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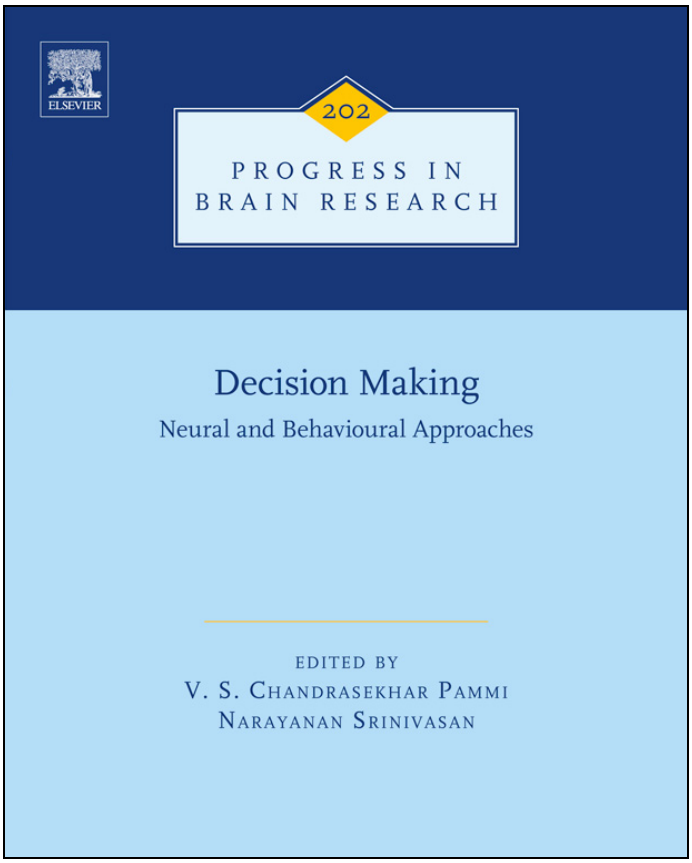

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CHAPTER

Contextual and social influences on valuation and choice

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Abstract

To survive in our complex environment, we have to adapt to changing contexts. Prior research that investigated how contextual changes are processed in the human brain has demonstrated important modulatory influences on multiple cognitive processes underlying decision-making, including perceptual judgments, working memory, as well as cognitive and attentional control. However, in everyday life, the importance of context is even more obvious during economic and social interactions, which often have implicit rule sets that need to be recognized by a decision-maker. Here, we review recent evidence from an increasing number of studies in the fields of Neuroeconomics and Social Neuroscience that investigate the neurobiological basis of contextual effects on valuation and social choice. Contrary to the assumptions of rational choice theory, multiple contextual factors, such as the availability of alternative choice options, shifts in reference point, and social context, have been shown to modulate behavior, as well as signals in task-relevant neural networks. A consistent picture that emerges from neurobiological results is that valuation-related activity in striatum and ventromedial prefrontal cortex is highly context dependent during both social and nonsocial choice. Alternative approaches to model and explain choice behavior, such as comparison-based choice models, as well as implications for future research are discussed.

Keywords

striatum, ventromedial prefrontal cortex, neuroeconomics, social neuroscience, context, valuation, decision-making

1 INTRODUCTION: THE IMPORTANCE OF CONTEXT

In everyday life, we maneuver through a variety of contexts with relatively little effort, such as our work environment, relationships with our romantic partners, friends, colleagues, children, and parents, as well as traffic, and even foreign cultures

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during travel and business interactions. All these contexts entail their own set of rules that inform us what behavior is expected from us and what is inappropriate. It has been known for a long time that modifying behavior according to context has important social and survival consequences (e.g., Bevan, 1968). In this chapter, we review evidence on the modulation of neural activation by different contexts. We define context as "the circumstances that form the setting for an event" (Oxford Dictionaries). This broad definition gives us the opportunity to discuss the various facets of context-dependent modulation that span learning environment, motivational and affective contexts, reference point, and social contexts.

Consider the example of extinction of Pavlovian conditioned fear, which was first mentioned in the original work of Pavlov (1927). Fear conditioning is a simple form of associative learning, in which an animal learns to associate the presence of a neutral stimulus, termed the conditioned stimulus (CS), such as a light or a tone, with the presence of a motivationally significant stimulus, termed the unconditioned stimulus (US), such as an electric shock to the foot. After only a few pairings of CS and US, the animal will show anxiety-related behaviors to the mere presentation of the previously neutral CS alone, indicating that the animal has learned to use the CS to predict the occurrence of the aversive properties of the US. This reaction can be eliminated by continued presentation of the CS alone, a process termed "extinction" (Holland and Bouton, 1999; Pavlov, 1927). Extinction has been shown to create an ambiguous memory of the CS, such that it attains two meanings, one predicting the impending presence of the US, and one where it is not predictive. Retrieval of a particular meaning is highly context dependent (Bouton, 1994, 2002), as context can help in resolving such ambiguity of multiple memory representations.

The phenomenon of the renewal effect clearly demonstrates the importance of context for extinction learning. Renewal occurs for instance when the association between CS and US is trained in context A (signified for instance by a particular place or odor), while extinction training occurs in context B until responding to the CS stops. When placing the animal in the original, or in a novel context, response rates to the CS return to preextinction levels, indicative of a renewal of fear (e.g., Bouton and Bolles, 1979a,b; for review see Bouton, 2002). Context dependence has also been used as an explanation for spontaneous recovery, first mentioned in Pavlov's original writings (Pavlov, 1927), as testing takes place in a novel temporal context (Bouton, 1988). Given that extinction training is a commonly used intervention method for drug dependence (Centonze et al., 2005; Kalivas and O'Brien, 2007), it is obvious how contextual factors that impact extinction have significant clinical relevance for preventing relapse in drug abusers (Bouton, 2002; Crombag et al., 2008). The example of extinction illustrates the importance of context for mechanisms that are crucial for an organism's survival, such as associative learning. Contextual cues, such as a location, time of day, or odors can indicate relative safety or threat and therefore allow an organism to engage in appropriate behaviors.

Given the importance and ubiquity of context in our daily lives, it comes as no surprise that contextual factors have been demonstrated to impact multiple perceptual and cognitive processes and their neural correlates. Consider for instance the

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center circles depicted in Fig. 1A and B. When asked to compare the center circles in Fig. 1A and B, you might be tempted to say that the circle in Fig. 1A is larger than that in Fig. 1B. The center circle in Fig. 1A appears relatively large when surrounded by small circles. When, however, surrounded by large circles, as in Fig. 1B, it appears relatively small. Figure 1C shows that these circles are in fact the same size. This simple example illustrates the importance of context within which perceptual

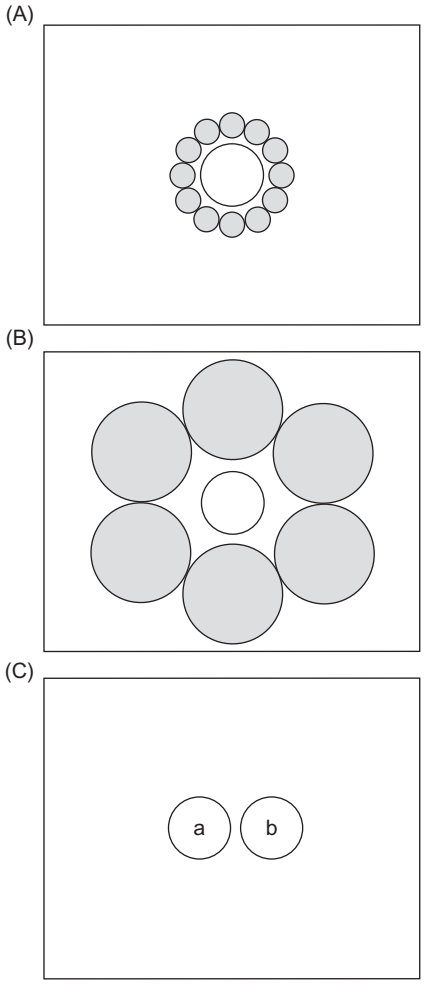

FIGURE 1

Illustration of contextual effects on perceptual judgments via the Ebbinghaus optical illusion. A circle surrounded by smaller circles (A) is typically judged to be bigger relative to a circle surrounded by larger circles (B), while they are, in fact, the same size (C). This analogy can easily be extended to contextual effects on valuation (see text).

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judgments are made. The psychophysics literature abounds with examples underlining contextual influences on judgment across all modalities (e.g., Jesteadt et al., 1977; Parducci and Perrett, 1971; Riskey and Parducci, 1979).

Recent neuroimaging evidence supports the claim that context influences perceptual judgments and provides information about the neuronal underpinnings of contextual modulation of behavior. One study presented surprised faces to subjects in two different contexts while undergoing functional Magnetic Resonance Imaging (fMRI; Kim et al., 2004). A verbal cue placed the surprised face either in a positive or negative context, that is, the cue indicated that a positive (e.g., a gain of $500) or a negative event (e.g., a loss of $500) happened to the person depicted in the subsequently shown image. Neuroimaging findings showed that signals in the amygdala, which were observed in response to viewing surprised faces, were significantly modulated by the valence of the preceding information. These results indicate context-dependent reactivity of the amygdala during a simple perceptual task. Interestingly, judgments of affect and affect intensities, particularly in ambiguous contexts, can be influenced by endogenous context, such as expectations about the degree and appropriateness of emotional expressions as formed by our cultural background (e.g., Matsumoto, 1989, 1992; Pogosyan and Engelmann, 2011). Recent neuroimaging evidence from the novel field of cultural neuroscience (e.g., Chiao, 2010) indicates that cultural differences in affect perception may in part be mediated by the amygdala (Chiao et al., 2008). Taken together, these results emphasize the importance of context for perceptual judgments.

Multiple experiments have demonstrated that contextual manipulations can also modulate cognitive control processes and their neural correlates (e.g., Engelmann and Pessoa, 2007; Engelmann et al., 2009b; Erk et al., 2003; Hare et al., 2005; Locke and Braver, 2008; Mohanty et al., 2008; Pochon, 2002; Small et al., 2005; Taylor et al., 2004). Examples include changes in motivational context, such that participants are paid large amounts in one condition and relatively smaller amounts in another for performance on the same task, as well as affective context, established for instance by presenting pictures showing emotional content. Motivational context has repeatedly been demonstrated to modify both brain responses and performance on tasks commonly employed to investigate executive (Pochon, 2002), attentional (Engelmann et al., 2009b; Small et al., 2005), and cognitive control (Locke and Braver, 2008), as well as working memory (Taylor et al., 2004, for review see Pessoa and Engelmann, 2010). Similarly, emotional context can alter brain responses and performance on a variety of cognitive control tasks, such as response inhibition (Hare et al., 2005) and episodic memory encoding (Erk et al., 2003).

Taken together, findings from these experiments demonstrate that different environmental cues provide contexts that impact behavioral performance, perceptual judgments and cognitive control processes. Neuroimaging evidence indicates that these behavioral effects are mediated by context-dependent alterations of concurrent responses in brain systems responsible for task performance. The goal of the current review is to outline recent evidence from the fields of Neuroeconomics and Social Neuroscience that demonstrate the impact of context on valuation and decision-making.

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We will provide a summary of results shedding light on the neurobiological basis of contextual effects on valuation and social choice and conclude with a number of hypotheses about neural systems that mediate the role of context across a variety of social and nonsocial settings.

2 CONTEXT CHANGES VALUATION

Standard economic theory assumes that decisions between choice alternatives are made by, at a minimum, ordinal-scale rank-ordering alternative options based on assessments of their utility by the decision-maker (an internal value that could in principle be represented by the vigor of neuronal activity and thus captured by electrophysiological and fMRI recordings). Once choice alternatives are rank-ordered in this fashion, a rational agent is assumed to choose the highest ranking option, thereby maximizing utility (e.g., Samuelson, 1937). A number of violations of this very basic assumption of rational choice theories will be discussed in this section. These demonstrate that, instead of value being an absolute measure, value may be much more of a relative measure that changes depending on context. Such violations include the influence of irrelevant choice options, intransitivity, preference reversals, as well as the endowment effect, and framing effects.

2.1 Value is relative

Ample evidence from neuroscience and psychology has demonstrated that, while rewards have clearly defined physical properties such as taste and smell, the motivational value of rewards can be relative (e.g., Black, 1968; Cox, 1975; Dunham, 1968; Reynolds, 1961). Recent neuroeconomic experiments have underlined the sensitivity of reward and cognitive control processes to contextual changes, such that reward value can depend on the availability of other, more or less preferred rewards as well as physiological state (e.g., Cromwell et al., 2005; Elliott et al., 2008; Grabenhorst and Rolls, 2009; Kalenscher et al., 2010; Plassmann et al., 2008; Tobler et al., 2005; Tremblay and Schultz, 1999).

Target brain regions for initial investigations of the neural underpinnings of context-dependent valuation were orbitofrontal neurons, for which response preferences to taste and odor had been previously mapped in monkey electrophysiology and human fMRI studies (O'Doherty et al., 2001; Rolls and Baylis, 1994; Rolls et al., 1996). Importantly, neurons in orbitofrontal cortex (OFC) that respond to rewarding tastes stop responding to foods fed to satiety (Rolls and Sienkiewicz, 1989). Similarly, in humans, satiety relative to hunger has been shown to inhibit responsiveness of OFC neurons (O'Doherty et al., 2000; Small et al., 2001). Findings from these experiments therefore suggest that relative preferences formed by interoceptive contexts modulate responses of OFC neurons, such that reward value is modulated by motivational states.

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Relative reward processing, where neural responses within reward-related regions depend on alternative outcomes, has been demonstrated previously in the striatum and OFC in both monkeys (Cromwell et al., 2005; Nakahara et al., 2004; Tobler et al., 2005; Tremblay and Schultz, 1999) and humans (Breiter et al., 2001; Grabenhorst and Rolls, 2009; Nieuwenhuis et al., 2005). Specifically, Tremblay and Schultz (1999) demonstrated that, on the one hand OFC neurons showed increased firing rates when anticipating receipt of a food item that was valued higher than a paired food item (context A: apple valued more than cereal). On the other hand, expectation of receiving the same food item when the alternative was a more preferred food led to decreased responding of OFC neurons (context B: apple valued less than raisin). In another seminal experiment (Tobler et al., 2005), monkeys learned to predict juice rewards with differing probabilities and magnitudes based on distinct visual stimuli while extracellular recordings from midbrain dopamine neurons (substantia nigra and ventral tegmental area) were taken. Paralleling findings indicating relative valuation in OFC neurons, results from this experiment suggest that dopamine neurons showed increased responses to a medium reward (0.15 ml) when monkeys expected a small (0.05 ml) or medium reward at equal probability. In contrast, decreased firing rates were observed to the same medium sized juice reward, when monkeys expected either a medium or a large (0.5 ml) reward. Similarly, relative reward responsiveness has been demonstrated in striatal targets of midbrain dopamine neurons, such as the putamen (Cromwell et al., 2005). It is of interest that these results also extend to aversive outcomes (Hosokawa et al., 2007) and probabilistic contexts during which the likelihood of current reward is predicted by the recent history of rewards (Nakahara et al., 2004). Finally, it has to be noted that a more recent experiment failed to demonstrate relative reward coding in OFC neurons (Padoa-Schioppa and Assad, 2007). Instead, results demonstrated that OFC neurons encoding the value or taste of a particular juice type did not change their firing patterns based on the availability of other more or less preferred juice types in a given choice set.

Recent neuroimaging studies provide supporting evidence for relative reward coding, demonstrating modulation of (1) valuation-related activity in medial OFC by regret (Chandrasekhar et al., 2008; Camille et al., 2004), (2) striatal activity by social comparison (Fliessbach et al., 2007) and (3) subjective pleasantness and concurrent activity in medial OFC by informational manipulations about the price of products (Plassmann et al., 2008). Furthermore, using cues predicting monetary reward pairs with different magnitudes in an experimental setup adapted from Tremblay and Schultz (1999) for fMRI, Elliott et al. (2008) demonstrated that Blood Oxygenation Level Dependent (BOLD) activity of the medial OFC increased in response to a stimulus predicting receipt of a medium amount of monetary gain when the alternative was a lower gain, relative to when a higher gain alternative was possible. Similarly, Nieuwenhuis et al. (2005) demonstrated context-dependent signals in a network of reward-sensitive brain regions that depended on a reward versus punishment frame. Specifically, activity in striatum and parietal cortex showed increased responding to a loss of 0 monetary units (MU), the best outcome when

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the alternatives were losses, but relatively decreased responding to a gain of 0 MU, the worst outcome when the alternatives were gains.

The neurobiological results demonstrating context-dependent neuronal correlates of utility reviewed above generally do not pose a threat to the validity of standard economic theory. They imply diminished marginal utility due to changes in interoceptive context, signified by decreased neuronal firing rates to food rewards when satiated, and monotonic preference curves, signified by increased firing rates to preferred relative to less preferred rewards (see however Tobler et al., 2005).[1] However, they also lend support to alternative accounts, such as comparison-based theories of choice, which hold that choices are made by directly comparing options present in a given choice set and choosing the best alternative. Contrary to standard economic models, some comparison-based choice-models do not require computation of the value of each choice option, but allow a much simpler comparison of which option is relatively better of worse (for review see Vlaev et al., 2011). Given the above results demonstrating that neurons encode relative, and not absolute value (Cromwell et al., 2005; Tobler et al., 2005; Tremblay and Schultz, 1999), this alternative account has intuitive appeal and finds support in a number of recent experiments demonstrating prospect relativity. In one experiment, participants were asked to judge the value of various prospects (framed as "probability P chance of winning magnitude X") in two contexts, created by presenting subjects with choice options that offered a range of values either below or above the mean certainty equivalent of the prospect (Stewart et al., 2003). Specifically, for the prospect offering a 60% chance of 400 MU, the most popular choice was 100 MU when choice options varied below the certainty equivalent (60–120 MU in 20 MU steps), while the most popular choice was 180 MU when choice options varied above the certainty equivalent (160–220 MU in 20 MU steps). The general pattern of results that choices depend on the available alternative choice options finds support in a variety of experimental settings investigating saving rates and investment risks (Vlaev et al., 2007), choices in game theoretical paradigms (Vlaev and Chater, 2007) and choices over levels of pain relief (Vlaev et al., 2009). Taken together, comparison-based theories of decision-making offer a parsimonious, computationally less expensive and, therefore, biologically plausible alternative to rational choice theories. Their attractiveness is underlined when considering empirical evidence questioning the underlying assumptions required by rational choice theories.

Rational choice theory assumes that preferences between options do not depend on the presence or absence of other options, a principle termed "independence of irrelevant alternatives" (Tversky and Simonson, 1993). At its foundation lies the assumption

[1]It is worth mentioning that, in addition to investigating neuronal encoding of relative value, Tobler et al. (2005) also demonstrated that the activation magnitude of midbrain DA neurons when receiving a reward larger than expected (up to 10 times) did not scale with the absolute magnitude difference between expected and received reward, but simply signaled whether the outcome was better or worse than expected. This result is inconsistent with predictions from rational choice theory, but follows those of comparison-based choice models.

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that a decision-maker represents an order of all choice alternatives from worst to best based on their utility. Given a choice between a number of options, the decision-maker is assumed to always select the best choice option, thereby maximizing utility. Behavioral experiments, however, have repeatedly shown changes in preferences when additional options are introduced into the choice set, even if these are less preferred than the original choice options and should therefore be irrelevant (Simonson and Tversky, 1992; Tversky and Simonson, 1993). Similarly, transitivity underlies the ability to monotonically rank-order choice alternatives and therefore is an important assumption of rational choice theory. It holds that a given choice alternative A that is preferred over another alternative B, should also be preferred over C, when C is less preferred than B. Simply put, transitivity states that if $A > B$, and $B > C$, then $A > C$ (where ">" indicates the direction of preference) and therefore, a given choice alternative cannot at the same time be better and worse than other choice alternatives. Intransitive choices, however, have repeatedly been demonstrated in the literature (Simonson and Tversky, 1992; Tversky, 1969). The empirical phenomena of intransitive choices and violations of independence of irrelevant alternatives imply context-dependent valuation of options. A recent and very elegant fMRI experiment investigated the neural underpinnings of intransitivity (Kalenscher et al., 2010). Using a binary choice task, in which probability and magnitude of prospects varied, the authors demonstrated intransitive choices in the majority of subjects (63%). Such context-dependent desirability was found to be driven by differential weighting of gain probability and gain magnitude as the difference between gamble attributes increased. Specifically, gain magnitude was weighted more heavily than probability for small differences, while probability dominated choices between options with large differences between gamble attributes. Neural correlates of context-dependent prospect desirability were obtained in a network of choice-related brain regions, such as dorsolateral prefrontal cortex (dlPFC), anterior cingulate cortex (ACC), and putamen (see Fig. 2A). Furthermore, these value-related signals were modulated by individual propensity for intransitivity. These results not only confirm prior findings on context-dependent valuation (e.g., Elliott et al., 2008; Tobler et al., 2005; Tremblay and Schultz, 1999), but also demonstrate that activity in choice-related regions can be modulated by contextual factors thus posing significant problems to the transitivity assumption of rational choice theories (Tversky, 1969).

Taken together, the behavioral and neural results reviewed above support the notion that valuation is relative and preferences are formed in reference to the available choice options. Comparison-based choice models (Vlaev et al., 2011) offer a parsimonious, computationally less expensive and biologically plausible alternative to rational choice theories that do not suffer from empirically falsified assumptions. Because this approach has been relatively understudied to date (but see work on drift diffusion models: e.g., Basten et al., 2010; Hare et al., 2011; Krajbich et al., 2010; for a detailed summary of race models see also Chapter 7), future experiments that assess predictions from computational models of comparison-based choice (e.g., Johnson and Busemeyer, 2005) against behavioral and neuroimaging data are required to investigate its relative strengths and shortcomings.

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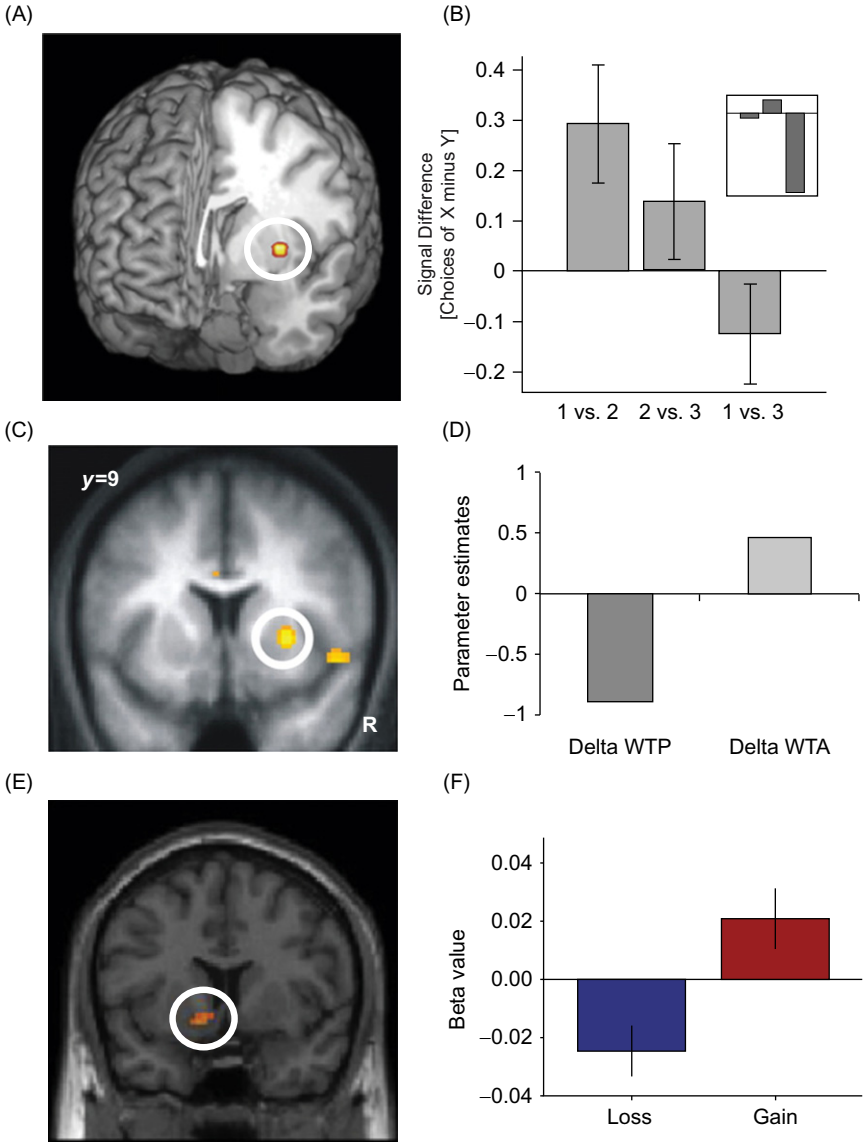

FIGURE 2

Contextual effects on valuation-related activity in ventral striatum. (A) Neural correlates of context-dependent prospect desirability reflective of intransitivity in putamen (from Kalenscher T, Tobler PN, Huijbers W, Daselaar SM and Pennartz CMA (2010) Neural signatures of intransitive preferences. Front. Hum. Neurosci. 4:49. http://dx.doi.org/10.3389/fnhum.2010.00049). (B) Activity in putamen shows decreased activity during intransitive choices, inset shows BOLD responses of individuals whose choices were classified as transitive (see Kalenscher et al., 2011 for more detail). (C) Reference-dependent activity patterns reflective of the endowment effect in putamen (from De Martino et al., 2009). (D) Reference-dependent activity in ventral striatum is reflected by an increase in activity as stated maximum buying prices decreased relative to the lottery's expected value (delta WTP) and an increase in activity as stated minimum selling prices

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2.2 Value is influenced by a context-dependent reference-point

Probably the most famous example of contextual influences on valuation is the "endowment effect" (Thaler, 1980), which is the tendency to assign greater value to products that are in one's possession. In an often-cited experiment demonstrating the endowment effect, Kahneman et al. (1990) randomly assigned a group of subjects to the role of either the seller or the buyer. Sellers were provided with coffee mugs of known value that buyers could choose to receive by foregoing sums of cash. Given that sellers and buyers faced identical choices (namely to obtain either money or a coffee mug), standard economic theory predicts that during such costless market transactions the price of the traded item should be determined solely by its value independent of ownership and about half the objects should change hands (Coase, 1960). The experiment and a number of laboratory and field replications (Ho et al., 2006; Kahneman, Knetsch, and Thaler, 1990), however, clearly show that context, that is, the participant's role as either seller or buyer during the transaction, has a significant impact on valuation. Specifically, the experimenters observed an increased Willingness-To-Accept (WTA) compensation to part from the mug and decreased Willingness-To-Pay (WTP) to obtain the mug relative to predictions. In fact, in Kahneman et al.'s experiment the ratio of median selling prices to median buying prices was 2.2, leading to substantial undertrading, namely an average of 2.25 of 22 expected trades.

Prospect theory offers one explanation for this discrepancy between WTA and WTP. Simply put, choice options are evaluated as either gains or losses relative to a reference point, typically the current state of wealth. Sellers that were given an object in the above experiment are assumed to have experienced a shift in their reference point, such that their updated status quo incorporates ownership of the coffee mug. From this new reference point, selling the mug is framed as a loss, while buying the mug is framed as a gain. It has repeatedly been demonstrated that losses are evaluated differently than gains. For instance, when giving participants the choice to play a mixed gamble that offers a probability (p) of losing some amount and a probability ($1-p$) of gaining another amount, symmetric gambles offering a loss and a gain of \$100 at $p=0.5$ are typically rejected. Only when the potential gain exceeds the potential loss by a factor of about two (e.g., a \$200 gain vs. a \$100 loss at $p=0.5$) are such gambles played (Tversky and Kahneman, 1991). This phenomenon, termed loss aversion, is such a stable empirical observation across a range of choice scenarios that it has been parameterized as a multiplicative weight (λ) for the Prospect Theory value function over losses (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992). As a consequence,

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increased relative to the lottery's expected value (delta WTA). (E) Reference-dependent activity patterns for aversive outcomes in ventral striatum (from Brooks AM, Pammi VSC, Noussair C, Capra CM, Engelmann JB and Berns GS (2010) From bad to worse: striatal coding of the relative value of painful decisions. Front. Neurosci. 4:176. http://dx.doi.org/10.3389/fnins.2010.00176). (F) Activity in ventral striatum shows decreased responding for outcomes worse than the reference shock amount and increased responding for outcomes better than the reference shock amount.

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the Prospect Theory value function, a power function that transforms objective value into subjective value, is steeper for losses than for gains (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992). Such relative overweighting of losses over gains in relation to a reference point then leads to the enhanced WTA observed in the coffee mug experiment. Interestingly, empirical results imply that losses loom larger than gains by a factor of greater than two (Tversky and Kahneman, 1991; although recent results indicate that this factor may be closer to 1.5, e.g., Sokol-Hessner et al., 2009), which is the same magnitude of the WTA–WTP ratio that was observed for the endowment effect by Kahneman et al. (1990).

The neural underpinnings of this phenomenon have been investigated by three recent fMRI studies (De Martino et al., 2009; Knutson et al., 2008; Weber et al., 2007; see also Tom et al., 2007). Weber et al. (2007) recorded BOLD responses while subjects indicated their WTA for selling digital copies of songs they were endowed with in half the trials, while in the other half, subjects indicated their WTP to purchase songs. Comparing brain activity at the time of choice indicated that both amygdala and caudate nucleus showed increased activity during selling compared to buying decisions. The authors interpret the activity pattern exhibited by the amygdala, which is associated with fear-related responses (e.g., LeDoux, 2000), as a neural correlate of loss aversion during selling decisions. However, while this is an important first investigation of the neurobiology of the endowment effect and results have a strong intuitive appeal given the role of the amydgala in fear-processing, results from this experiment need to be interpreted with caution as they suffer from a limitation: the endowment effect, as originally demonstrated by Kahneman et al., involves a comparison between the choice to keep an item or getting money for it in the seller's case and obtaining the same item or money in the buyer's case. In Weber et al.'s experiment, however, buying and selling both involved gains and losses, such that buying required giving up money for a good to obtain a song, while selling involved obtaining money for giving up a song (Loewenstein et al., 2008). This leads to difficulties in interpreting neural correlates of the WTA–WTP difference, as it is unclear whether neural responses are due to differences in greater perceived gain or loss in the selling versus buying condition. Such interpretations become especially difficult when considering the role of the amygdala in representing both positive and negative value and affect (e.g., Hamann et al., 2002; Paton et al., 2006).

This short-coming was elegantly addressed in a more recent experiment by De Martino et al. (2009). In this experiment, subjects traded lottery tickets with identifiable expected utilities by indicating their maximum buying price when in the role of the buyer and their minimum selling price when in the role of the seller. Importantly, the authors included an evaluation condition, which elicited the subjective value of each ticket that served as a context-free reference value from which to extract subject-specific endowment effect magnitudes. This feature allowed the authors to compute trial-by-trial endowment effect parameters that tracked the extent of each subject's deviation of buying and selling prices from their estimate of the subjective value of the lottery. Behaviorally, a robust endowment effect was demonstrated as an average increase in the WTA and an average decrease in the WTP relative to the subjective value of a lottery across subjects. At the neural level, the authors used

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parametric analysis to probe for regions whose activity tracked price changes reflective of context-dependent valuation related to the endowment effect. Reference-dependent activity patterns, reflected by an increase in activity as stated maximum buying prices decreased relative to the lottery's expected value and an increase in activity as stated minimum selling prices increased relative to the lottery's expected value, were revealed in bilateral ventral striatum (Fig. 2B). Importantly, these results could be dissociated from reference-independent activity in OFC and dorsal striatum. These results are corroborated by recent findings indicating reference-dependent activation changes in ventral striatum in the context of choices over purely aversive outcomes (Brooks et al., 2010). Specifically, subjects made choices over gambles offering more or less electric shocks relative to a reference amount of 10 shocks. The ventral striatum showed increased activity to gambles offering less shocks (better than reference amount) and decreased activity to gambles offering more shocks (worse than reference amount, Fig. 2C). This pattern of activity parallels the WTA–WTP-related activations observed in De Martino et al. (2009), indicating that reference-dependent valuation is also tracked by ventral striatum activity in the domain of losses.

Corroborating evidence from multiple fields spanning the subfields of neuroeconomics, such as (1) marketing research (Simonson and Tversky, 1992), (2) behavioral economics (Kahneman and Knetsch, 1990; Thaler, 1980), and (3) psychology (Stewart et al., 2003; Vlaev et al., 2009), monkey electrophysiology (Tobler et al., 2005; Tremblay and Schultz, 1999) and human neuroimaging (Kalenscher et al., 2010; Nieuwenhuis et al., 2005) demonstrate that value-based choice is highly context dependent and, in many instances, relative to other available options within a given choice set. Such empirical evidence clearly contradicts assumptions made by rational choice theory. While a number of alternative models have been offered that incorporate specific contextual effects (e.g., Tversky and Simonson, 1993), such approaches increase model complexity and thereby compromise biological plausibility. Future research using electrophysiology and fMRI is needed to test theories of context-dependent value-based choice. Comparison-based models of choice (Vlaev et al., 2011) offer a reasonable starting point in this endeavor.

3 SOCIAL CONTEXT

Humans interact with their social environment from the moment they are born. Long-term deprivation of social interaction causes utmost despair and neural damage (Innocenti, 2007), supporting the notion that human beings are innately social. Inspired by such results, recent neuroscience studies have started to investigate the impact of social context on decision-making.

Some studies focusing on the social context of decision-making have used game theoretical paradigms commonly employed in behavioral economics, for example the "trust game" (Delgado et al., 2005; King-Casas et al., 2005; Phan et al., 2010; Stanley et al., 2012). A typical trust game consists of two rounds of monetary

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exchanges between two partners (an investor and a trustee). In the first round, the investor is endowed with a monetary sum by the experimenter and can send all, a portion of it, or none, to the trustee. This sent amount is multiplied by a factor of two to four, before it is received by the trustee. In the second and final round, the trustee can reciprocate by sharing all, a portion, or none of her holdings with the investor. In the context of one-shot trust games played anonymously, trust is typically operationalized as the amount sent from investor to trustee. Given that the anonymous trustee has no financial incentive to return the money she received from the investor, the amount sent from the trustee to the investor is therefore considered a measure of pro-sociality (for more details see Fehr, 2009).

Other studies have manipulated the social context of decision-making using more natural social settings such as the induction of social conformity (Campbell-Meiklejohn et al., 2010; Klucharev et al., 2009), or combined natural social context manipulation with behavioral economics paradigms (Delgado et al., 2005; Stanley et al., 2012).

There is a set of brain regions which were found to play a prominent role in decision-making across many different experimental approaches, involving the striatum, the ventromedial prefrontal cortex (vmPFC), and the insula (Rilling and Sanfey, 2011). The following section provides an overview of the impact of social context on neural activation in these different regions associated with decision-making.

3.1 Social context and the striatum

A number of interesting results regarding the impact of social context on the neural response in the striatum have emerged from studies using the "trust game." For example, King-Casas et al. (2005) used this paradigm to investigate the impact of experienced reciprocity on behavioral and neural correlates of trust decisions. The formation of experience-based reputation over the course of 10 repeated interactions between the same investor and trustee correlated with a temporal shift of activity in the caudate nucleus of the striatum from the moment when investors received the outcome to the moment of decision. This means that the participants' anticipatory response at the time of decision began to reflect their expectation of reciprocity, or in other words, their partner's reputation based on previous interactions.

Phan et al. (2010) contrasted brain activations of the investors under conditions of reciprocated trust (i.e., the investor sent money and the recipient sends money back) and unreciprocated trust (i.e., the investor sends money but the recipient defects by keeping the entire amount). The results showed an increase in activation in the right OFC and bilateral ventral striatum when trust was reciprocated. Only the ventral striatum was selectively activated for partners who consistently returned the investment, suggesting that the neural response in human striatum is modulated by the reputation of one's partner that reflects a positive expectation about the partner's behavior in the context of social interactions.

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A recent study (Stanley et al., 2012) manipulated the social context of the trust game using a natural setting. Here, the trustee was either an ingroup member, indicated by a white face, or an outgroup member, indicated by a black face. At the time of choice, the investors' activity in the striatum correlated with individuals' trust bias—that is, the overall disparity in decisions to trust the ingroup or the outgroup member. The activity in the striatum was higher when deciding to trust partners from the race group that participants considered less trustworthy. The authors conclude that the striatum is involved in representing race-based reputations that shape trust decisions. The results of Stanley et al. (2012) are in line with the results of a previous study (Delgado et al., 2005), which used the trust game and manipulated the moral character of the trustees. At the time of decision, Delgado et al. (2005) found increased activation in the striatum when the investors interacted with a morally "bad" person, implicating striatal activity during trust decisions in more general representations of reputation. Interestingly, neural activation patterns related to reputation formation and updating parallel previous results on the reward prediction error in the striatum (McClure et al., 2003; Montague et al., 2004; Schultz et al., 1997). This is suggestive of similar learning mechanisms about the values of social and nonsocial stimuli (Behrens et al., 2008; King-Casas et al., 2005).

Additional evidence for the sensitivity of striatal response to social context was provided by the study of Harbaugh et al. (2007). This study employed a modified version of the dictator game, in which participants allocated money either to themselves or a charity. Giving to a charity correlated with increased activation in the ventral striatum, which was greater when participants gave voluntarily, as compared to mandatory allocation.

Studies using paradigms outside the domain of standard games from behavioral economics have provided interesting evidence for a modulation of striatal activation in the context of social conformity (Campbell-Meiklejohn et al., 2010). In these studies, participants were confronted with normative opinions related to the attractiveness of faces (Klucharev et al., 2009) or a piece of music (Campbell-Meiklejohn et al., 2010). The results showed that agreement between one's own and normative opinion modulates activity in the ventral striatum, similar to the dopamine-mediated reward signal observed in this region during reinforcement learning. Moreover, Klucharev et al. (2009) showed that the individual magnitude of the striatal response, elicited by conflict with the group opinion, correlated with individual differences in conforming behavior.

Taken together, the results reviewed above suggest that the striatum is important for evaluating social stimuli, as striatal activity has been shown to reflect social reward prediction during reputation formation. Furthermore, valuation-related activity in the ventral striatum can be modulated by social context, such as the presence of other's opinions.

3.2 Social context and the vmPFC

Together with the ventral striatum, the vmPFC has been shown to be involved in the valuation of monetary and primary rewards (O'Doherty, 2004). A number of recent studies have suggested that the neural response in vmPFC is altered by social

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contexts such as inequality (Tricomi et al., 2010), threat of sanction (Li et al., 2009), and received sponsorship (Harvey et al., 2010). Tricomi et al. (2010) created inequality between pairs of participants by giving only one of them a large monetary endowment. The results showed that activity in ventral striatum and vmPFC was more responsive to transfers to others than to self in the "high-pay" participants, whereas the "low-pay" participants responded stronger to transfers to self than transfers to others. These findings suggest that the magnitude of the neural response in ventral striatum and vmPFC is modulated by the context of advantageous and disadvantageous inequality.

Li et al. (2009) investigated behavioral and neural correlates of the trustees' decisions in the trust game in the context of threat or no threat of sanctions (i.e., monetary loss for not sending back the amount requested by the investor). The presence of sanctions reduced trustee's brain activity in the vmPFC, lateral OFC, and amygdala. Moreover, neural activity in a trustee's vmPFC area predicted the future level of cooperation under both sanction and no-sanction conditions.

Harvey et al. (2010) designed a task in which web-registered companies sponsored subjects' participation in a decision task involving the rating of a painting. The results showed that participants preferred the paintings presented next to the logo of the sponsoring company. The neural response in the vmPFC increased with increasing preference ratings, and was stronger for sponsor than nonsponsor paintings. Finally, a series of recent experiments demonstrated that social context provided by a risk-averse expert economist can modulate valuation-related activity in a network of structures that included striatum, anterior insula (AI) and ACC (Engelmann et al., 2009a), as well as vmPFC (Engelmann et al., 2012). Specifically, risk-averse advice from a trustworthy expert economist was demonstrated to increase the frequency of risk-averse choices and concurrently decreased correlations between vmPFC activity during choice and a model parameter reflective of risky choice alternatives in adult participants. Taken together, these results suggest that valuation-related activity in vmPFF can be modulated by a variety of social contexts, ranging from inequality, sanctions, and marketing actions, to the presence of advice.

3.3 Social context and the insula

Modulation of activation in insular cortex has been shown to correlate with decisions in economic games (Rilling et al., 2008; Wright et al., 2011), as well as the decision to help others (Hein et al., 2010; Ma et al., 2011). Rilling et al. (2008) investigated the neural response to nonreciprocation of cooperation, using an iterated version of the prisoners' dilemma (PD). In the PD, each of two players makes one of two choices: cooperate or defect. In case of mutual cooperation, both players receive an economic payoff with medium amount (e.g., 4 MU), in case of mutual defection both receive a low amount (e.g., 1 MU). If player A defects and player B cooperates, A receives an economic payoff with a maximal amount (e.g., 5 MU), whereas B receives 0 MU. The same holds for the opposite, that is, B defecting and A cooperating. If the PD is played sequentially, each of the players has the chance to punish the other player

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at cost to himself. According to Rilling et al. (2008), unreciprocated cooperation in the PD is associated with greater activity in bilateral AI, left hippocampus and left lingual gyrus, compared with reciprocated cooperation. Moreover, the functional connectivity between AI and lateral OFC in response to unreciprocated cooperation predicted subsequent defection (Rilling et al., 2008).

Wright et al. (2011) varied the social context to investigate the neural and behavioral correlates of objective and contextual fairness perception in the ultimatum game (UG). In the UG, one player (the proposer) makes an offer, which the other player (the recipient) can accept or reject. In the case of rejection, both players receive nothing. Wright et al. manipulated the context of the offers by presenting them either alone, interleaved with higher offers from different proposers, or interleaved with lower offers, thus varying the perceived fairness of objectively identical offers. The behavioral results showed increased acceptance when offers were contextually perceived as fairer (e.g., when presented in the context of low offers), despite being objectively identical. The imaging results suggested that the social context of the offer is integrated in posterior and mid-insula.

In the domain of prosocial decisions, Ma et al. (2011) investigated the impact of subjective socioeconomic status on empathy, and the willingness to make an anonymous monetary donation to a charitable organization. Empathy induced by painful faces correlated with activity in insula, inferior frontal and somatosensory cortices. In participants with subjectively high socioeconomic status, a stronger neural empathic response correlated with greater monetary donations, whereas the reverse pattern was found in participants with low socioeconomic status.

The authors of another study investigated the impact of group membership on empathy and later costly helping (Hein et al., 2010). In the first part of the study, soccer fans observed pain in a fan of their favorite soccer team (an ingroup member) or in a fan of the rival team (an outgroup member). The results showed a significant reduction of activation in the AI when the suffering other was an outgroup member as compared to the ingroup member. Moreover, participants who reported a particularly negative attitude towards the outgroup member displayed neural activation in ventral striatum when they saw the outgroup member suffering. In the second part of the study, the participant in the scanner could decide to alleviate the pain of the ingroup or the outgroup member by volunteering to receive half of that person's pain himself. The behavioral results showed an ingroup bias in helping, which was predicted by the individual group difference in AI signal. The stronger the difference in empathy-related AI activation in a direction favoring the ingroup member, the more likely the person was to help the ingroup member and not the outgroup member. Moreover, activation in nucleus accumbens when observing the outgroup member suffering predicted a lack of helping towards the outgroup member.

Taken together, these results implicate the AI in fairness- and empathy-related emotions that are modulated by social context, such as relative perceived fairness, socioeconomic status and group belonging.

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4 CONCLUSION

It is well known that context is an important determinant of behavior. Here, we have reviewed evidence demonstrating that contextual factors can have important modulatory influences on multiple processes underlying decision-making, including perceptual judgments across modalities, cognitive, and attentional control, as well as valuation of nonsocial and social stimuli. While all these processes are required for successful decision-making, particular emphasis was placed on evidence indicating contextual effects on valuation. Contextual factors that have been demonstrated to significantly modulate reward value include the availability of other (even putatively irrelevant) choice options, changes in reference point due to one's role during economic transactions, as well as a variety of social contexts. Findings from neuroimaging studies provide evidence for the modulatory role of nonsocial and social contextual factors in valuation-related brain activity. Neuronal activity in midbrain dopamine neurons and their striatal targets, as well as vmPFC/OFC have been shown to be modulated by a variety of nonsocial contexts using multiple neuroscientific approaches. Similar context-dependent modulations of valuation-related neuronal activity have been observed in social contexts, such as relative socioeconomic status, and reputation formation and updating. A consistent picture that emerges from the results reviewed above is that valuation-related activity in striatum and vmPFC is highly context dependent in both the nonsocial and social domain. These results are consistent with our previous proposal that motivational context modulates behavior and concurrent brain activity in task-relevant neural networks (Pessoa and Engelmann, 2010). This review of the neuroeconomic literature supports and extends this proposal by revealing consistent modulation of task-relevant valuation-related signals in ventral striatum and vmPFC by a range of contextual factors.

In conclusion, corroborating evidence from multiple fields including marketing research, behavioral economics, psychology, monkey electrophysiology and human neuroimaging indicate that context influences valuation at the behavioral and neural level. These results are inconsistent with important assumptions of rational choice theory. Alternative approaches to model and explain choice behavior have been applied successfully to nonsocial decision-making (Basten et al., 2010; Hare et al., 2011; Krajbich et al., 2010). Future research is required to further evaluate the potential and limitations of such models, such as their applicability to social decision-making.

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