.19	0.3270	−0.12	0.5420
Left AIC	0.18	0.3566	−0.08	0.6744
Right AIC	0.14	0.4591	−0.14	0.4571
Striatum	0.09	0.6362	0.11	0.5562
Dorsal striatum (caudate)	0.21	0.2718	0.11	0.5875
Left dorsal striatum	0.21	0.2695	0.21	0.2786
Right dorsal striatum	0.18	0.3585	−0.01	0.9613
Ventral striatum (nucleus accumbens)	−0.07	0.7293	0.10	0.5887
Left ventral striatum	−0.15	0.4435	0.23	0.2341
Right ventral striatum	0.01	0.9594	−0.06	0.7757
Posterior superior temporal sulcus (pSTS)	0.58	0.0011***	0.32	0.0928
Left pSTS	0.40	0.0312*	0.01	0.9485
Right pSTS	0.57	0.0013***	0.54	0.0027***
Anterior cingulate cortex (ACC)	0.26	0.1684	−0.08	0.6835
Left orbitofrontal cortex (OFC)	−0.45	0.0149*	0.27	0.1630
Ventromedial prefrontal cortex (VMPFC)	−0.12	0.5337	−0.06	0.7670
CORRELATIONS WITH CONTRIBUTION OF OTHER IN ROUND 21–25 (PREVIOUS COOPERATION SUCCESS)				
Anterior insular cortex (AIC)	−0.13	0.5160	−0.20	0.3105
Left AIC	−0.04	0.8382	−0.24	0.2062
Right AIC	−0.21	0.2732	−0.09	0.6486
Striatum	0.29	0.1209	0.01	0.9705
Dorsal striatum (caudate)	0.34	0.0684	0.02	0.9200
Left dorsal striatum	0.43	0.0201*	0.11	0.5619
Right dorsal striatum	0.19	0.3227	−0.07	0.7080
Ventral striatum (nucleus accumbens)	0.17	0.3664	−0.01	0.9707
Left ventral striatum	0.11	0.5854	0.01	0.9729
Right ventral striatum	0.19	0.3132	−0.02	0.9257
Posterior superior temporal sulcus (pSTS)	0.63	0.0003***	0.38	0.0413*
Left pSTS	0.68	0.0000***	0.22	0.2610
Right pSTS	0.38	0.0436*	0.42	0.0245*
Anterior cingulate cortex (ACC)	0.08	0.6826	−0.13	0.5135

(Continued)

Table 4 | Continued

Region of interest	Self gains at the expense of other		Other gains at the expense of self	
	Pearson	*p*-Value	Pearson	*p*-Value
Left orbitofrontal cortex (OFC)	−0.19	0.3304	−0.01	0.9397
Ventromedial prefrontal cortex (VMPFC)	0.04	0.8315	0.11	0.5656
CORRELATIONS WITH CONTRIBUTION OF SELF IN ROUND 26–28 (FUTURE INVESTMENT BEHAVIOR)				
Anterior insular cortex (AIC)	0.01	0.9629	0.14	0.4710
Left AIC	0.08	0.6689	0.11	0.5857
Right AIC	−0.10	0.5981	0.16	0.4176
Striatum	0.29	0.1209	0.33	0.0809
Dorsal striatum (caudate)	0.33	0.0793	0.34	0.0754
Left dorsal striatum	0.38	0.0420*	0.43	0.0185*
Right dorsal striatum	0.22	0.2444	0.19	0.3207
Ventral striatum (nucleus accumbens)	0.19	0.3285	0.27	0.1574
Left ventral striatum	0.14	0.4651	0.22	0.2530
Right ventral striatum	0.19	0.3279	0.22	0.2499
Posterior superior temporal sulcus (pSTS)	0.58	0.0009***	0.47	0.0108*
Left pSTS	0.60	0.0006***	0.29	0.1293
Right pSTS	0.39	0.0371*	0.48	0.0081**
Anterior cingulate cortex (ACC)	0.16	0.4054	0.21	0.2844
Left orbitofrontal cortex (OFC)	−0.12	0.5450	0.05	0.7980
Ventromedial prefrontal cortex (VMPFC)	−0.13	0.4989	−0.12	0.5288

$N = 29$.

**$p \leq 0.05$.*

***$p \leq 0.01$.*

****$p \leq 0.0043$, False discovery rate (FDR) corrected value of 0.05 over all correlations in the table.*

RELATIONSHIP TO PAST COOPERATION SUCCESS AND FUTURE INVESTMENT BEHAVIOR

To determine the degree to which these sharing-related responses are driven by past cooperation success, and/or predict cooperation in the continuation of the public good game after the second DOT, we correlated all post- minus pre-DOT responses with past cooperation success and future behavior (**Table 4**, second part). Previous cooperation success was defined as the other's mean contribution to the public good in the five rounds prior to administering the post-interaction DOT (van Dijk et al., 2002), while future cooperation was defined as one's own mean contribution to the public good in the three rounds after the second DOT (see Materials and Methods). Past cooperation success (**Figure 5**, middle) as well as future cooperation (**Figure 5**, bottom) in the public good game correlated only with the pSTS, again particularly for outcomes that entail gains at the expense of the other (past success: $r = 0.63$, $p = 0.0003$; future cooperation: $r = 0.58$, $p = 0.0009$).

REGRESSION ANALYSIS OF EMPATHY–TIE INTERACTION

Finally, we wanted to determine whether our empathy and interpersonal ties measures – or their interaction – might be used to predict cooperative behavior directly. We carried out a regression analyses, in which we regressed our behavioral measures for empathy and interpersonal ties, plus an interaction term, onto the average contribution to the public good in the rounds following the second DOT (our behavioral measure for cooperative behavior in the public good game). The overall model was significant: [$F(3,25) = 3.59$, $p = 0.0277$]. Moreover, it was driven only by our interpersonal ties measure ($p = 0.004$), and not by the BEES ($p = 0.184$) or by the interaction of the two ($p = 0.171$). This result confirms the influence of interpersonal ties – rather than empathy – in establishing prosocial behavior during interaction.

DISCUSSION

We isolated the influence of public good game interaction on neural responses in different sharing contexts, by subtracting normalized fMRI signals that were separated in time by the interaction. We investigated the post- minus pre-interaction difference signal in these sharing contexts (other gains at one's own expense and vice versa), subtracting out the raw neural responses to the division of monetary resources themselves. This somewhat unconventional analysis method allowed us to uniquely isolate the influence of intermediate public good game interaction on neural responses during imposed sharing, and determine the relation of these responses to empathy, interpersonal ties, past cooperation success, and future prosocial investment behavior. We found neural correlates of empathy and interpersonal tie measures in these interaction-related fMRI signals, showing that our neural correlates of these measures depend on the intermediate public good game interaction. Moreover, we show that the neural correlate of the interpersonal tie measure is uniquely related to past cooperation success and future prosocial investment behavior.

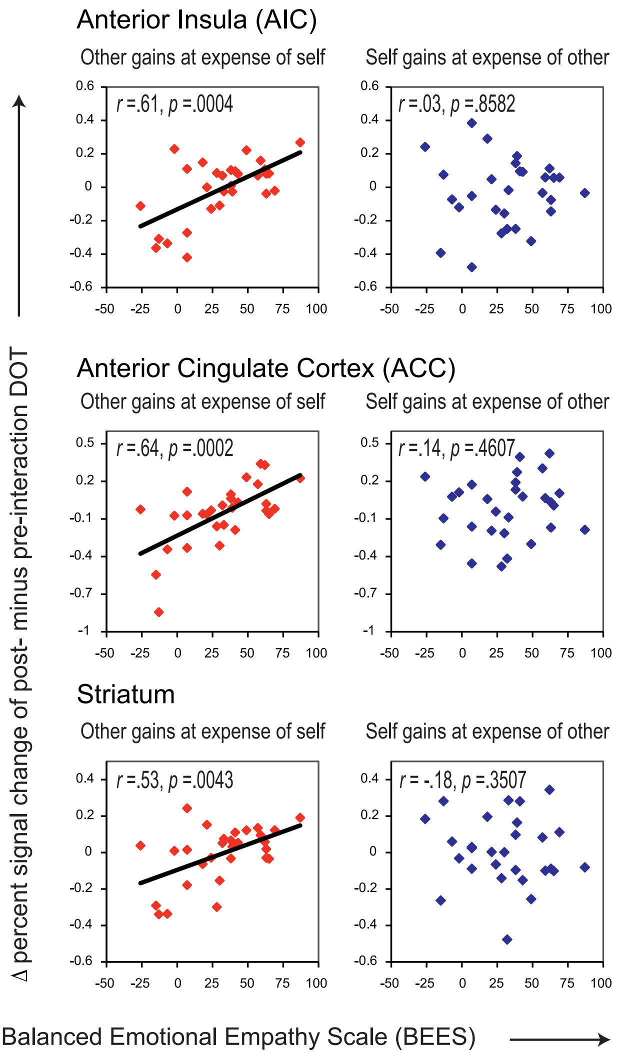

FIGURE 3 | Correlations between empathy scores (BEES) and Δ percent signal change of post- minus pre-interaction DOT. Correlations are shown for AIC (top) and ACC (middle) and striatum (bottom) for trials in which the other gains at the expense of oneself (left panels, in red), and for those in which oneself gains at the expense of the other (right panels, in blue). Correlations before and after public good game interaction separately can be found in **Figure 4**. All correlations are listed in **Table 4**.

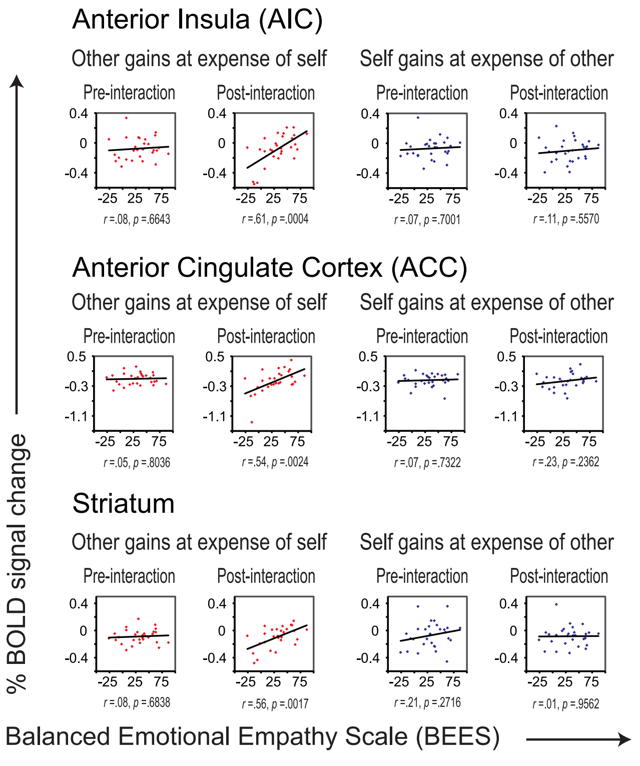

FIGURE 4 | Correlations between scores on the BEES and percent signal change in AIC (top), ACC (middle), and striatum (bottom), separately for the pre- and post-interaction DOT. Correlations are shown for sharing in which the other gains at the expense of self (in red), and for sharing in which oneself gains at the expense of the other (in blue), separately for the DOT prior to interaction (pre-interaction, first and third column) and for the second DOT (post-interaction, second and forth column).

Although neural correlates of empathy only emerged after having interacted with the other participant (**Figure 4**), these correlates could not be related to previous cooperation success or to future choice behavior (**Table 4**). Thus, while these correlates only emerged as a result of interaction, they do not seem to result from specific choice outcomes, or result in specific choices. This suggests that the relationship between trait empathy and economic interaction is more generic. One possibility may be that trait empathy is only expressed when the other person turns out to be a "real" actor in the world. Bear in mind that during the pre-interaction DOT, subjects are told that the "other" is a random anonymous subject from the experiment and that there is no interaction with that participant. The combination of anonymity and a lack of interaction may lead to dehumanization, lessening empathic responses during the pre-interaction DOT (Cehajic et al., 2009).

The pSTS correlate of the interpersonal tie on the other hand, exhibits a more specific interaction-related pattern. Like empathy, it only emerges as a result of public good game interaction. However, this signal could also be linked to previous cooperation success and to future cooperative choice behavior in subsequent rounds of the public good game. Moreover, tie-related activity only correlated with pSTS activation in the context of receiving a monetary reward at the expense of the other. This seems to link pSTS activation to positive choice outcomes. Possibly, the degree to which self-favoring outcomes engender activation in the pSTS depends directly on past cooperation success, extending previous findings on the role of the pSTS in tracking the effects of one's actions on other agents' decisions (Hampton et al., 2008). Similarly, Haruno and Kawato (2009) have shown that the degree to which subjects are able to exploit other agent's strategies is uniquely predicted by STS activity. We suggest that pSTS activation during forced sharing correlates with the interpersonal tie one has developed with another participant during previous interaction, even though this activation is captured outside and apart from the interaction. This alludes to a long-term representation of the

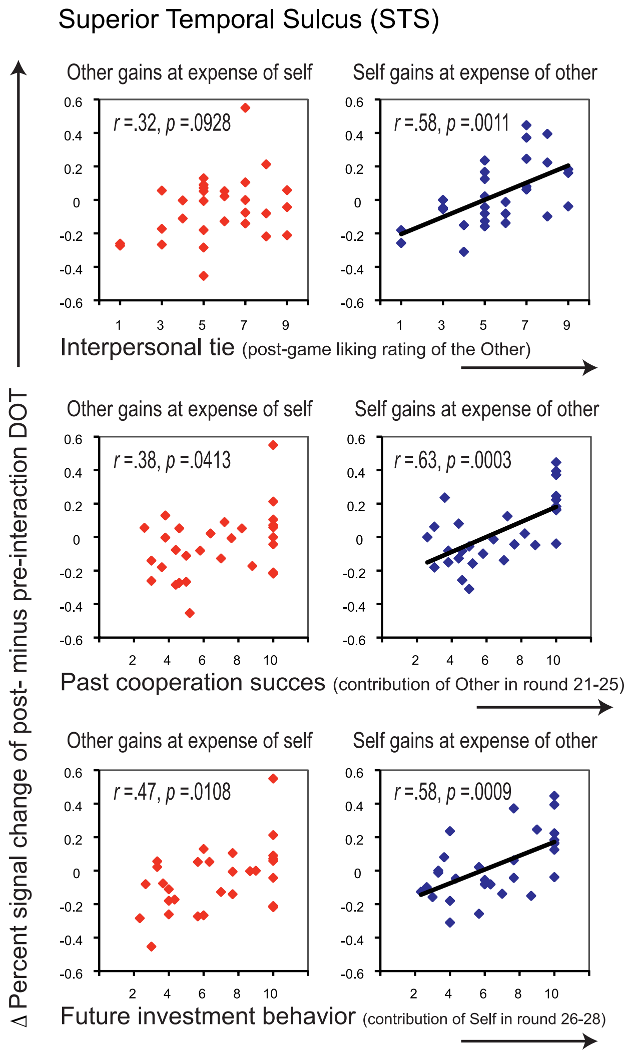

FIGURE 5 | Correlations between interpersonal tie-scores (top), past cooperation success (middle) as well as future investment behavior (bottom), and Δ percent signal change of post- minus pre-interaction DOT. Correlations are shown for the pSTS, for trials in which the other gains at the expense of oneself (left panels, in red), and for those in which oneself gains at the expense of the other (right panels, in blue). Correlations before and after public good game interaction separately can be found in **Figure 6**. All correlations are listed in **Table 4**.

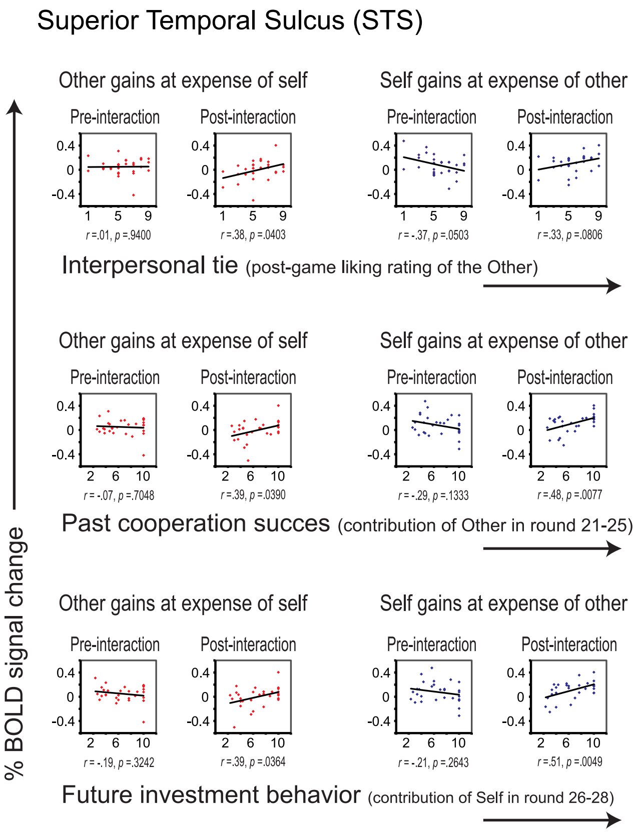

FIGURE 6 | Correlations between liking (top), past cooperation success (middle) and future investment behavior (bottom), and percent signal change in the pSTS, separately for the pre- and post-interaction DOT. Correlations are shown for sharing in which the other gains at the expense of self (in red), and for sharing in which oneself gains at the expense of the other (in blue), separately for the DOT prior to interaction (pre-interaction, first and third column) and for the second DOT (post-interaction, second and forth column).

interpersonal tie that outlasts representations that are temporally contained within the time frame of the interaction itself.

Taken together, our results suggest that during economic interaction, tie-related mechanisms are more closely involved in experience-based choice than trait empathy. As we established that our trait empathy measure and our interpersonal tie measure were uncorrelated, it seems unlikely that trait empathy plays a direct role in the formation of interpersonal ties and choice behavior during economic interaction. However, trait empathy might play a modulating role in determining the influence of interpersonal ties on experience-based choice. A regression analysis of our empathy and interpersonal ties measures together with an interaction term established that only interpersonal ties predicted cooperative behavior. This suggests that neither trait empathy, nor its interaction with interpersonal ties, determines subsequent choice behavior.

Importantly, we measured empathy in our experiment by establishing the degree to which someone is able to experience empathic emotions. Therefore, only trait-like aspects of empathy were considered. However, the degree to which empathy is experienced at any given moment in time can change depending on the situational context. For example, a person may feel more empathy toward a person that behaves nicely than toward a person that does not (Singer et al., 2006). As we did not measure the degree of empathy experienced during the experiment directly, we could not assess the influence of empathic experience on choice behavior directly. Other studies suggest that feelings of empathy or activity in empathy-related networks do play a role during prosocial behavior (Hein et al., 2010; Masten et al., 2011), which seems to be at odds with the findings we present here. Importantly however, these studies investigated non-interactive instances of prosocial behavior, in which the other is not expected to reciprocate the good deed bestowed onto them. Experiments like these often use verbal descriptions or passive viewing of characters. In our experiment, participants were involved in actual interaction with interaction partners. So even if feelings of empathic concern play a role during choice behavior, our results suggest that in interactive experience-based contexts such as the one investigated here, this influence cannot be traced back to a stable empathic trait.

We find correlations between trait empathy and the AIC and ACC only when the other gains at one's own expense, and not when resource transfer is in the opposite direction. In the DOT, negative (resource-losing) events for oneself go hand in hand with positive (resource-gaining) events for the other. Hence, outcomes that benefit the other at one's own expense can either be interpreted as "painful" (resource-losing) events for oneself, as positive (resource-gaining) events for the other, or as a combination of the two. AIC and ACC have been implicated in empathy for both positive (Jabbi et al., 2007) and negative (Wicker et al., 2003) events, but also in a more general brain network known as the "pain matrix," thought to be involved in the perception and appraisal of pain (Singer et al., 2004b). Following reverse inference, one interpretation might be that there is a correlation between trait empathy and one's own "pain" responses when having to share. If true, one would expect to also see them in the pre-interaction DOT. This is not the case (see **Figure 4**), suggesting that the correlations are driven by empathic concern for the other's benefit as a result of having interacted with that person, rather than by pain over one's own loss. In line with this interpretation, we not only found correlations in AIC and ACC, but also in striatal circuitry typically associated with reward processing (Moll et al., 2006; Haber and Knutson, 2010). Although speculative, another person's benefit may register more strongly as a reward signal for individuals with higher empathy levels.

This finding is interesting in light of common theorizing about empathy. Empathy is generally thought to be "other-oriented," being able to tune into or share the affective experiences of others (positive or negative; de Waal, 2008; Singer and Lamm, 2009). Here, we have the special situation where a positive event for the other is accompanied by a negative event for oneself and vice versa (sharing). We only see correlations with empathy when the other gains at one's own expense and not the other way around. This suggests that the "other-orientation" of empathy is modulated by the direction of the resource transfer involved in sharing. Empathic subjects engage empathy-related structures (AIC, ACC) during sharing – even when these events are painful for themselves – but only when their own suffering helps the other along, and not the other way around. Although speculative, empathic subjects may use their ability to empathize to help alleviate, counterbalance, compensate, or justify their own suffering when having to share, while empathy-related responses do not manifest when the tables are turned, possibly as a result of joy over one's own profit.

More generally, the expression of neural correlates of empathy and interpersonal ties in different sharing contexts may tell us something about their function in prosocial behavior. While the interpersonal tie correlate seems to be expressed more strongly in a sharing context where oneself benefits at the other's expense, the network structure involved in empathy seems to be engaged more strongly when one suffers loss that benefits another. This may point to different functional contributions of these regions to prosocial behavior. The pSTS may be used to keep track of the utility that other agents constitute in the short run, enabling immediate prosocial behavior during interaction. The empathy network on the other hand, may work to overcome negative emotions that are associated with loss. Although our study suggests that this is not translated into short-term investment choices during economic interaction, it may enable cooperative behavior in the long run, countering the adverse effects of absorbing temporary loss associated with social interactions.

Summarizing, previous cooperation success and future cooperation did not correlate with activations in structures related to empathy (AIC, ACC), reward (striatum), or social decision-making (OFC, VMPFC). However, previous cooperation success and future cooperation did correlate with pSTS activation, which we found to be related to interpersonal ties. This suggests that interpersonal ties and trait empathy may recruit different neural networks, of which only the former drives cooperative behavior during interaction. Moreover, individual differences in pSTS activation predicted individual differences in prosocial investment behavior in subsequent rounds of the public good game. This predictive value is important, as it suggests that the pSTS plays a role in keeping track of the dynamically evolving interpersonal tie underlying the willingness to invest in a shared public good. We conclude that during experience-based economic interaction, networks are engaged that keep track of interpersonal ties over longer periods of time, possibly enabling choice–outcome estimation in social settings, with the pSTS emerging as a key element.

A word of caution is also in order. The regions that were highlighted in our experiment have previously been related to many elementary operations, of which we discuss only a few. For example, the pSTS has also been linked to perception of biological motion (Perrett et al., 1989; Bonda et al., 1996), perception of intentional action (Castelli et al., 2000; Saxe et al., 2004) as well as speech perception (Demonet et al., 1992; Mottonen et al., 2006). AIC has been implicated in eye movements (Anderson et al., 1994), speech production (Dronkers, 1996; Ackermann and Riecker, 2004), higher-order learning (Seymour et al., 2004), interoceptive awareness (Critchley et al., 2004; Khalsa et al., 2009), and even consciousness at large (Craig, 2009). Likewise, the ACC has been implicated in interoception (Critchley et al., 2004; Khalsa et al., 2009), reward based decision-making (Bush et al., 2002), error detection and conflict monitoring (Gehring et al., 1993), and various related cognitive and emotional processes (Lane et al., 1998; Bush et al., 2000). The striatum has traditionally been implicated in planning and modulation of movement (Rolls, 1994), but recently more prominently in reward processing (Moll et al., 2006; Haber and Knutson, 2010), novelty-based choice behavior (Wittmann et al., 2008), and higher-order learning (Seymour et al., 2004). Together, this paints a picture of a highly complex network in which regions work together to achieve certain functions, plausibly providing different functions in different contexts and at different moments in time. Although we have attempted to isolate empathy and tie-related mechanisms, the idea that these mechanisms are solely implemented in the regions that we highlight is most likely an oversimplification. More likely, these functions are achieved through interactions between and within regions, executing various more elementary subprocesses to provide more complex higher-order functions. Our study does not allow us to tease apart empathy and tie-related mechanisms into their elementary processes. However, it does provide pointers as to where these higher-order functions seem to be expressed most strongly, and what their role is in interactive experience-based choice. Relatedly, it deserves mention that we did not have a control group in which the other participant in the post-interaction DOT was either a non-human player (computer) or another anonymous participant from the experiment. Although it is unlikely that the specific activation patterns we observed can be attributed to non-specific effects such as game repetition, boredom or exhaustion, future studies employing a similar design might do well to include such controls.

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Positive interaction of social comparison and personal responsibility for outcomes

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We formulate and test a model that allows sharp separation between two different ways in which environment affects evaluation of outcomes, by comparing social vs. private and personal responsibility vs. chance. In the experiment, subjects chose between two lotteries, one low-risk and one high-risk. They could then observe the outcomes. By varying the environment between private (they could observe the outcome of the chosen lottery and the outcome of the lottery they had not chosen) and social (they could observe the outcome of the lottery chosen by another subject) we can differentiate the response and brain activity following the feedback in social and private settings. The evidence suggests that envy and pride are significant motives driving decisions and outcomes evaluation, stronger than private emotions like regret and rejoice, with ventral striatum playing a key role. When we focus on the outcome evaluation stage we demonstrate that BOLD signal in ventral striatum is increasing in the difference between obtained and counterfactual payoffs. For a given difference in payoffs, striatal responses are more pronounced in social than in private environment. Moreover, a positive interaction (complementarity) between social comparison and personal responsibility is reflected in the pattern of activity in the ventral striatum. At decision stage we observe *getting ahead of the Joneses* effect in ventral striatum with subjective value of risk larger in social than in private environment.

Keywords: envy, pride, social comparison, responsibility, regret

INTRODUCTION

We investigate neural correlates of envy and pride during choice and evaluation of outcomes. Envy is a negative emotion experienced when an individual receives a worse outcome than someone else; correspondingly, pride is a positive emotion experienced when that outcome is better than the other's. Human subjects may feel envy and pride for different reasons. A classical view (Social Comparison Theory; Festinger, 1954) is that comparing our performance with others' can give us a useful signal about our skill, information that we may want to have even if we are not interested in relative comparisons, and envy and pride simply help us to learn from such experience. The other classical view is formulated for example by Veblen (1899): individuals strive for social dominance, which is their ultimate objective, and envy and pride reflect responses to differences in social status.

Until recently economics has focused mainly on situations where social comparison is not considered, and the utility of an economic agent depends only on one's obtained outcomes and is independent of others' outcomes. The works on conspicuous consumption in quest for social status (Veblen, 1899) or relative-income theory of consumption (Duesenberry, 1949) were rather isolated examples of incorporating social comparison into economics. More recently the empirical literature on subjective well-being shows importance of relative-income (Blanchflower and Oswald, 2004; Luttmer, 2005; Dynan and Ravina, 2007). The experimental work on other-regarding preferences suggests that players in simple strategic situations are influenced by relative outcomes (Fehr and Schmidt, 1999; Charness and Rabin, 2002). Social comparison was demonstrated to matter potentially in many applications like internal wage structure in a firm (Frank, 1984), use of prizes instead of wages as optimal motivation devices (Dubey et al., 2005), or pro-cyclical tax policy as a stabilization tool (Ljungqvist and Uhlig, 2000), and many others. In finance, social comparison can account for the observed under-diversification of households' portfolios (Roussanov, 2010). Social comparison has a potentially broad impact in economics because it affects the central concept of utility function. In this light the more important becomes thorough understanding of social comparison including its neurobiological basis.

Neuroeconomics focuses on understanding neural basis of reward system (neurobiological utility), beliefs formation and emotions that impact decisions, *ex post* evaluations, and learning (Glimcher et al., 2008). Numerous studies point to ventral striatum and orbito-frontal cortex as essential regions that process reward and values in the brain (McClure et al., 2003; O'Doherty et al., 2003; Preuschoff et al., 2006; Glimcher et al., 2008; Caplin et al., 2010). Social aspects of reward processing were addressed by several papers in neuroeconomics (Sanfey et al., 2003; Knoch et al., 2006; Singer et al., 2006; Takahashi et al., 2009). Two most related papers to ours show that ventral striatum is sensitive to social comparison (Fliessbach et al., 2007; Dvash et al., 2010). The first paper (Fliessbach et al., 2007) demonstrates that BOLD signal in ventral striatum increases as the ratio of relative-income increases to subject's advantage (1:2, 1:1, 2:1). In the second paper (Dvash et al., 2010) the effect of social comparison in ventral striatum is demonstrated by benchmarking social treatment to the treatment with absolute payoff only (no information about others' outcomes). The limitation of these fMRI studies is that one cannot exclude the possibility that the main effect comes from a different type of comparison than social one, i.e., counterfactual comparison reflected by activity in ventral striatum (Camille et al., 2004; Coricelli et al., 2005). Using counterfactual comparison as a benchmark social comparison was demonstrated in skin conductance responses (Bault et al., 2008).

There are at least four factors that distinguish our fMRI study from the related work in neuroeconomics we mentioned. First, we consider envy and pride in social comparison as social correspondents of regret and rejoice in counterfactual comparison, which we use as a benchmark for the former. This is a much higher bar for social comparison to pass as compared to those in the mentioned papers. Second, the present study is the first in neuroeconomics to weigh two classical explanations of social comparison described in the first paragraph: Veblen's social status and Festinger's drive to compare abilities. Third, thanks to large variability in outcomes we are able to test robustness of social comparison to loser/winner effect. Forth, using a two-lottery choice task allows us to investigate social comparison at decision stage unlike earlier studies (Fliessbach et al., 2007; Dvash et al., 2010). The studies (Bault et al., 2008, 2011), where a similar design is used, are closely related. Differently from Bault et al. (2011), in the current study the emphasis is in the decomposition of the counterfactual comparison in chance and personal responsibility, based on a specific formal model that we now present.

THEORETICAL FRAMEWORK

Our work can be conceptualized within the axiomatic framework of social decision theory laid out in Maccheroni et al. (forth coming), hereafter MMR, who extend regret theory (Loomes and Sudgen, 1982) into social context, with envy and pride as social correspondents of regret and rejoice. The theory considers a decision-maker that observes both the outcome x obtained from his choice, and the counterfactual outcome y, that is an outcome he could have had alternatively. The value function $V(x, y)$ of outcome profile (x, y) is a sum of personal utility $u(x)$ from the obtained outcome x and relative utility $G(x-y)$. The latter part captures importance of counterfactual comparison of the obtained outcome x vs. the counterfactual outcome y. This is a generalization of classical expected utility theory, incorporating relative utility. How important relative utility is for well-being of decision-maker, given x and y, potentially depends on the nature of counterfactual outcome y.

The model allows a distinction between private and social environments. In private environment a counterfactual outcome y is just what the individual could have had. In social environment a counterfactual outcome y is what he could have had, but someone else obtained. Independently of distinction between private vs. social environment, this setup may distinguish between chance and personal responsibility. In case of chance, a decision-maker obtained x rather than y due to pure luck. This occurs for example when x and y are outcomes of the same chosen lottery, but drawn independently. As for personal responsibility a decision-maker could have obtained a counterfactual outcome y if he had made a different choice. In general, the *ex post* value function is:

$$V_j^i(x, y) = u(x) + G_j^i(x - y) \tag{1}$$

where the superscript i denotes private or social environment, and j denotes chance or personal responsibility. To evaluate lotteries *ex ante*, before choice is made, a decision-maker uses expectation of a value function $V_j^i(x, y)$ with respect to a subjective belief over states of nature. One of the main features of the model is that it provides separation of the personal $u(x)$ and relative $G_j^i(x-y)$ utility: here we focus on the latter. The G_j^i functions have natural interpretation, for example: the function G_0^0 is the disappointment/elation function (private environment and chance responsibility), the function G_1^0 the regret/rejoice function (private environment and personal responsibility), and G_j^1 the envy/gloating function (social environment, and either chance or personal responsibility).

HYPOTHESES

Our primary objective is to investigate social comparison at outcome evaluation stage. To simplify the analysis we assume that functions $G_j^i(x - y)$ are linear, and we refer to G_j^i as a slope. If this model is taken as a model of the *ex ante* choice, then a linear G function would make the model identical to expected utility: that is, it would produce the same choice as that of an individual that ignores inter-personal comparisons. For this reason we rather interpret linear functions $G_j^i(x - y)$ as approximations to true non-linear functions. We state now formally our hypotheses:

1. Counterfactual comparison: $G_j^i > 0$ for all i, j.
2. Social comparison: $G_j^1 - G_j^0 > 0$.
3. Personal responsibility: $G_1^i - G_0^i > 0$.
4. Positive interaction (complementarity) between social comparison and personal responsibility effects: $G_1^1 - G_1^0 > G_0^1 - G_0^0$.
5. Correspondence between behavioral and neural effects.

The first hypothesis asserts that the subjective value of the obtained outcome x, while a decision-maker could have had the outcome y, depends on the comparison of x and y, or $G_j^i \neq 0$. In addition, we hypothesize that the functions G_j^i are increasing. In other words, the subject's relative utility G_j^i is increasing in the subject's advantage (that is the difference $x-y$) over the counterfactual payoff. The second hypothesis of social comparison states that the counterfactual comparison matters more in a social than in a private environment. Simply, if a subject earns \$1 more than the other person his relative utility is larger as compared to earning \$1 more than the counterfactual outcome in private environment. The third hypothesis concerns personal responsibility effect, which states that the counterfactual comparison is more important in case of personal rather than chance responsibility. Intuitively, the subject is more affected in terms of relative utility if advantage (or $x-y$) in counterfactual comparison is due to his choice

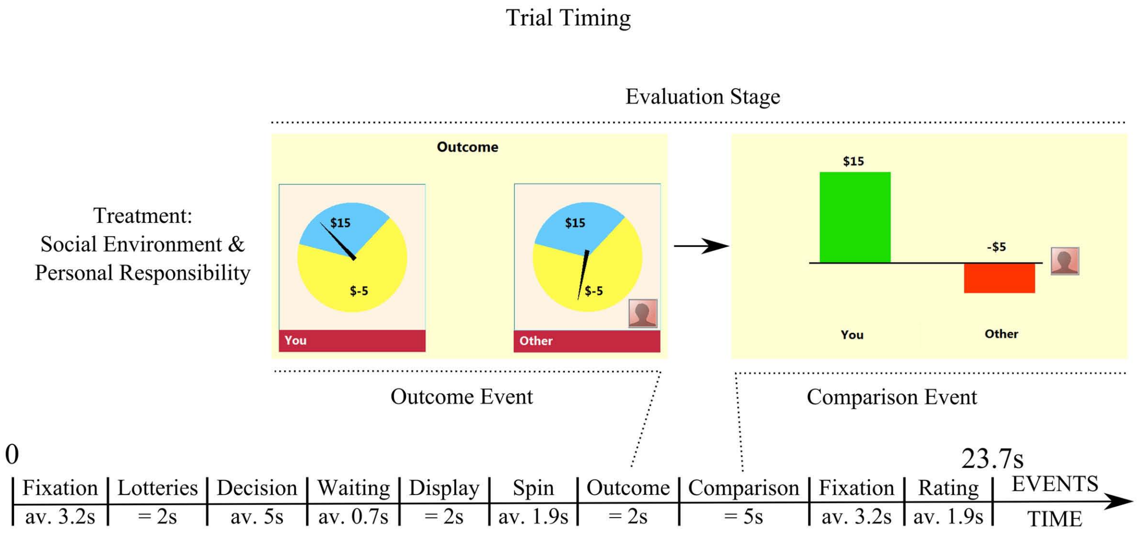

FIGURE 1 | Trial timing with duration and sequence of events. The study focuses on *ex post* evaluation stage that is divided into two events: outcome event and comparison event. The events presented in this Figure refer to the treatment of social environment and personal responsibility. At comparison event, a subject ("you") conducts counterfactual comparison of "*what you got*" as compared to "*what you could have had, but the other got.*" The clause "*but the other got*" extends counterfactual comparison into social comparison.

rather than just pure chance. The forth hypothesis is positive interaction (complementarity) between social comparison and personal responsibility effects. It is about personal responsibility effect being stronger in the social than in the private environment. The last fifth hypothesis is the correspondence between the neural and behavioral effects.

MATERIALS AND METHODS

PARTICIPANTS

We recruited 63 participants from introductory courses in microeconomics and macroeconomics at University of Minnesota to participate in 21 experimental sessions. In each session one participant was placed inside magnetic resonance imaging (MRI) scanner and two other at computers outside the scanner in a separate room. All subjects in each experimental session faced otherwise the same task. The 21 scanned participants were right-handed, healthy males, aged 18–20 years old (mean 18.5, SD 0.6). Forty-two subjects (18 females and 24 males) participated in the experiment outside the scanner. We later discovered that the subject in the scanner and one of the other two had a personal relationship, so we drop this session from analysis and analyze data from 20 sessions. All subjects gave informed consent to participate according to the procedures approved by University of Minnesota Institutional Review Board.

EXPERIMENTAL TASK

Subjects chose between two lotteries in each of 70 consecutive rounds. Each lottery had two possible outcomes ranging from a minimum value of −$5 to a maximum of $25. Three subjects performed the same task in each experimental session. One male subject was placed inside MRI machine. The two others made choices at computers through a remote connection in a separate room. We dropped one session from analysis due to violation of experimental procedures. The main focus of this paper is on the 20 scanned subjects, for whom we collected both behavioral and neural data according to the study procedures. Subjects were connected over computer network. No deception was used at any time. Subjects chose repeatedly a lottery from a pair of lotteries, a low-risk and a high-risk one. In a typical trial each subject had 2 s to evaluate lotteries, and then made a decision without time constraints: see **Figure 1**. Choice was followed by display of lotteries for 2 s, and then determination of outcome for each. Lotteries together with final outcomes were then shown for 2 s (outcome event). Subjects then observed for 5 s two bars representing the obtained payoff and the counterfactual payoff (comparison event). Each of 70 trials ended with a subjective rating on the integer scale 0–10 (we labeled 0 as bad, 5 as neutral, 10 as good) without time constraints. The outcomes of lotteries were drawn once and for all using the actual probabilities for each of 72 trials. These outcomes were the same in all 21 experimental sessions.

TIMING

Each of 70 periods started with a fixation screen pre-announcing either the social or the private environment. Next, we asked the subject to choose from two lotteries. After a display of 2 s, a cue was given indicating that a choice could be made. The subject had unlimited time to decide his choice of lottery. The average choice time was 5 s. The lottery chosen by the subject was highlighted for 2 s for decision confirmation. Sometimes, a subject in addition learned the choice of lottery by one other subject selected randomly. This could lead to the delay of presentation of choices that last 0.7 s on average. After that an arrow appeared over the pie chart describing each lottery on the screen, started to spin instantly, and stopped pointing to the outcome of lottery after an average spinning time of 1.9 s. Pie charts and arrows pointing to outcomes were kept on the screen for 2 s. After that, a subject was presented for fixed 5 s with his obtained payoff vs. the counterfactual payoff he could have had according to the relevant condition. This event, called comparison event, is the main focus of brain data analysis. The period ended with the question "How did that make you feel?" that a subject answered on the integer scale 0–10, with 0 – "Bad," 5 – "Neutral," and 10 – "Good."

PAYMENTS

Subjects received a fixed participation payment of $15; the subject in the MRI machine received additional $25. In addition subjects were paid the outcomes of three randomly determined out of those they had chosen during 70 periods. Outcomes of lotteries varied from −$5 to $25, so losses were possible. To cover potential losses a participant received an additional payment of $15. The three paid lotteries were drawn at the end of the session. The total fixed payment was $55 to a scanned subject and $30 to a subject participating outside MRI scanner. The average additional payment from the three paid lotteries to subjects scanned in MRI was $11.25, with minimum −$4, maximum $39, and SD $10.97. The average performance payment to subjects participating outside MRI was $12.80, with minimum −$7, maximum $46, and SD $12.39.

ANALYSIS

At the decision stage there was only one factor with two levels: private vs. social environment. In the social environment each subject was choosing a lottery expecting to learn its outcome as well as choice and obtained outcome of the other randomly matched subject. In contrast in private environment a subject was not provided with any information about others. At the evaluation stage we used 2 × 2 factorial design.

The two independent factors were: environment and responsibility. Each factor had two levels: private vs. social environment, and chance vs. personal responsibility. There were 20 trials in each of three treatments: (private, personal), (social, chance), and (social, personal). There were 10 trials in the treatment (private, chance). The order of treatments in a session was random. We used the set of 20 different pairs of lotteries shown at most once in each treatment, see **Table A1** in Appendix.

We now explain the four treatments present at the evaluation stage, the stage consisting of outcome and comparison events, see **Figure A1** in Appendix for displays used in different treatments. In treatment (*private*, *chance*) a subject saw at outcome event only the lottery he chose, and at comparison event the obtained outcome vs. the unrealized outcome within the chosen lottery. In contrast in treatment (*private*, *personal*) a subject observed at outcome event both the lottery he chose and the lottery he did not choose, followed with comparison event presenting the outcome of chosen lottery vs. the outcome of lottery he could but did not choose. Treatment (*social*, *chance*) occurred if subjects in a random match chose the same lottery. In this case we resolved the same lottery independently for each subject in the match. Consequently, a subject in the match observed at outcome event the two instances of the same lottery, one instance applying to him and other instance applying to other subject. The outcome event was followed with comparison event presenting subject's outcome vs. other's outcome. Finally, treatment (*social*, *personal*) occurred if subjects in a random match chose different lotteries. At outcome stage a subject observed a lottery he chose and a lottery chosen by the other subject in a random match. This was followed with a comparison event presenting subject's outcome against the outcome obtained by the other.

fMRI ACQUISITION AND PREPROCESSING

We collected data at Magnetic Resonance Research Center at University of Minnesota using 3T Siemens Trio scanner. High resolution anatomical images were obtained using Siemens T1-weighted 3D flash 1 mm sequence. Functional images were acquired using echo planar imaging with repetition time (TR) 2000 ms, echo time (TE) 23 ms, flip angle 90°, 64 × 64 matrix, 38 slices per scan, axial slices 3 mm thick with no gap, voxel size 3 mm × 3 mm × 3 mm. Functional images were acquired with an oblique 30° angle to the anterior commissure–posterior commissure (AC–PC) line to optimize signal acquisition from orbito-frontal cortex. The data were preprocessed and analyzed using Brain Voyager QX 1.8. The anatomical images were transformed into Talairach space in two steps: first the cerebrum was rotated into AC–PC plane using trilinear transformation, second we identified eight reference points (AC, PC, and six boundary points) to fit the cerebrum into Talairach template using trilinear transformation. We preprocessed functional data performing slice scan time correction, 3D movement correction relative to the first volume using trilinear estimation and interpolation, removal of linear trend together with low frequency non-linear trends using high-pass filter. Next, we co-registered functional with anatomical data to obtain Talairach referenced voxel time courses, to which we applied spatial smoothing using Gaussian filter of 7 mm.

fMRI ANALYSIS

The analysis was performed in Brain Voyager QX; the statistical analysis in Stata. We used GLM model with continuous predictors of interest convolved with two-gamma hemo-dynamic response function (Bvϋchel et al., 1998). We proceeded in three steps separately for decision and outcome evaluation stages. First, we performed whole-brain analysis with treatments collapsed using random-effects General Linear Model (RFX GLM) to identify functional region-of-interests (ROIs). We then examined treatment effects in the regions identified in the first step. We finally performed whole-brain analysis with RFX GLM focusing on relative treatment effects. At *ex post* outcome evaluation stage we focused on two events of interest: *outcome* and *comparison*, while controlling for the remaining events of no interest with dummy variables. We implemented model designs with continuous predictors of product of delta function (a box car function over 500 ms) and value of advantage at event *comparison*. In model designs differentiating between treatments we used separate predictors of advantage for each treatment considered. We controlled for the obtained payoff by a subject with a continuous predictor being a product of delta function (2000 ms) and value of the obtained payoff by a subject at event *outcome*. In analyzing *ex ante* evaluation of choice alternatives we focused on the event *lotteries*. We implemented model designs with continuous predictors of product of delta function (500 ms) and value of risk-adjusted return of high-risk lottery at the event *lotteries*.

Table 1 | Counterfactual comparisons in behavioral data.

	Private ($i = 0$)	Social ($i = 1$)
Personal ($j = 1$)	$G_1^0 = 0.169$ ($t = 7.7$)	$G_1^1 = 0.185$ ($t = 6.2$)
Chance ($j = 0$)	$G_0^0 = 0.098$ ($t = 6.1$)	$G_0^1 = 0.113$ ($t = 6.8$)

The coefficients G_j^i on advantage (with t-values in brackets) from the regression analysis of affective ratings as a function of the obtained outcome (payoff = x), and counterfactual comparison (advantage = x – y) of the obtained outcome (x) and counterfactual outcome (y) made in different conditions. The constant is 4.896 (t = 55.84) and the coefficient of the payoff is 0.147 (t = 9.06) with $R^2 = 58.9\%$.

RESULTS

BEHAVIORAL RESULTS

We focus on the question how self reported affective ratings (variable *affect*) depend on subjects' obtained outcome (variable *payoff*) and counterfactual comparison relevant to treatment (variable *advantage*). The variable advantage is the difference between the payoff obtained by the subject and the counterfactual payoff. We estimate the model given by Eq. 2 using OLS with robust SE corrected for in-subject correlation in observations:

$$affect = \alpha + \beta \cdot payoff + \sum_{i,j=0,1} G_j^i \cdot advantage_j^i \tag{2}$$

The results reported in **Table 1** confirm hypothesis that counterfactual comparisons matter in the evaluations of outcomes of choices, for example the estimated G_j^i coefficients are positive and significantly different from 0. The affective rating of outcome profile depends not only on the obtained payoff but also on the counterfactual comparison.

To investigate the effect of personal responsibility we test whether the importance of counterfactual comparisons is higher in personal than in chance responsibility separately for the private $(G_1^0 - G_0^0) > 0$ and the social $(G_1^1 - G_0^1) > 0$ environment using the above estimates of G_j^i. The personal responsibility effect is highly significant in both cases according to a two-sided Wald test: $F(1, 19) = 26.28$ with $p < 0.001$ and $F(1, 19) = 13.28$ with $p = 0.002$, respectively. Similarly for the social comparison effect we test whether the importance of counterfactual comparisons is higher in the social than in the private environment separately for chance $(G_0^1 - G_0^0) > 0$ and personal $(G_1^1 - G_1^0) > 0$ responsibility treatments. The social comparison effect has the right sign but is not significant in both cases using two-sided Wald test: $F(1, 19) = 1.24$ with $p > 0.1$ and $F(1, 19) = 0.77$ with >0.1, respectively. To check the forth hypothesis of positive interaction between social comparison and personal responsibility we construct the complementarity index CI:

$$\mathrm{CI} = \frac{\left(G_1^1 + G_0^0\right) - \left(G_1^0 + G_0^1\right)}{0.25 \cdot \left(G_1^1 + G_0^0 + G_1^0 + G_0^1\right)} \tag{3}$$

The numerator in Eq. 3 captures the degree of complementarity between two factors. If it is positive then factors are complementary (positive interaction), if zero they are independent (no interaction), and if negative they are substitutable (negative interaction). The denominator in Eq. 3 is a normalization introduced so that CI is independent of scaling of variables. We estimated CI individual by individual finding mean CI = 0.21, which is positive as hypothesized. However, we cannot reject the hypothesis that the two factors: environment and responsibility are independent (Wilcoxon signed-rank test, $z = 0.34$, $p > 0.1$).

fMRI RESULTS

We performed whole-brain analysis of *ex post* evaluation of outcomes. The evaluation stage was partitioned in two distinct events: outcome event (which lasted 2 s) followed immediately by comparison event (5 s), see **Figure 1**. During the outcome event subjects were shown the lotteries, relevant to treatment, and their outcomes. In the comparison event subjects observed the obtained outcome vs. the counterfactual outcome, with the latter varying according to treatments. In the statistical models we test we use the outcome event to control for the obtained payoff, while during the comparison event we focus on counterfactual comparison. The partitioning of the outcome evaluation stage into two events allowed us to better control the nature of counterfactual comparison between the obtained and counterfactual outcomes, while also temporally decouple the predictors of the obtained and counterfactual payoffs.

UNIVERSAL NETWORK FOR COUNTERFACTUALS

Our strategy is to first identify brain areas that are involved in counterfactual comparisons in general, without differentiating between different treatments. To this end we use model design with linear predictors (Bv̈chel et al., 1998) in the obtained payoff and the advantage (with all treatments collapsed) and consider the contrast of advantage against the baseline. With conservative threshold of $p < 0.01$ (Bonferroni corrected) we find increased activations only in striatum bilaterally, see **Figure 2A**. However, with more liberal threshold of $p < 0.02$ (FDR corrected) we find also other clusters associated with reward processing like mPFC and OFC, see **Table 2**, among other regions, see **Table A2** in Appendix. In the second step we extract average BOLD time-series from the regions identified above and perform ROI analysis to test our hypotheses. We

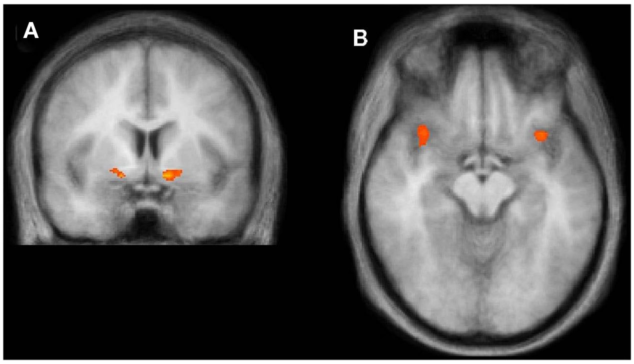

FIGURE 2 | Regions of interest identified. (A) Ventral striatum bilaterally shows increased activity at the contrast of linear advantage against the baseline with $p < 0.01$ (Bonferroni corrected). **(B)** Anterior insula bilaterally shows increased activity at the contrast with dummy predictors: Social Loss less Private Loss with $p < 0.001$ (uncorrected), where Loss = 1 if advantage <0, and 0 otherwise. Details of coordinates in **Table 2**.

Table 2 | Areas in universal network for counterfactuals.

ROIs	Average coordinates			Max *t*	Size	*p*-Value
	x	*y*	*z*			
l LGP	−14	2	−4	8.7	350	$p < 0.01$ Bonf.
r LGP	17	2	−3	6.0	66	$p < 0.01$ Bonf.
OFC	−4	23	−12	4.1	150	$p < 0.02$ FDR
mPFC	−2	43	−2	4.8	572	$p < 0.01$ FDR

l/r, left/right; LGP, lateral globus pallidus; OFC, orbito-frontal cortex; mPFC, medial prefrontal cortex.

differentiate between different treatments by considering model designs with one factor at the time, instead of two, in order to increase power. For clarity we report below the results on the left ventral striatum, and very similar results on the right ventral striatum are reported in the Appendix.

We ran random-effects panel regression to explain average BOLD time-series in the cluster of left striatum with linear predictors (convolved with standard two gammas hemodynamic response function) in private advantage (coefficient $G^0 = 0.77$ with $z = 7.79$, $p < 0.001$) and social advantage (coefficient $G^1 = 1.07$ with $z = 11.31$, $p < 0.001$), while controlling for the obtained payoff. Both coefficients are positive and significantly different from zero, which demonstrates the involvement of left striatum in counterfactual comparisons.

The difference in coefficients on social less private advantage is positive and statistically significant (two-sided Wald test, $\chi^2 = 5.45$, $p = 0.02$). The same analysis after the introduction of a responsibility factor shows that the coefficients on chance advantage (coefficient 0.79, $z = 7.93$, $p < 0.001$) and personal advantage (coefficient 1.05 with $z = 11.14$, $p < 0.001$) are significantly different from zero, with the difference between the latter and the former positive and statistically significant (two-sided Wald test, $\chi^2 = 4.18$, $p = 0.04$). The results confirm again the involvement of left striatum in counterfactual processing and show that it is stronger for personal rather than chance responsibility, see **Figure 3**. To exclude the possibility that correlation of payoff and advantage drives the results we consider the model designs with advantage normalized to mean 0 and SD 1, without controlling for payoffs. We run subject by subject regressions to explain BOLD time-series convolved with HRF linear predictors in normalized advantage, so that we obtain individual by individual coefficients allowing us to perform non-parametric statistical tests. Considering environment factor we find that coefficients on normalized private (coefficient 4.30, Wilcoxon signed-rank test, $z = 3.73$, $p < 0.001$) and social advantage (coefficient 6.03, Wilcoxon signed-rank test, $z = 3.92$, $p < 0.001$) are positive and statistically significant. The difference between the latter and the former is also positive and significant (Wilcoxon signed-rank test, $z = 1.79$, $p = 0.07$). Switching to responsibility factor we observe that coefficients on normalized chance (coefficient 3.49, Wilcoxon signed-rank test, $z = 3.21$, $p = 0.001$) and personal advantage (coefficient 6.52, Wilcoxon signed-rank test, $z = 3.92$, $p < 0.001$) are positive and significantly different from 0. The difference between coefficients on personal less chance normalized advantage is positive and statistically significant (Wilcoxon signed-rank test, $z = 2.02$, $p = 0.04$). The non-parametric analysis of normalized advantage, without controlling for payoff, confirms the results obtained in panel analysis when we controlled for payoffs.

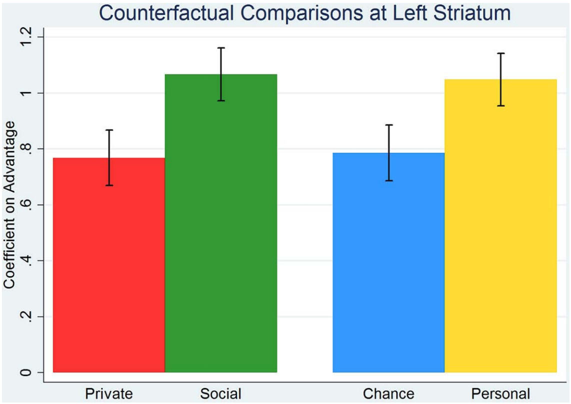

FIGURE 3 | We performed ROI analysis, considering one factor at the time, on the cluster of left ventral striatum, identified earlier as a part of universal network for counterfactuals, showing that coefficients on linear predictors in advantage are positive in all treatments. The coefficient on advantage is larger in social than in private environment and with personal than with chance responsibility.

To investigate the interaction between the two factors, environment and responsibility, we consider the disaggregated model design with all four treatments. We estimated neural CI (Eq. 3) in left ventral striatum cluster to be 1.82 and significantly different from zero (Wilcoxon signed-rank test, $z = 2.46$, $p = 0.01$). Further, for each participant we compute CI in the left striatal cluster and based on affective ratings, and found that the neural CI is positively correlated with behavioral CI with Pearson correlation coefficient 0.4 see **Figure 4**. The OLS regression of neural CI against behavioral CI gives a significant positive coefficient 0.94 ($p = 0.08$). The robust regression of neural CI vs. behavioral CI, that weights away outliers and leverage points, gives very similar results to OLS regression with coefficient on behavioral CI of 0.92 ($p = 0.03$). However, this result is not robust to entirely removing the two extreme points from the right or two extreme outliers (see **Figure 4**) from the OLS regression.

NEURAL TREATMENT EFFECTS

The previous analysis focused on the regions of interest involved in the counterfactual comparisons in all conditions. However, some

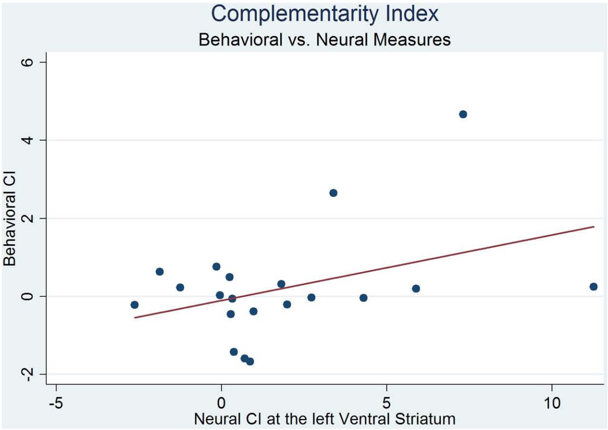

FIGURE 4 | BOLD data in the left ventral striatum exhibit positive interaction, or complementarity between responsibility and environment factors as measured by complementarity index CI = 1.82 (Wilcoxon signed-rank test, $z = 2.46$, $p = 0.01$), see Eq. 3 for definition of CI. The Figure shows that neural CI (*x*-axis) predicts behavioral CI (*y*-axis).

brain regions may be involved selectively only in some treatments, or may deviate from baseline in the opposite directions in different treatments. To account for these possibilities we use model design differentiating between private vs. social environment in order to identify the regions of interest involved. We performed the whole-brain analysis looking at the contrast between social less private advantage, while controlling for payoffs (all being linear predictors). In terms of MMR model we are looking for brain regions in which $G^1 - G^0 \neq 0$. At the threshold $p < 0.005$ (uncorrected) and cluster size 50 voxels we find increased activity in right striatum (left striatal cluster is slightly above threshold), superior frontal gyrus (SFG), and right dorsolateral prefrontal cortex (right DLPFC) among other regions. Confirming above findings the ROI analysis of right striatal cluster reveals that the coefficients on private $G^0 = 0.1$ (Wilcoxon signed-rank test, $z = 3.6$, $p < 0.001$) and social advantage $G^1 = 0.21$ (Wilcoxon signed-rank test, $z = 3.85$, $p < 0.001$) are positive and significantly different from 0. In addition, the difference between coefficients on social less private advantage $G^1 - G^0$ is positive and significantly greater than 0 (Wilcoxon signed-rank test, $z = 3.3$, $p < 0.001$). In the ROI analysis we computed for each participant a gloating index $(G^1 - G^0)/(G^0 + G^1)$ in the right striatal cluster and separately a behavioral one based on affective ratings. Using robust regression we found behavioral gloating index to be predicted by its neural counterpart individual by individual: a constant -0.21 ($p = 0.07$) and a coefficient 0.22 ($p = 0.01$). As caution is necessary when using robust regression, we find positive correlation of neural and behavioral gloating indices at individual level to strengthen the finding of social comparison effect at aggregate level documented above. In addition to right striatum we found also SFG and right DLPFC to exhibit increased activity at the contrast between social less private advantage, while controlling for payoffs. However, in contrast to right striatum neither SFG nor right DLPFC was identified to be part of universal network for counterfactuals. The ROI analysis reveals that both SFG and right DLPFC show positive linear response only to social advantage. In case of SFG the coefficients on private advantage $G^0 = -0.06$ (Wilcoxon signed-rank test, $z = -1.8$, $p = 0.07$) and social advantage $G^1 = 0.1$ (Wilcoxon signed-rank test, $z = 2.3$, $p = 0.02$) are significantly different from zero, but have opposite signs. The last fact explains why we did not detect SFG to be part of the universal network for counterfactuals. The difference between coefficients on social less private advantage $G^1 - G^0$ in SFG is positive and significant (Wilcoxon signed-rank test, $z = 3.36$, $p < 0.001$). ROI analysis of right DLPFC exhibits similar pattern. The similar exercise along chance vs. personal responsibility dimension has not led to identification of other regions than those already found in the universal network for counterfactuals.

LOSER AND WINNER EFFECT

There exists a possibility that, rather than being more linearly responsive to advantage in social than in private environment, the brain regions are only more responsive to a win or a loss in social than in private environment, no matter how large the advantage is. In our experiment the variable advantage varied from -22 through $+21$, with 34 intermediate discrete values, and contiguous values in the interval from -11 to 11. Given this variability in advantage we are able to run robustness check of the above findings by considering the model design with both linear and dummy predictors of interest. In addition to linear predictors in payoff, private, and social advantage we include dummy predictors: social win (equal to 1 if social advantage is strictly larger than 0, and equal to 0 otherwise), and similarly defined variables social loss, private win, and private loss.

The ROI analysis in the clusters of right stratum, SFG, and right DLPFC, identified above shows that greater positive linear response to social than private advantage in these regions is robust to private/social win/loss effects. The difference in coefficients on linear predictors of social less private advantage $G^1 - G^0$ was positive and significant in all three regions: right striatum (Wilcoxon signed-rank test, $z = 2.9$, $p = 0.004$), SFG (Wilcoxon signed-rank test, $z = 1.8$, $p = 0.07$), and right DLPFC (Wilcoxon signed-rank test, $z = 2.2$, $p = 0.03$). Further, we looked at contrasts between dummy predictors. In the whole-brain analysis in the contrast social loss vs. private loss we found increased activity in anterior insula bilaterally, see **Figure 2B**. The ROI analysis of left insula cluster reveals a percentage BOLD change only to social loss to be positive and significantly different from zero (Wilcoxon signed-rank test, $z = 3.3$, $p < 0.001$), while in cases of private loss, private win, and social win we fail to reject the hypothesis that percentage BOLD change is zero (Wilcoxon signed-rank test, $p > 0.6$), see **Figure 5**.

GETTING AHEAD OF THE JONESES

Until now we presented behavioral and neural evidence that counterfactual comparisons matter in *ex post* evaluations of choice outcomes. They are stronger in social than private environment and with personal than chance responsibility. We predict similar results during the *ex ante* evaluations of choice alternatives, that is, in the process leading to choice. In the analysis of *ex post* evaluations we considered two factors: environment (private vs. social)

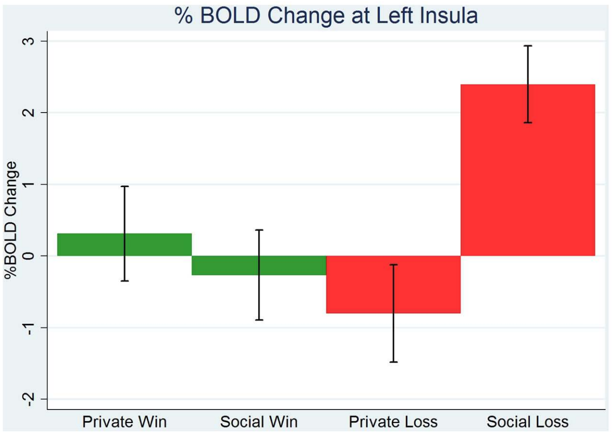

FIGURE 5 | Region-of-interest analysis of left anterior insula shows increased activity only to social loss (equal to 1 if advantage is strictly less than 0 in social environment, and equal to 0 otherwise), and around zero or slightly negative activity in cases of social win or private win/loss.

and responsibility (chance vs. personal). In contrast, in the analysis of *ex ante* evaluations of choice alternatives we considered environment factor only. In the beginning of a trial subjects learned whether they are in private or social environment but not whether the trial involves chance or personal responsibility. The analysis of the *ex ante* evaluations of choice alternatives, two binary lotteries in our case, is complicated by the fact that outcomes of lotteries are risky at the evaluation stage. In the previous analysis we assumed for simplicity that relative utility in MMR model is linear. However, under the linearity assumption MMR model applied to *ex ante* evaluations is equivalent to expected utility model, meaning that both models generate the same choices and counterfactual comparisons do not matter for choice behavior. Therefore, it is necessary to adjust risk attitudes of subjects in the *ex ante* analysis. Our empirical strategy is to consider risk-adjusted return as a variable of interest. Recall that each choice situation in our study involved two binary lotteries with similar expected values, low-risk vs. high-risk one. We focus on the question how the choice of high-risk lottery depended on its risk-adjusted return. We define risk-adjusted return as expected value of lottery divided by SD. The view that risk-adjusted return drives decisions has been supported in the literature (Weber and Johnson, 2009), which justifies our approach.

We first examine behavioral data with logit regression aiming to explain the choice of high-risk rather than low-risk lottery with risk-adjusted return of high-risk lottery in private vs. social environment. Borrowing intuition from finance one can interpret the regression coefficient on risk-adjusted return as the subjective value of risk. We run logit regression subject by subject obtaining the average subjective value of risk to be 0.14 (SEM 0.22) in private and 0.68 (SEM 0.2) in social environments. The former is not significantly different from 0 (Wilcoxon signed-rank test, $z = 0.3$, $p = 0.79$), while the latter is positive and significantly different from zero (Wilcoxon signed-rank test, $z = 2.9$, $p = 0.004$). The subjective value of risk is significantly larger in social than in private environment (Wilcoxon signed-rank test, $z = 2.4$, $p = 0.02$). This may suggest that subjects choose more often high-risk lotteries in social than in private environment. However, high-risk lotteries are not all the same. Focusing on high-risk lotteries we can consider those with below and above median risk, namely the median of SD of high-risk lottery in the pair of lotteries presented to subjects. The median value was $6.58. High-risk lotteries with below median risk are chosen with lower frequency in social (47%) than in private (52%) environment. The reverse pattern holds for high-risk lotteries with above median risk as subjects choose the high-risk lotteries with higher frequency in social (42%) than in private (38%) environment. A Wilcoxon signed-rank test shows that the first difference is not significant ($z = 1.01$ and $p > 0.1$, while the latter is significant ($z = -2.02$, $p = 0.04$).

This analysis suggests that subjects adjust their decisions in social as compared to private environment in order to get ahead of others. Our findings are consistent with the literature on experience based tasks showing social exposure to increase risk-taking (Yechiam et al., 2008).

Guided by the behavioral results we performed analogical analysis of neural data at the decision stage. Given our interest in reward system, and especially in ventral striatum, our use of risk-adjusted return as predictor in neural analysis can be justified by the finding that ventral striatum tracks both expected reward and variance (Preuschoff et al., 2006). We first consider the model design with linear predictor in risk-adjusted return, without distinction between private and social environments. In the contrast of risk-adjusted return against the baseline, with threshold $p < 0.005$ uncorrected, we found increased activity in ventral striatum bilaterally and decreased activity in OFC (see **Table 2**). In the ROI analysis of the left cluster of ventral striatum we looked at the linear response to risk-adjusted return in private vs. social environment. In both cases the coefficients were positive and significantly different from 0: private coefficient 0.04 (SEM 0.032, Wilcoxon signed-rank test, $z = 1.75$, $p = 0.08$) and social coefficient 0.14 (SEM 0.025, Wilcoxon signed-rank test, $z = 3.5$, $p < 0.001$). Crucially, the difference between the coefficients in social vs. private environment was positive and highly significant (Wilcoxon signed-rank test, $z = 3.1$, $p = 0.002$). The similar results apply to right cluster of ventral striatum. As for OFC the analogical ROI analysis revealed that the coefficients on risk-adjusted return were negative and significant with private coefficient −0.17 (SEM 0.12, Wilcoxon signed-rank test, $z = -3.6$, $p < 0.001$) and social coefficient −0.05 (SEM 0.11, Wilcoxon signed-rank test, $z = -3.1$, $p = 0.04$). The difference between social and private coefficients was positive and significant (Wilcoxon signed-rank test, $z = 2.4$, $p = 0.02$). Subsequently, we considered the model design with linear predictors in risk-adjusted return, both in private and social environments. Looking at the contrast social less private risk-adjusted return with threshold $p < 0.005$ uncorrected we found increased activity in striatum bilaterally and OFC as above. In addition we found also increased activity in anterior cingulate cortex (ACC) and right dorsolateral-cortex (rDLPFC) among other regions. The ROI analysis shows that BOLD activity is decreasing in risk-adjusted return in ACC and rDLPFC in private environment.

The coefficients on private risk-adjusted return are negative and significant, with coefficient in ACC equal to −0.1 (SEM 0.04, Wilcoxon signed-rank test, $z = -2.2$, $p = 0.03$). The coefficient in rDLPFC was −0.07 (SEM 0.04, Wilcoxon signed-rank test, $z = -1.5$, $p = 0.13$). In contrast coefficients on social risk-adjusted return are positive and significant with coefficient in ACC 0.07 (SEM 0.03, Wilcoxon signed-rank test, $z = 1.8$, $p = 0.08$) and the coefficient in rDLPFC 0.08 (SEM 0.03, Wilcoxon signed-rank test, $z = 2.9$, $p = 0.004$).

CONCLUSION

Our results put social comparison in new light and strengthen existing findings. We document as in existing literature a crucial role of ventral striatum, a part of brain reward system, in social comparisons. Focusing on outcome evaluation stage we showed that social emotions like envy and pride are stronger than corresponding private emotions like regret and rejoice as measured by ventral striatum responses. First, this confirms Veblen's view of envy and pride as reflecting differences in social status. Second, this is important finding as other studies established social comparison effect in ventral striatum only against the baseline (Fliessbach et al., 2007; Dvash et al., 2010), without reference to any other alternative comparison process, i.e., counterfactual comparison (Camille et al., 2004; Coricelli et al., 2005). More, social comparison in ventral striatum is stronger in case of personal than chance responsibility for outcomes, which amounts to positive interaction of social environment and personal responsibility. We favor interpretation that difference between personal and chance responsibility for outcomes is about how much can be inferred about skill vs. luck of decision-maker during comparison process. Given this interpretation, positive interaction of social environment and personal responsibility confirms Festinger's view of envy and pride as helping people to learn skills from others. We show that larger linear response in social than in private environment to difference in outcomes is robust to winner/loser effect. At the same time we find social loser effect in anterior insula, a region associated with negative emotions. Interestingly, we did not find for this region similar loser effect in private environment or winner effects in either environment. Nor we found differential linear response in private vs. social environment. This suggests that the very social loss, no matter how large evokes strong negative emotion. These findings fit well with increased activity in anterior insula predicting rejections of unfair offers (worse than 50:50) in ultimatum game (Sanfey et al., 2003). We find also increased activity in areas related to Theory of Mind reasoning in social vs. private environment. At decision stage we observe *getting ahead of the Joneses* effect with subjective value of risk as measured by activity in ventral striatum being larger in social than in private environment. Not surprisingly subjects assume extreme risk more often in social than in private environment. One another interesting aspect of brain response to risk-adjusted return at decision stage is increased activity in rDLPFC and ACC in social vs. private environment. Both regions were shown previously to exhibit increased activity the higher the decision conflict present (MacDonald et al., 2000). In this light one interpretation of our results would be that the subjects have decision conflict in social environment whether to assume extreme risk and possibly *get ahead of others* or keep taking reasonable risks only.

Further research on social comparisons is needed to understand it better. It may have far reaching consequences as social comparison affects utility function, a central concept in economics. A direction of future research would be to focus on decision stage and investigate idiosyncratic as compared to systematic risk in private vs. social environment. Another interesting direction of research to pursue is the relationship between temporal discounting and social comparison, topics that independently received considerable attention in neuroeconomics. Motivated by personal responsibility effect in our study the hypothesis is that patient individuals are more envious and proud if differences in relative outcomes are mainly due to different skills. The intuition is that patient individuals would weigh more the future differences in relative outcomes. Yet another intriguing question is the relationship between social comparisons in different domains: me-vs.-others as compared to among others. One possibility is that the more envious and proud individual the higher is his preference for equality among others, for this increases chances he is in better situation than anyone else.

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APPENDIX

In the section on the universal network for counterfactuals we focus on reporting results concerning the left ventral striatum. However, the results concerning the right ventral striatum are very similar, and we omitted them in the main text in order not to flood the reader with too many statistics, which we report here in the Appendix. The cluster of right ventral striatum identified as a part of the universal network for counterfactuals included 66 voxels at $p < 0.01$ (Bonferroni corrected). The coefficients on private ($G^0 = 0.61$ with $z = 5.68$, $p < 0.001$) and social advantage (coefficient $G^1 = 1.08$ with $z = 10.56$, $p < 0.001$) are positive and statistically significant. The difference in coefficients on social less private advantage is also positive and statistically significant (two-sided Wald test, $\chi^2 = 11.61$, $p < 0.001$). The analysis for responsibility factor shows the coefficients on chance advantage (coefficient 0.73, $z = 6.79$, $p < 0.001$) and personal advantage (coefficient 0.97 with $z = 9.46$, $p < 0.001$) to be positive and statistically significant, with the difference between the latter and the former positive and statistically significant (two-sided Wald test, $\chi^2 = 2.86$, $p = 0.09$).

As we did for the left ventral striatum in the main text to exclude the possibility that correlation of payoff and advantage drives the results we consider the model designs with advantage normalized to mean 0 and SD 1, without controlling for payoffs.

Considering environment factor we find that coefficients on normalized private (coefficient 3.39, Wilcoxon signed-rank test, $z = 3.14$, $p = 0.002$) and social advantage (coefficient 6.47, Wilcoxon signed-rank test, $z = 3.92$, $p < 0.001$) are positive and statistically significant. The difference between the latter and the former is also positive and significant (Wilcoxon signed-rank test, $z = 2.54$, $p = 0.01$). Switching to responsibility factor we observe that coefficients on normalized chance (coefficient 3.61, Wilcoxon signed-rank test, $z = 3.25$, $p = 0.001$) and personal advantage (coefficient 6.52, Wilcoxon signed-rank test, $z = 3.70$, $p < 0.001$) are positive and significantly different from 0. The difference between coefficients on personal less chance normalized advantage is positive but not significant as in the left ventral striatum (Wilcoxon signed-rank test, $z = 1.38$, $p = 0.17$). The nonparametric analysis of normalized advantage, without controlling for payoff, in principle confirms the results obtained in panel analysis when we controlled for payoffs.

To investigate the interaction between the two factors, environment and responsibility, we consider the disaggregated model design with all four treatments. We estimated neural CI (Eq. 3) in right ventral striatum cluster to be 2.12 and significantly different from zero (Wilcoxon signed-rank test, $z = 1.98$, $p = 0.05$). Further, for each participant we compute CI in the right striatal cluster and based on affective ratings, and found that the neural CI is positively correlated with behavioral CI (Pearson correlation coefficient is 0.22). The OLS regression of neural CI against behavioral CI gives positive coefficient 0.78 but not significant ($p = 0.36$). In the analogical robust regression the coefficient is 0.75 ($p = 0.17$), also not being significant. In contrast at the left ventral striatum the analogical coefficients were significant in both regressions.

Table A1 | Lotteries used in the experiment.

Pair number	Lottery $X = (X_1, p, X_2)$			Lottery $Y = (Y_1, q, Y_2)$		
	X_1	$p = \text{Prob}(X_1)$	X_2	Y_1	$q = \text{Prob}(Y_1)$	Y_2
1	−5	0.25	0	−1	0.50	−1
2	−4	0.67	1	−2	0.50	−2
3	4	0.33	−4	−3	0.25	0
4	4	0.33	−4	−2	0.33	0
5	12	0.25	−5	1	0.50	1
6	10	0.25	−4	1	0.50	1
7	9	0.33	−5	0	0.50	1
8	8	0.25	−3	0	0.75	2
9	18	0.50	−4	9	0.67	5
10	17	0.50	−3	8	0.67	6
11	10	0.25	−1	3	0.75	1
12	12	0.33	−2	4	0.83	2
13	16	0.25	−4	2	0.50	2
14	15	0.33	−5	2	0.50	2
15	24	0.33	3	12	0.67	6
16	25	0.33	2	10	0.75	8
17	22	0.14	3	7	0.67	7
18	24	0.17	4	8	0.75	8
19	13	0.25	2	6	0.75	2
20	12	0.33	1	7	0.67	1

There are two lotteries in each choice: $X = (X_1, p, X_2)$ and $Y = (Y_1, q, Y_2)$, where in the lottery X the prize X_1 realizes with probability p and the prize X_2 realizes with probability $(1 - p)$, with similar notation applying to the lottery Y. The lottery pairs with odd numbers are distinct. The lottery pairs with even numbers are slightly perturbed ones relative to the preceding odd-number pairs. We used these pairs of lotteries in all treatments, with exception of the treatment (private, chance), where odd numbered pairs were used only. No pair was repeated within a treatment.

Table A2 | Areas in universal network for counterfactuals.

ROIs	Average coordinates			Size
	x	*y*	*z*	
Superior temporal gyrus	59	−7	−1	858
Inferior parietal lobule	55	−30	31	53
Culmen	44	−36	−26	211
Pyramis	41	−68	−32	142
Superior temporal gyrus	37	−1	−16	61
Medial frontal gyrus	21	30	26	152
Medial frontal gyrus	17	−44	15	56
Anterior cingulate	−1	42	−2	1559
Subcallosal gyrus	−4	23	−12	150
Middle frontal gyrus	−30	27	45	433
Middle temporal gyrus	−33	−57	16	140
Middle temporal gyrus	−35	−49	9	56
Middle frontal gyrus	−39	52	6	161
Inferior frontal gyrus	−48	39	−2	70

The regions of interest in the universal network for counterfactuals identified in the contrast of advantage against the baseline at comparison event. The threshold is $p < 0.02$ FDR corrected.

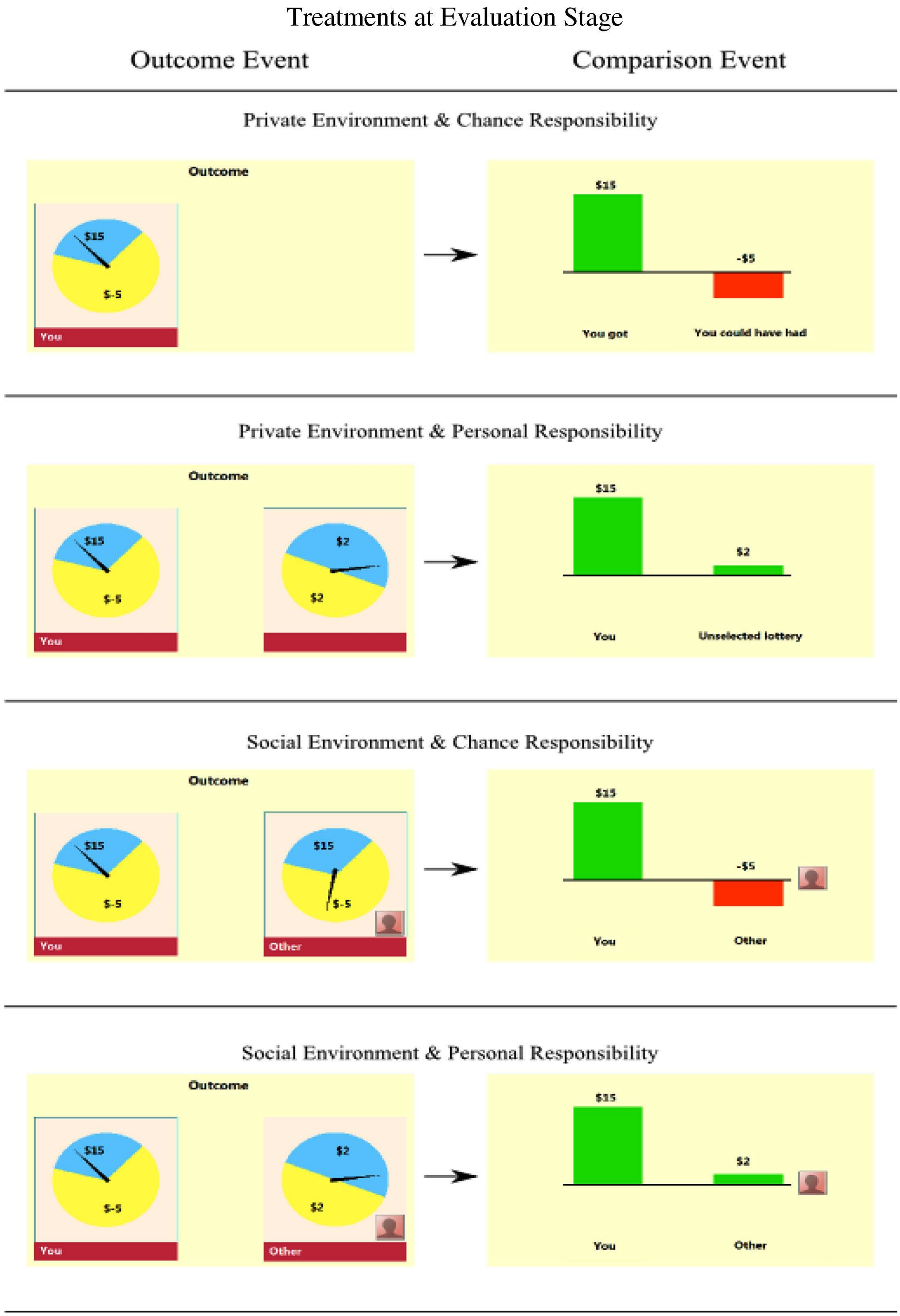

FIGURE A1 | Treatments at evaluation stage as displayed to subjects. First outcome event is presented and then followed with comparison event.

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Is your error my concern? An event-related potential study on own and observed error detection in cooperation and competition

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Electroencephalogram studies have identified an error-related event-related potential (ERP) component known as the error-related negativity or ERN, thought to result from the detection of a loss of reward during performance monitoring. However, as own errors are always associated with a loss of reward, disentangling whether the ERN is error- or reward-dependent has proven to be a difficult endeavor. Recently, an ERN has also been demonstrated following the observation of other's errors. Importantly, other people's errors can be associated with loss or gain depending on the cooperative or competitive context in which they are made. The aim of the current ERP study was to disentangle the error- or reward-dependency of performance monitoring. Twelve pairs ($N = 24$) of participants performed and observed a speeded-choice-reaction task in two contexts. Own errors were always associated with a loss of reward. Observed errors in the cooperative context also yielded a loss of reward, but observed errors in the competitive context resulted in a gain. The results showed that the ERN was present following all types of errors independent of who made the error and the outcome of the action. Consequently, the current study demonstrates that performance monitoring as reflected by the ERN is error-specific and not directly dependent on reward.

Keywords: performance monitoring, response ERN, observed ERN, cooperation, competition, reward

INTRODUCTION

Human behavior is prone to errors. We slip, trip, push incorrect buttons, and drop things on a regular basis. Fortunately, people are in general able to detect these errors in a fast and efficient manner. This fast error detection process is enabled by a continuous monitoring of our performance and thus importantly facilitates goal-directed behavior. Electroencephalogram (EEG) studies have identified an event-related potential (ERP) component immediately following own errors known as the error-related negativity or ERN (Falkenstein et al., 1990; Gehring et al., 1993). The ERN is elicited 50–70 ms following an erroneous button press and is thought to originate from areas in posterior medial frontal cortex (pMFC), including anterior cingulate cortex (ACC) and pre-supplementary motor area (pre-SMA; Holroyd et al., 2004; Ridderinkhof et al., 2004; De Bruijn et al., 2009). Research and theories on the ERN and performance monitoring have proposed a close link between error and reward processing. The goal of the current study is to disentangle the error- or reward-dependency of performance monitoring using ERPs.

One of the most influential theories on the ERN in performance monitoring is the reinforcement learning (RL) theory proposed by Holroyd and Coles (2002). The ERN can be elicited immediately following response onset, the so-called response ERN or rERN or following negative feedback, the so-called feedback related negativity or FRN. The RL theory proposes that depending on the knowledge available to the system, the ERN is elicited at the first moment in time the error can be detected. Importantly, this theory proposes a direct relation between performance monitoring or error detection and reward processing. In short, the RL theory states that whenever an error is made, the outcome of an action turns out to be worse than expected, resulting in a loss of reward and hence eliciting the ERN. However, as own errors are always negative events associated with some loss of reward, disentangling whether the ERN is error- or reward-dependent has proven to be an extremely difficult endeavor.

Humans are social animals and for a large part of the day involved in some form of social interaction. Experience teaches us that people are not only able to detect their own errors, but that they are also extremely skilled in detecting other people's mistakes. However, for long, research focused on performance monitoring in individual settings, thus only reporting findings on monitoring of our own performance.

More recently, performance monitoring research has expanded into more social settings and an ERN, the so-called observed ERN (oERN) has also been demonstrated following the observation of other's errors (Miltner et al., 2004; van Schie et al., 2004; Bates et al., 2005). These initial ERP studies suggested that similar neural processes are responsible for the detection of one's own errors as well as the detection of other's errors. This assumption was later confirmed in fMRI studies showing that indeed overlapping areas in pMFC were stronger activated for own and observed errors in comparison to correct performance and observations (Shane et al., 2008; De Bruijn et al., 2009).

Importantly, depending on whether the observed errors are made in cooperative or competitive contexts they are associated with loss or gain for the observer, respectively. Thus, we realized that by using the overlapping mechanisms for observed and own error detection we had a method to disentangle the error- or reward-dependency of performance monitoring. For this aim, we recently conducted an fMRI study in which we directly compared monitoring of own and other's performance in both a cooperative and a competitive setting (De Bruijn et al., 2009). As in real-life, own errors were associated with a loss of money in both settings, while observed errors also resulted in a loss of money in the cooperative setting, but led to a monetary gain in the competitive context. The results from this study demonstrated that the areas in pMFC involved in detecting own errors were similarly involved in detecting other's errors independent of the award associated with the cooperative or competitive context, thus demonstrating the error-specificity of these areas. On the other hand, areas known to be involved in reward processing, like ventral striatum, were sensitive to the nature of the context and responded in a reward-specific manner.

Although some recent studies have investigated ERP correlates of observed performance monitoring in cooperative and competitive contexts, the focus so far has mainly been on the FRN elicited by negative feedback. Two recent studies demonstrated increased FRN amplitudes in a cooperative compared to a competitive setting, suggesting that the FRN in these tasks were more sensitive to the loss of reward associated with the outcome (Itagaki and Katayama, 2008; Marco-Pallares et al., 2010). Importantly, however, a focus on the FRN has some consequences for the analyses and the choice of paradigm. First of all, unlike the response-locked oERN, it is difficult to fully dissociate between the FRN and the following stimulus-locked P300 ERP component as both are involved in processing unexpected, but task-relevant events (see, e.g., Hajcak et al., 2005). This is especially the case when the FRN is analyzed at a more central electrode like Cz. Second, the focus on the FRN has important consequences for the paradigms used. Speeded-choice-reaction tasks are mainly used in rERN and oERN tasks to elicit a reasonable amount of errors. Studies aimed at investigating the FRN, however, usually employ gambling tasks in which participants have little or no control over the correctness of their responses and thus need to fully rely on the feedback information. So although it is generally assumed that the FRN and ERN are reflections of the same performance monitoring process (see, e.g., Holroyd et al., 2004; Mars et al., 2005), important differences in quantification and experimental design exist that may importantly affect the exact outcomes of these observed error studies.

To our knowledge, only one recent study did investigate observed errors relative to the moment of the actor's response in a cooperative and competitive context. The results from this go/no-go study by Koban et al. (2010) were more in line with our recent fMRI findings, by demonstrating an oERN of similar amplitude for observed errors in both contexts. The study did demonstrate a latency difference, with the oERN peaking later in the competitive setting. However, when directly comparing the ERP waveforms from the original observed error monitoring study by van Schie et al. (2004) and those in the study by Koban et al. large differences become apparent. Importantly, the waveforms in the Koban et al. may alternatively be interpreted as resembling stimulus-locked ERPs more than response-locked ERPs. These differences in ERP waveforms raise the question whether the exact same processes are investigated in the two paradigms.

In the observed Flanker paradigm in the van Schie et al. (2004) study participants were seated facing each other and observed the actor's actual thumb movements, which were taken as the moment of response onset. In the Koban et al. (2010) study, participants were seated next to each other, looking at a computer screen and inferred the correctness of the actor's response on the basis of a visual stimulus presented on the screen (i.e., a black frame appearing around the target stimulus indicating that a response had been given). So although ERPs were in theory time-locked to the moment of the actor's response, this time-point was visualized for the observer by the presentation of a stimulus. The observer thus had to process this abstract visual stimulus and then infer the correctness of the given response. It is plausible that this explains why the ERP waveforms from the observation condition in the Koban et al. study differ from the initial oERN study by van Schie et al. as the presentation and subsequent processing of the visual stimulus may result in a stimulus-locked ERP pattern. Consequently, it is rather difficult to determine whether the negativities analyzed in the Koban et al. paper are superimposed on response-locked or stimulus/feedback-locked error-related ERPs.

An important explanation for the presence of the oERN in the van Schie et al. (2004) study was based on sub-threshold simulation of the goal movement and comparing this to the actual observed movement. This was supported by dedicated analyses investigating the relative activation of the left or right motor cortex during observation. These so-called lateralized readiness potential (LRP) analyses demonstrated covert lateralized activation of the motor cortex. In other words, while observing, participants activated the correct response at a sub-threshold level even before the actor started responding and thus generated a representation of the appropriate response following stimulus presentation. However, when they subsequently observed an error from the actor this initial correct activation was inhibited and the observers showed increased activation of the incorrect response. So, following the response of the other participant, the observer's motor system was differentially activated as a function of the accuracy of the observed response. This covert motor simulation may thus play a central role in the mechanisms underlying observed error detection. Another advantage of the setup by van Schie et al. was that it represented a situation which was more comparable to real-life performance monitoring in a social context, as the relation between the observed erroneous movement and the process of performance monitoring was very direct. This relation was more indirect in the Koban et al. (2010) study, as the error detection process was mediated by the presentation of a more abstract visual stimulus. As a result, the motor simulation processes underlying observed performance monitoring might have been weakened in the later study. In our view, the existing differences in paradigms used and the processes involved as well as the forthcoming uncertainties importantly warrant investigating the error- or reward-dependency of the ERN using the observed flankers paradigm.

The aim of the current study was to disentangle the error- or reward-dependency of performance monitoring using ERPs. This was achieved by investigating the ERN following own and observed errors in a cooperative and competitive context using the observed Flankers paradigm. Based on our previous fMRI study (De Bruijn et al., 2009) and the results by Koban et al. (2010) we expected to find similar rERN and oERN amplitudes in both contexts, reflecting the error-dependency of this ERP component.

MATERIALS AND METHODS

PARTICIPANTS

Twelve pairs of participants ($N = 24$; 14 women; mean age = 23.1 years, SD = 2.9) participated in the experiment. All subjects were healthy volunteers recruited on the campus of the Radboud University in Nijmegen, the Netherlands and were either paid or awarded course credits for participation. All participants gave their informed consent after the nature of the study had been fully explained to them. The study was carried out in accordance with the latest version of the Helsinki Declaration and was approved by the local ethics committee of the university.

DESIGN AND PROCEDURE

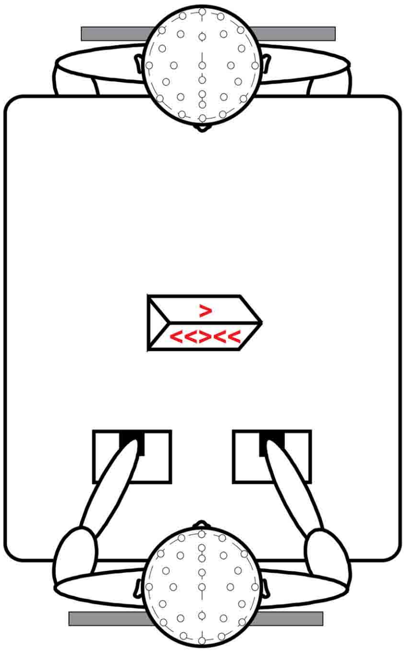
The experimental setup can be seen in the left panel of **Figure 1**. Two participants were scheduled for one meeting and randomly assigned to start the task as an actor or observer. They were seated face-to-face at a table. In the middle of the table, between the two participants, a wooden box with a LED display was placed. The actor responded with joystick movements in one horizontal axis. The stick had a central position and moved back to this position when the force was removed. The joysticks were positioned, such that (1) the actor could easily reach the sticks with his/her thumbs and that (2) the observer was able to see the joysticks and thumbs well. On the actors' side of the LED display, arrow stimuli from a modified Flankers task were presented (Eriksen and Eriksen, 1974). On the observers' side of the display, only the target arrow was presented, indicating which joystick had to be moved.

Stimulus presentation was controlled with Presentation software (Neurobehavioral Systems). Each trial began with the presentation of a fixation circle (300 ms), followed by an empty display (300 ms). Next, the stimulus was presented for 300 ms. All stimuli consisted of five arrows. The central target arrow indicated the goal direction of the actor's movement. The two flanking arrows on each side could either be congruent or incongruent with the target. Following the stimulus, an empty display was presented for 900 ms.

Actors were instructed to touch the two joysticks with their thumbs and respond to the target arrow as fast as possible. When the central arrow on the display pointed to the right, they had to press the right stick with their right thumb to the right. Analogously, they were required to press the left stick with their left thumb to the left, when the central arrow pointed to the left.

Observers were instructed to count the errors made by the actor (see van Schie et al., 2004). They were told that the initial response counted and that any corrective behavior of an error was invalid. They were asked to keep the amount of errors in mind and write it down during the break between the blocks. After the first condition, a break was held, and participants switched their tasks.

The task was performed in both a cooperative and a competitive context. The order of these two contexts was counterbalanced between pairs. Participants started the cooperative context with



Pay-off matrix

	Cooperation	Competition
Own errors	- $$	- $$
Observed errors	- $$	+ $$

FIGURE 1 | Setup of the observed Flankers task. Participants both performed and observed 600 trials in a cooperative and in a competitive context. Own errors were always associated with a loss of money. Observed errors in the cooperative context also resulted in a loss of reward, but observed errors in the competitive context resulted in a gain.

a shared bonus of 10 Euros, but for each error 10 cents were deducted from this bonus, irrespective of whether a participant made the error or whether they observed their partner make an error (see **Figure 1**, right panel and De Bruijn et al., 2009). In the competitive context each participant started out with an individual bonus of five Euros. Again 10 cents were deducted when they made an error themselves, but they would gain 10 cents when their opponent made an error.

Participants performed and observed six blocks of 100 trials in each context. As a result, the entire experiment consisted of 2400 experimental trials and 160 test trials (40 before each new condition). Congruent and incongruent stimuli were presented in a random order and equally distributed in each block (each stimulus type was presented 150 times in each context). After each block, there was a break of approximately 1 min.

DATA ACQUISITION AND ANALYSES

The EEG was recorded from the two participants using 27 tin electrodes mounted in an elastic electrode cap (Electrocap International). Electrodes were placed at 7 midline (FPz/AFz/Fz/FCz/Cz/Pz/Oz) and 20 lateral (FP1–2/F7–8/F3–4/FC5–6/T3–4/C3–4/CP5–6/T5–6/P3–4/O1–2) locations in accordance with an extension of the international 10–20 system. All signals were referenced to the left mastoid, but later re-referenced to the average of both mastoids. The vertical electro-oculogram (EOG) was recorded bipolarly from electrodes placed above and below the right eye. The horizontal EOG was also recorded bipolarly from electrodes lateral to both eyes. All electrode impedances were kept below 5 kΩ. The EEG and EOG signals were amplified using a time constant of 8 s (high pass 0.02 Hz) and were filtered off-line with a bandpass of 1–14 Hz. All signals were digitized with a sampling rate of 500 Hz.

Trials with response times faster than 150 ms were excluded from all analyses (1.5%). For the behavioral analyses, we analyzed performance and response times of the actors by entering individual mean error rates and reaction times in a repeated measures general linear model (GLM) with Context (cooperative vs. competitive), Congruency (congruent vs. incongruent), and Correctness (correct vs. incorrect) as possible within-subject factors.

Before averaging EEG signals to ERPs, error and correct trials were matched for reaction times (±4 ms; see van Schie et al., 2004) to control for possible differential effects of the stimulus-locked ERP components. Eye movements were corrected using the procedure described by Gratton et al. (1983) and averaged to ERPs separately for each subject and each condition, relative to a 100-ms pre-response baseline. Note that a peak measure implies the presence of a negative peak on correct ERP waveforms as well. However, inspection of our individual averages revealed that this was often not the case for both the actor and observer data. Therefore, we conducted ERN analyses in which the ERN was quantified as a mean amplitude measure. Based on the grand averages, we defined the rERN as the mean amplitude of the interval from 0 to 150 ms after response onset and the oERN as the mean amplitude in the 150- to 300-ms time window after the response. Individual rERN and oERN amplitudes were entered into 2×2 repeated measures GLMs with Context (cooperative vs. competitive) and Correctness (correct vs. incorrect) as within-subject factors. Finally, latencies of the rERN and oERN peaks on incorrect responses were analyzed by entering the individual latencies into repeated measures GLMs with Context (cooperative vs. competitive) as within-subject factor.

RESULTS

BEHAVIORAL ANALYSES

As expected, the analyses on error rates demonstrated a main effect of Congruency, indicating increased error rates for incongruent trials (22.2%) than for congruent ones [6.7%; $F(1,23) = 124.08$, $p < 0.001$]. There was neither a main effect of Context present [$F(1,23) = 1.85$, $p = 0.186$], nor a significant interaction between Congruency and Context ($F < 1$).

When investigating reaction times for correct responses only, we found the expected main effect for Congruency, with slower reaction times for responses to incongruent stimuli (352 ms) compared to responses to congruent stimuli [312 ms; $F(1,23) = 97.05$, $p < 0.001$]. Neither the main effect of Context, nor the interaction between the two was significant (both $F\text{s} < 1$). When incorrect responses were also included in the analysis, an additional effect of Correctness was found, reflecting the usually found faster reaction times for erroneous responses (273 ms) compared to correct ones [332 ms; $F(1,23) = 273.37$, $p < 0.001$].

ACTOR ERP ANALYSES (rERN)

The ERP waveforms for the actor in the performance condition are depicted in **Figure 2**. The well-known rERN component is visible following incorrect responses at midline electrodes with the expected frontocentral distribution (**Figure 3**, upper panel) peaking around 70 ms. The peak latencies were not different for the two contexts ($F < 1$).

As expected, the amplitude analyses demonstrated a main effect of Correctness, with more negative amplitudes for incorrect responses (−2.76 μV) compared to correct ones [3.08 μV; $F(1,23) = 75.25$, $p < 0.001$]. Neither the main effect of Context [$F(1,23) = 2.66$, $p = 0.117$], nor the interaction between Correctness and Context ($F < 1$) reached significance, indicating that rERN amplitudes did not differ between the two contexts.

OBSERVER ERP ANALYSES (oERN)

The ERP waveforms for the observer in the observation condition are depicted in **Figure 4**. The oERN component is visible following incorrect responses at the midline electrodes and also shows the typical frontocentral distribution (**Figure 3**, lower panel). The oERN peak latencies did not differ between the two contexts ($F < 1$; cooperative = 232 ms; competitive = 237 ms).

Similar to the rERN outcomes, the amplitude analyses demonstrated a main effect of Correctness, with more negative amplitudes for incorrect responses (−2.75 μV) compared to correct ones [−0.74 μV; $F(1,23) = 43.71$, $p < 0.001$]. Neither the main effect of Context ($F < 1$), nor the interaction between Correctness and Context [$F(1,23) = 2.32$, $p = 0.141$] reached significance, indicating that oERN amplitudes did not differ between the two contexts.

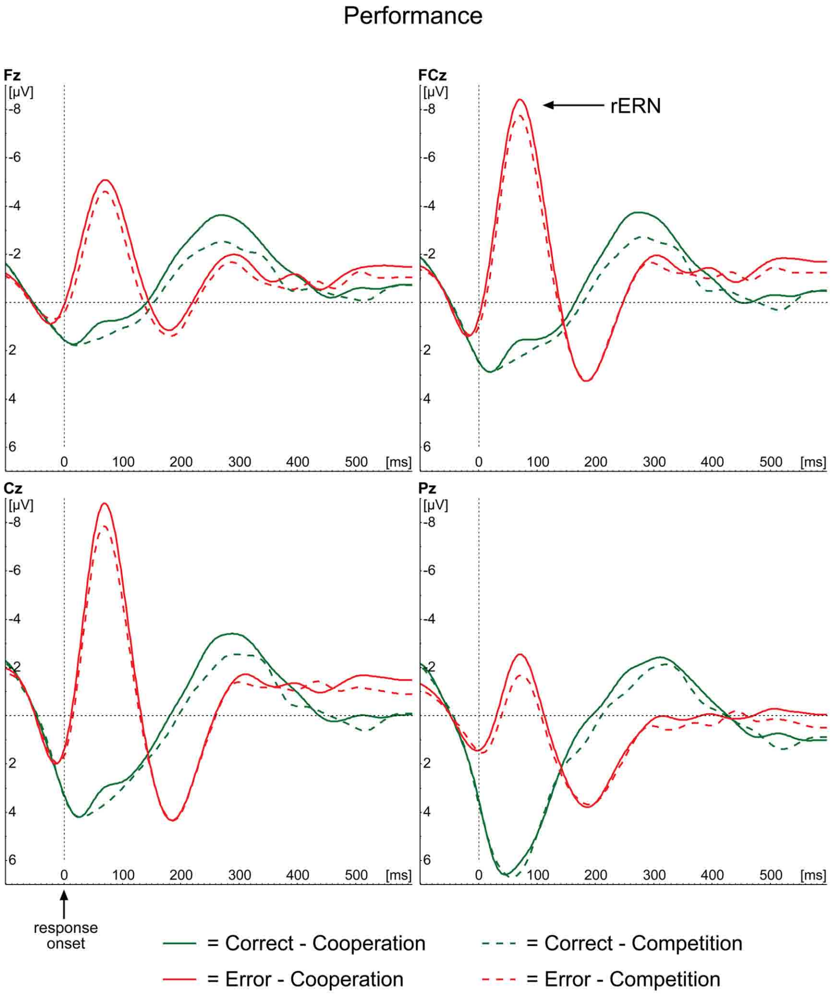


FIGURE 2 | Grand average ERP waveforms for the performance condition, time-locked to the onset of the actor's response for correct (green lines) and incorrect (red lines) responses separately. Midline electrodes Fz, FCz, Cz, and Pz are depicted.

DISCUSSION

The current study aimed at determining the error- or reward-dependency of performance monitoring by examining response-locked own and observed errors in a cooperative and competitive setting. The setup was designed with the aim to resemble real-life interactive behavior, by enabling EEG onsets to be time-locked to the actual actor's movement onset in a direct and comparable manner both for own and observed actions.

The results demonstrated the well-known rERN following own errors in the performance condition. The amplitude and latency of the rERN was comparable for both contexts. Moreover, a clear oERN was present following other's errors in the observe condition. The ERP waveform patterns for the observed actions time-locked to movement onset were very similar to those originally reported by van Schie et al. (2004), thus supporting our assumption that we are currently investigating the same processes and mechanisms. Importantly, the current study showed that the amplitudes and the latencies of the oERN did not differ between the cooperative and competitive context. As the reward-dependency was crucially manipulated for the observed errors (loss vs. gain) in the two contexts, our results are in favor of an error-specific explanation of the ERN. We do not find evidence supporting the reward-specificity of performance monitoring as suggested by the RL theory (Holroyd and Coles, 2002).

Notably, the current outcomes are in line with a previous fMRI study from our lab, which also revealed error-dependent activations in anterior cingulate and pre-SMA for own and observed errors in both contexts (De Bruijn et al., 2009). Previous studies have repeatedly demonstrated the source of the ERN to originate from areas in pMFC, including anterior cingulate (see, e.g., Ridderinkhof et al., 2004; Debener et al., 2005). Reward-dependent activations were found in the previous fMRI study in striatal areas including nucleus accumbens. Please note that, to enable a more direct comparison, the payoff matrix for errors in the two contexts used in the fMRI study was the same as the one currently used. Obviously, it is very well plausible that the reward-related activations are not reflected in the scalp-recorded ERN waveforms. Furthermore, the current results are in line with a recent study by

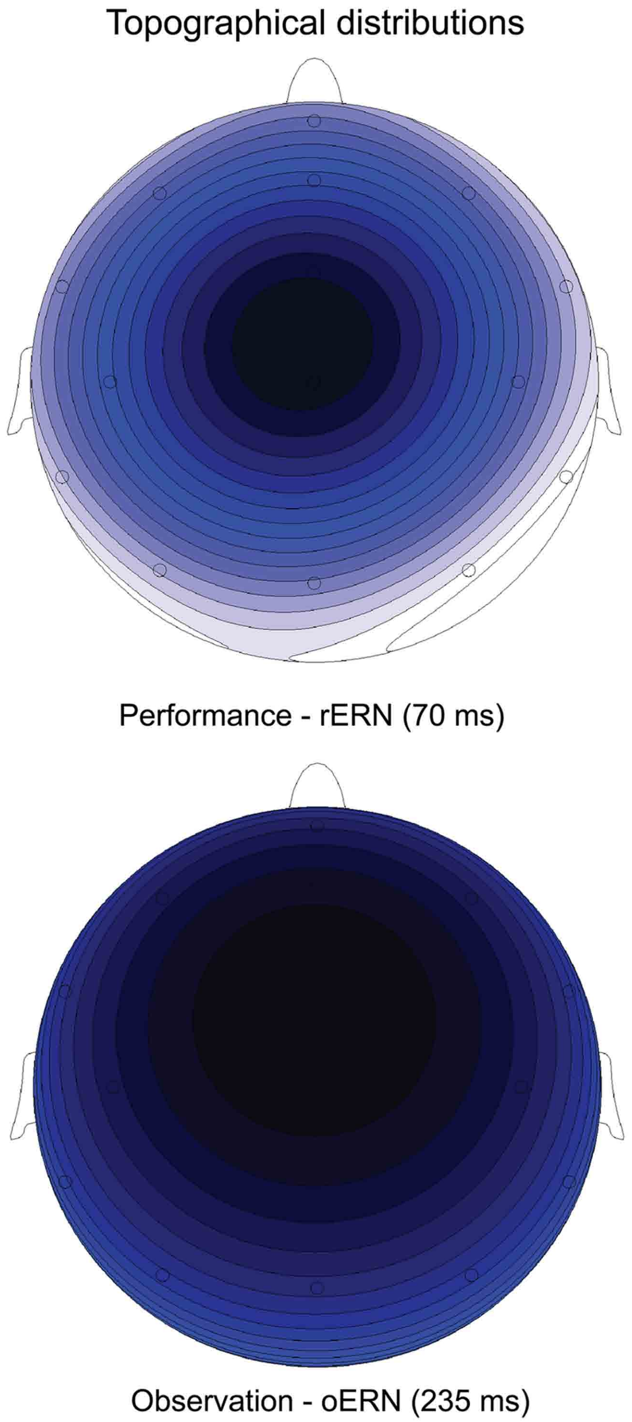


FIGURE 3 | Topographical distribution of the difference waves (incorrect minus correct) showing the expected frontocentral distribution for the rERN at peak onset (70 ms) in the Performance condition (upper panel) and for the oERN at peak onset (235 ms) in the Observation condition (lower panel). Darker colors indicate more negative amplitudes.

Koban et al. (2010), which also demonstrated similar amplitudes for observed errors in a cooperative and competitive context. The results from that study did however demonstrate a latency difference between the two contexts, with a later oERN peak in the competitive compared to the cooperative context. This finding was not present in the current data. Given the differences in methodology and resulting ERP waveforms between the current study and the one by Koban et al. it is difficult to draw conclusions regarding this aspect. It is, for example, not entirely clear whether the two paradigms measure the exact same processes.

To our knowledge, no other studies investigated the context-sensitivity of the oERN measured relative to response onset. Two recent studies did investigate the feedback-locked FRN in comparable cooperative and competitive settings (Itagaki and Katayama, 2008; Marco-Pallares et al., 2010). The current findings are not in line with these recent studies that demonstrated the FRN to be sensitive to the actual reward outcome. Although it is generally assumed that the rERN and the FRN are reflections of the same performance monitoring process (see, e.g., Holroyd et al., 2004; Mars et al., 2005), these divergent outcomes might suggest that the feedback-locked and response-locked ERNs actually reflect different processes in social performance monitoring. However, based on currently available evidence, we would like to refrain from concluding this. Importantly, experimental paradigms used in rERN and FRN studies are very different and thus the exact performance monitoring processes needed to perform the task may crucially differ. The studies by Itagaki and Katayama and Marco-Pallares et al. made use of gambling tasks to investigate the FRN during social performance monitoring. Importantly however, performing a gambling task does not require internal performance monitoring, as participants do not have a representation of the correct response at the moment of response onset. Participants need to fully rely on the external feedback information to determine the correctness of their response and have no control over the outcome. Moreover, in complete gambling tasks, participants cannot optimize their behavior in any way, as associated feedbacks are predetermined by a computer program and thus each trial requires a new gamble.

Recent theories have proposed pMFC to be implicated in regulating adaptive behavior rather than performance monitoring alone. Rushworth and Behrens (2008) proposed pMFC to be crucially involved in updating of action values, optimizing performance, and subsequent strategy changes on the basis of reward information. Support for this more general role comes from studies that demonstrated amongst others pMFC to be similarly involved in processing correct actions associated with a high predictive value, as is the case in the beginning of learning (Walton et al., 2004). It also explains why pMFC is often found to be activated by other signals besides errors that also trigger the need for a behavioral change, like response conflict (Botvinick et al., 2004), error likelihood (Brown and Braver, 2005), or pain (Eisenberger and Lieberman, 2004; Singer et al., 2004). So, if indeed the central role of pMFC and associated ERP components is regulation of adaptive behavior, the exact function of the FRN elicited in tasks lacking behavioral control may thus be open for investigation.

A recent study by Holroyd et al. (2008) recently investigated this issue, by focusing on positive and negative ERP components elicited by different types of stimuli and feedback. Crucially, the authors concluded that the FRN is actually the same component

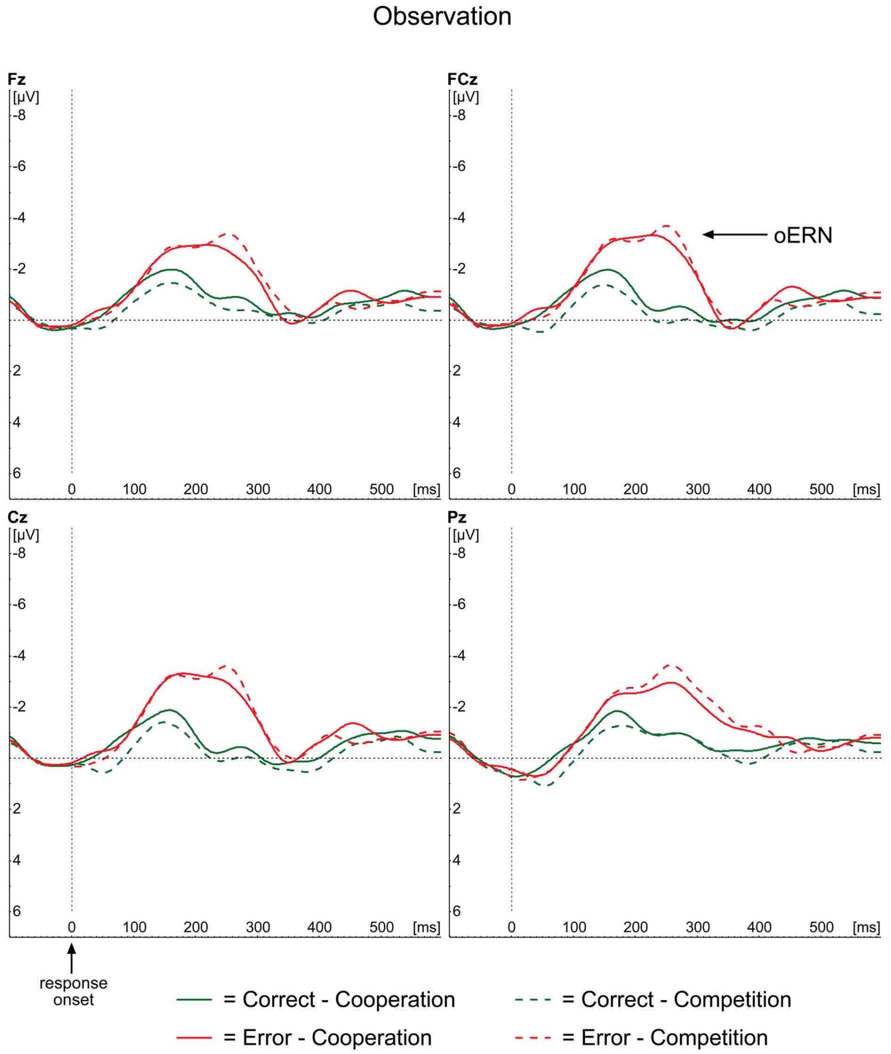


FIGURE 4 | Grand average ERP waveforms for the observation condition, time-locked to the onset of the actor's response for correct (green lines) and incorrect (red lines) responses separately. Midline electrodes Fz, FCz, Cz, and Pz are depicted.

as the stimulus-locked N200, a standard visual ERP component that is typically present in all stimulus-locked ERP waveforms. The important consequence of this interpretation is that the FRN is not – as generally assumed – additionally elicited on erroneous trials, but is always present and may be reduced or even absent on correct feedback trials. This more parsimonious interpretation may explain, for example, why the FRN is also commonly found on non-informative neutral feedback stimuli. Thus, the crucial conclusion was that "events that fail to indicate that a task goal has been achieved (including the occurrence of both neutral and error feedback stimuli) elicit the FRN (or N200), whereas events that do indicate that a task goal has been achieved elicit a positive ERP component," the so-called feedback correct-related positivity or fCRP, significantly reducing or even canceling out the FRN/N200 (Holroyd et al., 2008). The consequence of this interpretation is that the important neural activity is actually happening on correct feedback trials that signal that a goal has been achieved. Although this interesting proposal needs further investigation, it may explain the recent FRN findings in cooperative and competitive contexts. When participants focus on winning in a gambling task, this goal will be achieved when an opponent receives negative feedback. This "negative" feedback signal may thus result in increased positive amplitudes as reflected in the fCRP, importantly reducing the FRN. This alternative interpretation of the FRN may thus explain the reported opposite patterns of FRNs in cooperative and competitive settings using gambling tasks.

It is obvious that future research is needed to test these theories and hypotheses by investigating differences and possible overlap between these ERP components in social settings with more directly comparable experimental paradigms. Instead of using gambling tasks, employing for example RL or probabilistic learning paradigms may be a way to accomplish this, as participants crucially have to use the information derived from the feedback to optimize their behavior.

A limitation of the current study may be that the blocked observation design does not allow for measurements on behavioral adjustments following observed errors. However, we do believe that the current results may also be relevant in the light of recent behavioral work demonstrating different behavioral adjustments following observed errors in cooperative and competitive contexts (De Bruijn et al., 2011; Núñez Castellar et al., 2011). Post-error slowing, i.e., slowing down following an erroneous response, is a well-known strategic adjustment in speeded-choice-reaction tasks (Rabbitt, 1966). It has repeatedly been shown in individual choice-reaction paradigms like the Flankers task, but recent studies have also demonstrated slowing down following other's errors in more social settings (Schuch and Tipper, 2007; De Bruijn et al., 2011; Núñez Castellar et al., 2011). While Shuch and Tipper demonstrated post-error slowing in response to other's errors in a neutral setting, we recently showed that the amount of post-error slowing in response to observed errors critically depends on the context in which the interaction is taking place (De Bruijn et al., 2011). In this behavioral study, we measured both post-error slowing following own and observed errors in both contexts. The results of the cooperative context showed a clear relationship between own and observed post-error slowing: people who slowed down the most following their own errors also slowed down following their partner's errors. However, a different pattern was found in the competitive context. Participants still slowed down following their own errors, but they actually speeded up following errors from their opponents. Núñez Castellar and co-workers recently reported a comparable finding by demonstrating reduced post-error slowing following a co-actor's errors in the competitive context compared to the cooperative one. Based on the previous fMRI study from our lab, we concluded that the findings from our behavioral study indicated that although the error signal itself is insensitive to the context of the social interaction, the exact formalization of the behavioral adjustments are largely dependent on the context. The current ERP findings are in line with this interpretation, by demonstrating the insensitivity of the error signal to the social context at an electrophysiological level.

To conclude, the present results demonstrate that monitoring other's errors that are time-locked to the actor's response is independent of the reward associated with the observed error. This outcome does not fit with a strict interpretation of the RL theory stating that the ERN should only be generated after a loss of reward. However, we suggest the current findings to be more in line with theories assuming pMFC to be crucially involved in predicting outcomes and adjusting behavior (Rushworth and Behrens, 2008). In our view, the current findings may also be relevant in the light of recent behavioral work demonstrating the social context-specificity of the exact formalization of behavioral adjustments following observed errors (De Bruijn et al., 2011; Núñez Castellar et al., 2011). Both the context-insensitivity of the error signal and the context-sensitivity for the following behavioral responses make sense in daily life, as it is obvious that different actions may be required in response to an error from one's partner than in response to an error made by an opponent. The current study thus adds further support to the assumption that humans use the same neural and cognitive mechanisms to detect observed errors independent of the associated reward. However, we do propose that the type of behavioral adjustments in response to those observed errors might importantly depend on the role of the co-actor as determined by the social context.

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Experience-based decisions and brain activity: three new gaps and partial answers

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Experience-based decisions can be defined as decisions emanating from direct or vicarious reinforcements that were received in the past. Typically, in experience-based decision tasks an agent repeatedly makes choices and receives outcomes from the available alternatives, so that choices are based on past experiences, with no explicit description of the payoff distributions from which the outcomes are drawn. The study of experience-based decisions has long roots in the works of mathematical psychologists during the 1950s and 1960s of the last century (e.g., Estes and Burke, 1953; Bush and Mosteller, 1955; Katz, 1964). This type of task has been viewed as a natural continuation of the behaviorist tradition involving animals as subjects, and multiple trials in which feedback is obtained on each trial. During the 1970s and 1980s seminal studies focusing on choices among descriptive gambles began to dominate the field of Judgment and Decision Making, paving the wave for the successful and influential works of Tversky and Kahneman (e.g., Kahneman and Tversky, 1979). Indeed, a review of the decision making literature from 1970 to 1998 conducted by Weber et al. (2004) shows prominent use of description-based tasks over experience-based tasks.

Yet the study of experience-based decisions has continued to evolve. Some of the workers in this subfield were neuropsychologists who used experience-based tasks as a natural way to evaluate individual differences owing to these tasks having many choice trials (e.g., Bechara et al., 1994). Others were interested in the complex relations between learning and decision making (Erev and Roth, 1998). An interesting finding that has finally defined the importance of contrasting the two types of tasks – experience-based decisions and description-based decisions, was obtained by Ido Erev and his colleagues. Kahneman and Tversky (1979) showed that individuals overweight small probability events in their decisions from description. For instance, in selecting between an alternative producing $3 for sure or a gamble producing 10% chance to receive $32 (and otherwise zero), most people pick the riskier alternative, behaving as if they give greater weight to the relatively rare event (see Hau et al., 2009). Erev and colleagues have demonstrated a reverse phenomenon in decisions from experience (Barron and Erev, 2003; Hertwig et al., 2004; Yechiam et al., 2005). People tend to experientially select alternatives as if what happens most of the time has more weight than the rare event. Thus, people overweight small probability events in decisions from description while underweighting them in decisions from experience. This has been referred to as the description–experience (D–E) gap (Hertwig et al., 2004). The studies exploring the D–E gap were followed by further investigations examining the divergent and convergent processes in these task types (e.g., Rakow et al., 2008; Barron and Yechiam, 2009; Wu et al., 2011).

In parallel to the recent advancements in experience-based decisions within the field of Judgment and Decision Making, there have been numerous studies of this type of decisions in Neuroscience. For example, the feedback-based error-related negativity (fERN; see below; e.g., Gehring and Willoughby, 2002) and the role of non-declarative knowledge in selecting advantageously (Bechara et al., 1997) were found in experience-based decisions. Several studies have explicitly showed that that experience-based tasks result in higher correlation between studied brain variables and over behavior. For example, in Aharon et al.'s (2001) fMRI study, participant evaluated the attractiveness of face images either descriptively or by making choices and receiving feedback. Brain activation levels in the reward circuitry (particularly, the nucleus accumbens) matched the evaluation patterns only in the experiential condition. Similarly, severe damage to the orbitofrontal cortex was found to lead to decision impairments in experience-based tasks, but not in description-based tasks (Leland and Grafman, 2005). Still, many of the investigations of these neuroscientific aspects have borrowed their theoretical underpinning from the study of decisions from description, and have not been guided by relevant theories of experience-based decisions. At the same time, many of the decision making studies of experience-based tasks have taken place without awareness of the relevant brain studies using this paradigm.

In an attempt to highlight the necessity of integrating the two bodies of research (JDM and neuroscience studies), we present three dissociations (or "gaps") between brain activation patterns and behavioral choices in these tasks. The majority of this paper is devoted to describing the three gaps in order to encourage further research. Additionally, we also suggest some directions for exploring and explaining these inconsistencies.

THREE BRAIN-BEHAVIOR GAPS IN EXPERIENCE-BASED DECISIONS

BRAIN ACTIVATION AND BEHAVIORAL RESPONSES TO RARE EVENTS

The very famous "oddball" paradigm examines people's brain responses following low-probability events compared to more frequent events. The typical result is an elevated fronto-central signal approximately 300 ms following the rare event, which is known as P300. The original oddball paradigm normally required a response following the rare event, and thus confounded the rarity of the event and its performance requirements (Squires et al., 1975). Yet the same findings were also replicated in task-irrelevant rare events (Debener et al., 2005) and in reward prediction tasks (Karis et al., 1983). The elevated neural activation following the rare event appears to be inconsistent with the tendency to *underweight* rare events in experience-based decisions. One might argue, though, that the dependent variable in decision tasks (i.e., the choice proportion) is also affected by the size of the rare payoff, and this component may be insufficiently integrated upon making choices. Still, this would be inconsistent with the standard way in which the underweighting phenomenon is explained (Hertwig et al., 2004). Moreover, as we shall see below, inconsistency between brain activation and behavior also emerges when the target event (e.g., a loss) is similar in size to the control event (e.g., a gain).

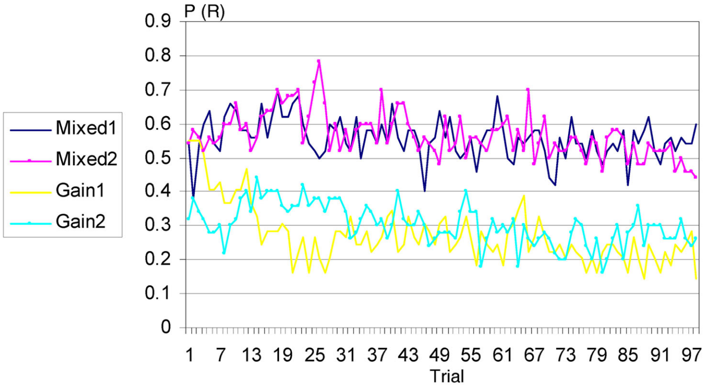
BRAIN ACTIVATION AND BEHAVIORAL RESPONSES TO LOSSES

In a seminal EEG study, Gehring and Willoughby (2002) demonstrated that a large portion of the frontal cortex exhibits greater rapid activation following losses than following equivalent gains. This event-related brain potential (ERP) has been referred to as medial frontal negativity (MFN; Gehring and Willoughby, 2002) or fERN (Yeung and Sanfey, 2004). Gehring and Willoughby (2002) suggested that the existence of the increased cortical response following losses is consistent with the behavioral principle of "loss aversion," which denotes an increased subjective weight of losses compared to gains (Kahneman and Tversky, 1979). Furthermore, they argued

The payoffs in Ert and Yechiam (2010):

Condition	Safe alternative	Risky alternative
Mixed1	Get 0	50% to win 1000, 50% to lose 1000
Mixed2	Get 0	50% to win 2000, 50% to lose 2000
Gain1	Win 1000	50% to win 2000, 50% to get 0
Gain	Win 2000	50% to win 4000, 50% to get 0

The results in Ert and Yechiam (2010):



The payoffs in Yechiam and Telpaz (in press):*

Condition	Safe alternative	Risky alternative
Mixed	Get 0	50% to win 200, 50% to lose 200
Gain	Win 200	50% to win 400, 50% to get 0
Loss	Lose 200	50% to lose 400, 50% to get 0

* A noise factor of -1,0, or +1 was added to each outcome.

The results in Yechiam and Telpaz (in press):

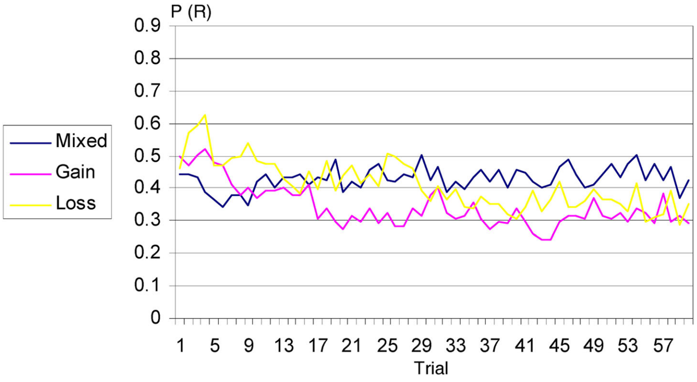


FIGURE 1 | Risk taking in two studies of experience-based decisions. Top: Ert and Yechiam (2010). Bottom: Yechiam and Telpaz (in press). Each task involves the selection among a Safe option (S) and a Risky option (R). The results show the mean proportion of selections from the risky alternative in each trial [P(R)] in different conditions. The participants take less risk over time when payoffs are predominantly gains or losses but not in mixed gains and losses.

that the asymmetric fERN response to losses represents the brain mechanism directly contributing to the representation of subjective value, or "instant utility." However, in Gehring and Willoughby's (2002) research, as in other studies of experience-based decisions (e.g., Erev et al., 2008; Silberberg et al., 2008; Hochman and Yechiam, 2011; Yechiam and Telpaz, 2011, in press), participants actually made behavioral choices as if they were loss neutral and not loss-averse. Specifically, the fERN was observed in choices between an alternative producing +5 or −5 US cents and a second alternative producing +5 or −25 cents. Loss aversion implies that in choice between a pair of alternatives with symmetric gains and losses, individuals should prefer the alternative producing lower losses. However, the two choice alternatives were selected at about the same rate.

This gap was replicated in follow-up ERP studies, some using higher payoffs (e.g., Nieuwenhuis et al., 2004; Yeung and Sanfey, 2004; Masaki et al., 2006). It has also been demonstrated in studies of autonomic arousal: Losses were found to have greater effect on pupil diameter and heart rate, even in the absence of reliable loss aversion (Hochman and Yechiam, 2011; Yechiam and Telpaz, 2011). Interestingly, the ERP studies noted above did not make a big issue out of this discrepancy, and did not consider it as deserving special attention. Yet we feel that it is a critical issue because participants make experiential choices as if they are loss neutral while their brain acts as if it is loss sensitive.

THE EFFECT OF EXPERIENCE ON RISK TAKING

The third brain–behavior gap we would like to draw attention to involves a discrepancy between what is known about the dynamic function of the dopaminergic system and experiential choice behavior. Under current models of the striatum, the dopaminergic system adapts to reinforcement using a "Delta" learning rule (Rumelhart et al., 1986), whereby a new outcome from a given alternative is compared to the expectancy of the alternative prior to the outcomes, and the expectancy is updated as a function of the difference between the new outcome and the old expectancy. Brain areas within the striatum were found to exhibit activation patterns consistent with the implied mechanism of the delta rule (Schultz et al., 1997). This rule axiomatically leads to a clear behavioral prediction involving the effect of experience on risk taking behavior (Niv et al., 2002; Denrell, 2007): Under the Delta rule, decision makers should be more risk averse with experience because they invariably sample the risky alternative in a biased fashion. For example, say that in an experience-based decision you have a choice between getting zero for sure and a risky alternative producing equal chances to win or lose $10. In the first 10 trials in which the risky alternative is chosen there is about 40% chance that *in reality* the likelihood of winning $10 will be less than 50%. This can lead participants to avoid the risky alternative in future choices. Moreover, as soon as the risky alternative is avoided, there is no mechanism that reduces this bias. The chance of biased sampling from the risky alternative continues in the next trials as well, and under the Delta learning rule, it is expected to slowly lead participants away from the risky alternative. But this is not how participants behave in experiential tasks! In several studies involving such symmetric risky alternative (with equal chance of winning or losing) participants were found to show remarkable flatness in their learning curves (see **Figure 1**). This gap between the mechanism considered to govern learning and actual experiential behavior in tasks involving mixed gains and losses bears some similarity to the issue of loss sensitivity because in both cases the brain activation pattern is in the direction of avoiding risk (and potential losses) while behavior leans toward risk neutrality[1].

PARTIAL ANSWERS

A technical way out of theses gap involves the typically different temporal resolution of brain activation measures and behavioral choices. The fERN patterns, for instance, were revealed in the first 300 ms after the choice outcomes are presented. However, in most studies, decision makers are given much more time to make behavioral decisions. Thus, behavioral loss neutrality might be the product of delayed brain processes implicated in executive control. For instance, some executive functions of verbal working memory have been known to result in activation peaks approximately 600 ms after the relevant stimuli (Gunter et al., 2000) and even later (Tu et al., 2009). Still, while this is a possible interpretation for these gaps, it is quite tentative as the relevant delayed processes have not been uncovered.

An alternative suggestion is that the rapid fronto-central activation following monetary outcomes does not represent "instant utility" weighting of these outcomes (as proposed, for instance, by Gehring and Willoughby, 2002). Possibly, it could represent an attentional phenomenon. We (Yechiam and Hochman, 2011; Yechiam and Telpaz, 2011) suggested that an encompassing increase in frontal activation may represent the intensity of the attentional orienting response. Attention may be drawn by losses for instance, and this may increase the overall investment of cognitive resources in the task, in a symmetric fashion to both gains and losses. A related explanation involves the surprise value of incentives (Nevo and Erev, 2011). Under these explanations, the noted gaps are accounted for by the assertion that brain activation to incentives may represent cognitive processes that do not have a direct effect on the subjective valuation of the stimuli that have elicited them.

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[1] Risk neutrality over time is also inconsistent with Kahneman and Tversky's (1979) "loss aversion" hypothesis. As noted in Section "Brain Activation and Behavioral Responses to Losses," studies of experience-based decisions (e.g., Erev et al., 2008) typically do not find reliable behavioral manifestations of loss aversion. The studies reported in Figure 1 replicate this pattern.

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