Do you make a difference? Social context in a betting task

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Social context strongly influences human motivated behavior. The triadic model implicates three major nodes in the regulation of motivated behavior, i.e. amygdala, medial prefrontal cortex (mPFC) and striatum. The present work examines how social context modulates this system. Nineteen healthy subjects completed an event-related functional magnetic resonance imaging study of a monetary betting task in the presence (social trials) and in the absence of a social peer (nonsocial trials). In the social trials, the scanned subject played along with another subject, although their performances were independent from one another. In the nonsocial trials the scanned subject played alone. Although behavioral performance did not differ between social and nonsocial trials, BOLD signal changes during betting were significantly greater in the amygdala bilaterally and the right dorsolateral prefrontal cortex (BA 9) in the social condition relative to the nonsocial condition. In contrast, activation was greater in ventral striatum in the nonsocial condition relative to the social condition. These findings suggest that social context modulates the triadic neural-systems ensemble to adjust motivated behavior to the unique demands associated with the presence of conspecifics.

Keywords: amygdala; ventral striatum; BA 9; decision-making; social context

INTRODUCTION

John is playing a game of chance—a slot machine—in a casino. There is another slot machine sitting beside his machine—sometimes it is vacant, other times there is another person playing it. Even though the two games are independent, does the presence of this other person affect John? The question posed in this study is whether social presence induces an implicit state of alertness that influences the neural substrates of decision making and choice behavior.

Studies of decision making in social contexts have largely employed frameworks of strategic interaction (Lee, 2008), in which two individuals perform actions that reciprocally affect each other. However, in the absence of reciprocal interactions, questions remain concerning the degree to which the mere presence of a ‘social other’ affects one’s decision making (Aiello and Douthitt, 2001), along the lines of the notion of social facilitation (Zajonc, 1965). Understanding the underlying neural correlates of these effects may help to clarify the neurobiology underlying fundamental aspects of human behavior.

A growing literature has examined the neural underpinnings of decision making (Ernst and Paulus, 2005). A triadic neuroscience systems-based model has been proposed for the mechanisms underlying changes in motivated behavior during development (Ernst et al., 2006), based on formulations of the mechanisms of motivated behavior from neurophysiological evidence (Damasio, 1996; Rogers et al., 1999; Clark et al., 2004). The triadic model posits that motivated behavior is the product of the integrated activity of three distinct, although overlapping, systems serving three functions, approach, avoidance and modulatory (Ernst et al., 2006; Ernst and Fudge, in press). Striatum, amygdala and medial/ventral prefrontal cortex have been identified as mapping to these three functions, respectively, with the understanding that each one is part of its own network. This formulation was based on the recognition of a dominant role of these structures from lesion and activation studies (Ernst and Fudge, in press). This concept of functional dominance is critical as it implies, correctly, that each node serves other functions, including those carried by the other two nodes. The triadic model is a platform specifically conceived to guide functional neuroimaging studies that examine how critical factors—such as social context—influence mechanisms underlying motivated behavior.

Motivated behavior is thus understood as the output of the integrated activity among three systems whose overall balance may be uniquely set for each individual. This idea is central to the mechanisms underlying the regulation of
motivated behavior, and is particularly suited for examining the influence of social factors. Highly relevant is the recognition of a set of structures associated with the coding of social information that have substantial commonality with those involved in the triadic model (Nelson et al., 2005). A host of studies have identified the amygdala as a critical structure for the coding of affective social information (Adolphs, 2003; Amaral, 2003). The medial frontal cortex has been identified to be particularly involved in social cognition processes (Amodio and Frith, 2006). Self-referential processes—cognitive processes that involve the generation, manipulation or processing of a model of the ‘self’—are also thought to engage midline areas of the prefrontal cortex (Gusnard et al., 2001; Northoff et al., 2006). In addition, there is a great overlap between areas involved in the so-called ‘theory of mind’ processes (Siegal and Varley, 2002; Frith and Frith, 2006) and the frontal circuits underlying decision-making processes. Rewarding social stimuli involve the activation of the striatum (Insel, 2003; Depue and Morrone-Strupinsky, 2005; Nelson et al., 2005). Moreover, different aspects of social contexts, such as trust (Rilling et al., 2004), social comparison (Fliesbach et al., 2007), and the acquisition of favorable reputation (Izuma et al., 2008) seem to modulate activity in the striatum as well.

The presence of an unfamiliar other is expected to activate a system of alertness that prepares the organism for a rapid response to a potential danger. This prediction is consistent with data showing innate fear responses to un-encountered conspecifics (Misslin, 2003), and weaker amygdala activity to familiar faces than to novel faces, in line with the notion that the amygdala subserves the guarded attitude when meeting someone unknown (Gobbini and Haxby, 2006). During a game of chance that engages the reward (approach) circuitry (Wise and Rompre, 1989; Mogenson and Yang, 1991; Di Chiara, 1999; Delgado et al., 2000), an unfamiliar presence might recruit the amygdala and fear-related circuitry, and dampen activation of the striatum and reward-related network. In contrast, a game of chance played alone might set the brain to a reward mode that enhances striatal responsiveness to stimuli.

To the best of our knowledge, no study has yet investigated the effects of a passive, noninteracting social other on the neural substrates of decision making. To address this question, we used functional magnetic resonance imaging (fMRI) paired with a monetary betting task that is performed either concurrently with a social peer (social trials) or alone (nonsocial trials). We predicted in the social vs nonsocial contrast (i) greater activation of amygdala, based on its role in affective and behavioral responses to threat and social stimuli (Price et al., 1996; Amaral, 2003; Schwartz et al., 2003; Fox et al., 2005; Satpute and Lieberman, 2006); (ii) greater activation of medial prefrontal cortex based on its role in social cognition (Amodio and Frith, 2006) and self-referential processes (Northoff et al., 2006); and (iii) lower activation of the striatum based on the dampening of approach behavior associated with the emergence of a state of alertness (Ernst et al., 2006).

MATERIALS AND METHODS

Subjects

Nineteen healthy Japanese volunteers (nine females; mean age 21.6, range 19–24), recruited from local universities, participated in an event-related fMRI experiment. Two subjects were studied at each experimental session. Both subjects played the task twice, once in the scanner and once outside the scanner, in a randomized order (one subject only performed the task in the scanner). Only the data of the subjects in the scanner were analyzed. Pairs of subjects were college students of same gender who met for the first time in the day of the experiment. In the scanner, stimuli were projected onto a screen at the head of the scanner bed via an LCD projector. The fMRI-subject viewed the screen via a mirror attached to the head coil, and responded via a response pad placed inside the scanner. Straps were used to reduce head motion. The non-fMRI subject saw the same stimuli displayed on a computer monitor in the control room, and responded via keyboard.

The study was approved by the local institutional review board and carried out in accordance with the Declaration of Helsinki. All subjects gave written informed consent after receiving detailed explanation about the study. Subjects were trained on the task outside the scanner to obviate any learning effects. All subjects were right-handed, as determined by the Edinburgh Handedness Inventory, and had normal or corrected-to-normal vision. None reported any medical or psychiatric problems or to be on any medications. Subjects were told that after the experiment they would receive the initially agreed amount (4000 yen), plus an additional bonus depending on their performance. At the end of the study, all subjects were given a set amount of 5000 yen (for practical reasons we were unable to pay different amounts to each subject. This fact was explained to the subjects at debriefing time).

Task

The social/nonsocial betting paradigm (SNSB task) was programmed using Presentation (Neurobehavioral Systems, Inc., Albany, CA, USA). The SNSB consists of making bets on the color of a card. The rule was always the same: the subject won the amount that was bet if the card was green, but lost that amount if the card was red (Figure 1). Cards were initially presented on their back. Subjects were told that each card had 50% chances of being green, and 50% chances of being red. Two point values were presented to the subjects at the onset of each trial as possible bets. Subjects were asked to select one of the amounts as their bet. The goal of the game was to maximize the cumulative number of points.

At the onset of each trial, participants were cued to the trial type: nonsocial trials were indicated by displaying the visual cue representing the fMRI-subject (e.g. A), whereas
the social trials were indicated by displaying both visual cues representing the fMRI-subject and the non-fMRI subject (A and B). Letters were assigned at random to each pair of subjects, and remained the same for the whole experiment.

In the nonsocial trials, fMRI-subjects selected their bet and then feedback was presented, i.e. the color of the card was revealed along with the cumulative number of points. In the social trials, the fMRI-subject selected their bet, then the non-fMRI subject selected a bet from the remaining option and a newly available option, and finally, during feedback, the color of the card was shown revealing whether both subjects won or lost. During feedback, the cumulative number of points for each player was displayed as bar graphs.

The period of interest for this study was the selection phase, which was identical in both social and nonsocial trials. The selection phase included the evaluation of the options (500 ms) and the betting (3000 ms). The details of the task are depicted in Figure 1.

As already mentioned, the bets were placed on point values. Pairs of point values were presented at each trial: either both values were high (253, 252 or 251 points), both values were low (68, 67 or 66 points), or one value was high and the other low. Subjects were told that the total cumulative points at the end of the game were to be converted into a monetary bonus.

The SNSB task comprised 256 trials, distributed into four runs of 64 trials each. Each run included 42 social trials and 22 nonsocial trials, presented in pseudo-random order. The greater number of social vs nonsocial trials was to accommodate the greater number of potential combinations of bets in the social vs nonsocial conditions. In addition to the social and nonsocial trials, 32 fixation trials (white crosshair at the center of the screen) of 3000 ms duration were pseudo-randomly interspersed among trials and served as baseline. Trials were separated by intertrial intervals of 1500 ms average duration, which were jittered between 0 and 3000 ms.

**FMRI data acquisition**

Subjects were scanned on a 1.5T scanner (Shimadzu-Marconi Magnex Eclipse 1.5T Power Drive 250). T2-weighted anatomical images were acquired in the same plane as the functional images using a fast spin echo sequence.

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**Fig. 1** Two successive trials are presented in this figure. The upper panel represents the timeline for a social trial, and the bottom panel the timeline for a nonsocial trial. The type of trial, social vs nonsocial, is announced by the first screen. In the social trial, both ‘A’ (fMRI subject) and ‘B’ (peer) are highlighted. In the nonsocial trial, only ‘A’ (the fMRI subject) is highlighted. This screen stays on for 500 ms. The next screen presents the bets (here 66 and 68), one of which is selected by the fMRI subject (3500 ms). This 3500 ms period is the time window under study. The next screen either remains unchanged (nonsocial) (1000 ms); or, for the social condition, is updated with a third choice for the peer selection, since one of the two previous choices has already been taken, and the peer bets on one of the two available point amounts (3500 ms). The last screen displays the feedback (3000 ms), during which the subject sees two bar graphs. One bar graph represents the fMRI subject’s cumulative point amount (in percent of the highest possible amount), and the other bar graph represents either the peer’s cumulative amount in the social trial, or a set 50% amount in the nonsocial trial. Next, a central fixation point appears for an intertrial interval of a jittered duration averaging 1500 ms.
right before the start of the experimental task (TR = 5468 ms, TE = 80 ms, FA = 90°, FOV = 224 x 224 mm, matrix size = 256 x 256, in plane resolution 0.875 x 0.875 mm). Functional images were acquired in 30 contiguous 3 mm axial slices parallel to the AC-PC line (TR = 3000 ms, TE = 49 ms, FA = 90°, FOV = 224 x 224 mm, matrix size = 64 x 64, in plane resolution 3.75 x 3.75 mm). This sequence permitted coverage of the brain between a superior horizontal plane at z = 45 mm, and an inferior horizontal plane at z = −45 mm. The slices were acquired in descending interleaved order. A total of 255 volumes were acquired in each of the four runs. At the start of each session, the screen remained blank for 18 s to allow time for magnetization to stabilize (the corresponding six volumes were discarded from the analysis). Whole-brain T1-weighted anatomical images (voxel size 1 x 1 x 1 mm) were also acquired after the completion of the experimental runs.

FMRI data preprocessing

Image preprocessing and all subsequent image analyses were done using the Statistical Parametric Mapping software (SPM5, Wellcome Department of Imaging Neuroscience, UK). Images were corrected for nonsimultaneous slice acquisition (the first slice used as the reference slice), and realigned for motion correction to the first image of the corresponding run. The subject’s T2-weighted co-planar anatomical image was first coregistered to the mean functional image, and then coregistered to the subject’s T1-weighted anatomical image while keeping the functional images in alignment. Functional images were then spatially normalized (resampled voxel size 2 x 2 x 2 mm) by using the SPM T1 template defined in the Montreal Neurological Institute (MNI) space, and smoothed using a 6 mm FWHM Gaussian kernel. No subjects moved more than the length of a voxel in any one direction, thus none was excluded from the analysis.

FMRI analysis

Analyses were based on blood oxygen level dependent (BOLD) contrasts. At the individual-level (i.e. time series), event-related response amplitudes were estimated on a voxel-by-voxel basis using the General Linear Model (GLM) implemented in SPM5 and other routines written in Matlab 7.1.0.183 (MathWorks, Inc., Natick, MA, USA). The time series for each voxel was high-pass filtered to 1/128 Hz, and serial correlations were corrected by an autoregressive AR(1) model (global signal changes were not removed).

The GLM consisted of the three regressors of interest, two regressors for the selection phase (selection-social, selection-nonsocial and one regressor for the fixation period), plus six regressors describing residual motion, and four regressors of no interest for the feedback phase (win-social, win-nonsocial, lose-social and lose-nonsocial). The waveform used to model each type of event-related response in the GLM was a rectangular pulse of the duration of the event (i.e. 3500 ms for the selection phases, and 3000 ms for the fixation periods) convolved with the synthetic hemodynamic response function provided by SPM5. Contrast images of (selection-social vs selection-nonsocial) were generated for each subject using pairwise comparisons of the event-related BOLD responses across event types.

A random effects model was employed to permit population-level inferences (Penny et al., 2003). Subject-specific contrast images of parameter estimates were used as inputs (subject as a random factor). Based on a priori hypotheses, we conducted analyses of the following regions of interest (ROI): amygdala, mPFC [encompassing Brodmann Areas (BA), 8, 9, 10, 11, 24 and 32] (Amadio and Frith, 2006), and ventral striatum. Because the mPFC is a relatively large area, we additionally included two ROIs that were found in a previous study to be linked with decision making involving probabilistic rewards (Eshel et al., 2007). That study found that the orbitofrontal/ventrolateral prefrontal cortex (OFC/VLPFC) and the dorsal anterior cingulate cortex (ACC) of adult subjects responded preferentially to risky choices as opposed to safe choices. We chose the voxels in the ACC because they sit in the cortical midline. The voxels are (x, y, z MNI coordinates) 0, 4, 26 and 4, 26, 32. The functionally determined ROIs were defined as 10 mm spheres centered in those voxels.

The amygdala and mPFC ROIs were defined using the Anatomical Automatic Labeling (AAL) system (Tzourio-Mazoyer et al., 2002) and applied in the second-level analyses. The ventral striatum, because it is not included in the AAL system, was ascertained from standard anatomical criteria (Talairach and Tournoux, 1988; Duvernoy, 1999). Voxel-wise tests were performed in the ROIs using small volume correction (SVC) implemented in SPM5 (Worsley et al., 1996). Statistical significance of activation in the regions of interest was set to P < 0.05 corrected for family-wise error as implemented in SPM5 and an extent threshold of 10 adjacent voxels. In addition, significant findings were decomposed by extracting the individual mean parameter estimates around the peak voxels (6 mm sphere) from the contrast images (selection-social vs fixation) and (selection-nonsocial vs fixation).

Behavioral analysis

We assessed the degree to which social context influenced risk-taking behavior by analyzing the rate of selection of the high bet when the options were high-low in social and non-social trials using a repeated measures ANOVA with Context (social vs nonsocial) as the within subjects factor. In addition the percent selection of low bets was used as a measure of loss aversion to examine individual differences on this variable.

A second repeated measures ANOVA with social Context and bet Selection as the within subjects factors was
conducted for the selection reaction times in the four different bet combinations: high bet when high–low, low bet when high–low, low bet when low–low and high bet when high–high.

In addition, subjects' answers to a series of questions like 'Did you employ a strategy when making choices in the social trials?' were collected at debriefing time.

RESULTS

Behavioral measures

The high-risk selection rate—rate of selection of the high bet when the choice was between a high and a low bet—did not significantly differ between social and nonsocial trials \(F(1,18) = 0.04, P = 0.85\). In both contexts, in average subjects selected about 50% of the times the high amount of points in the high–low combination (social: 52.5% ± 20.9; nonsocial: 53.2% ± 18.1). The percentage of times the high bet was chosen when the options were high–low was normally distributed across subjects. No differences regarding the variance (standard deviation) in choice behavior were found between social and nonsocial trials \(F(1,18) = 0.50, P = 0.49\), variance of the percent of times the high bet was chosen when the options were high–low: social: 45.6% ± 7.1; nonsocial: 46.7% ± 5.3.

Similarly, reaction times did not differ between social and nonsocial trials \(F(1,18) = 0.21, P = 0.65\) (Figure 2). However, reaction time on similar bets (high–high and low–low) was longer than reaction time on differing bets (high–low) [main effect of bet Selection, \(F(3,54) = 6.7, P = 0.0006\)], suggesting that more cognitive resources were devoted to decision making when subjects were required to select between options of similar values, relative to when they were required to select between options of substantially different values. There was no interaction of social Context with bet Selection on reaction time \(F(3,54) = 0.94, P = 0.43\).

![Fig. 2](image_url)  
**Mean reaction times (±SEM) by trial type:**

Table 1 Regional activation in the contrast social selection > non-social selection and non-social selection vs social selection

| Location          | MNI Voxel coordinates (mm) | T    | Z    | K    |
|-------------------|-----------------------------|------|------|------|
| Social vs Nonsocial | L amygdala                  | -28  | -4   | -12  | 3.94 3.3 11 |
|                   | R amygdala                  | 28   | 2    | -14  | 3.71 3.16 48 |
|                   | R dorsolateral PFC (BA 9)   | 44   | 26   | 38   | 5.76 4.28 31 |
| Nonsocial vs Social | R ventral striatum (nucleus accumbens) | 18   | 8    | -10  | 3.86 3.25 41 |

Table shows the peaks of activity in a priori regions of interest that survive a threshold of \(P < 0.05\), corrected for family-wise error inside the region.

Functional imaging data

The results of the imaging analyses in the regions of interest are presented in Table 1, and Figures 3 and 4. Because we were interested in the modulation of the circuits involved in motivated behavior as proposed by the triadic model, we examined the brain activity during the selection phase in the social vs nonsocial conditions. The contrast between the social trials vs nonsocial trials revealed significant activation in the right and left amygdalae, consistent with our predictions. Moreover, a cluster of activation was found in the right dorsolateral prefrontal cortex (DLPFC), in BA 9. The contrast nonsocial vs social selection revealed significant activation in the right ventral striatum (VS), also in line with our predictions. In all regions, inspection of the mean parameter estimates obtained for choice in social and nonsocial trials indicated that there were increases, and not decreases, in activation relative to fixation, in both trial types. No voxels survived the thresholds of acceptance in the functionally determined ROIs in the ACC.

DISCUSSION

The current study examined the modulation of the brain circuits involved in decision making by the social context. Subjects performed a binary monetary betting task in an fMRI setting either in conjunction with another player or in social isolation. Our predictions were that the presence of another person would induce a state of alertness in the subjects, which would enhance activation of the threat system and reduce activation in the reward system during the betting task. In addition, medial regions of the brain associated with reflective cognitive processes were expected to be more responsive in the social condition than in the nonsocial condition.

Findings were partially in line with predictions. As predicted, the left and right amygdalae were recruited more strongly in social trials than in nonsocial trials, and ventral striatum was recruited more strongly in nonsocial trials than in social trials. However, the focus of activity in the PFC...
found in the social trials vs nonsocial trials, though inside one of the predetermined ROIs (BA 9), was not medial but dorsolateral ($x = 44$).

Against this background of differential neural activation, the behavioral pattern of decision making and reaction time did not differ between conditions. The lack of performance difference suggests that the neural coding of social context, when kept to a low level (noninteractive player), is not translated readily at the behavioral level. Another possibility for the absence of behavioral differences could be due to the design of the task that purposely was devoid of an optimal strategy. This design was chosen to minimize having subjects anticipating the strategy of the other player. Finally, a study with a larger sample or with a higher number of experimental trials might have provided more power to detect performance difference.

On the other hand, the absence of a behavioral difference between conditions also presents some advantages. If performance had differed between the two conditions, any differences in brain regions could have been attributed to differential rewards across the two conditions or differences in overall processing devoted to the task, as opposed to a specific effect of social context. As such, in the absence of performance difference the observed differences in neural activation might be more easily interpreted as a direct consequence of the social manipulation rather than as an artifact of differential task performance across conditions. Making inferences from brain activation findings alone in the

Fig. 3 Activations in the contrast social selection vs nonsocial selection. The top panel represents activation of right dorsolateral prefrontal cortex (BA 9) and bilateral amygdalae rendered on a single-subject T1-image provided by SPM5. The bottom panel represents the mean parameter estimates ($\pm$ s.e.m.) in a 6 mm sphere centered in the respective peak voxels (Table 1).
absence of behavioral differences is not novel and such findings have been found to be quite informative (Hariri et al., 2002; Hariri and Weinberger, 2003; Schmitz et al., 2004; Wilkinson and Halligan, 2004).

It is important to highlight that even though the betting task did not have a ‘winning strategy’, according to answers to the debriefing questionnaires, 16 out of 19 subjects reported that they were following a strategy when making choices in the social trials. Likewise, 16 subjects reported having a choice strategy when playing the nonsocial trials (out of which 14 of them said they had a strategy in the social trials). Taken together, these data indicate that the great majority of the participants were not placing bets at random, and were attending to the other player in the social trials, all despite the randomness of the outcomes in the task.

The preferential recruitment of the amygdala in the social trials is consistent with the role of this structure in socially elicited emotions (Adolphs et al., 2002). In addition, based on the specialized function of the amygdala in processing threat stimuli (LeDoux, 2000), its recruitment may reflect the coding of a warning signal (Holland and Gallagher, 1999; Davis and Whalen, 2001) associated with the detection of an unknown ‘social other’. This signal is expected to modulate actions to enhance safety, by controlling approach and facilitating avoidance behavior. However, it is also possible that the differential amygdala activation reflects the greater salience or motivational value of the social trials over the nonsocial trials, as opposed to a feature of social valence (Zald, 2003). Dissociating social-salience from nonspecific salience effects might be addressed in future work.

Fig. 4 Activation of the ventral striatum in the contrast nonsocial selection vs social selection. The left panel represents activation of ventral striatum (nucleus accumbens) rendered on a single-subject T1-image provided by SPM5. The right panel represents the parameter estimate (±s.e.m.) in a 6 mm sphere around the peak voxel (Table 1).
through the use of parametric designs that manipulate separately the social factor and the salience of the trials.

A warning signal that controls approach behavior would be consistent with a relatively reduced engagement of the neural circuitry that facilitates approach, i.e. ventral striatum. Research in rodents has shown that the ventral striatum facilitates approach-behavior (Wise and Rompré, 1989; Di Chiara, 1999; Di Ciano et al., 2001), and human studies report greater ventral striatal activation in response to positive than in response to negative outcomes, i.e. stimuli that stimulate approach rather than avoidance (Breiter et al., 2001; Knutson et al., 2001). In short, the presence of an unfamiliar ‘social other’ might promote a state of alertness that mitigates approach behavior.

Given that the ventral striatum, similarly to the amygdala, is sensitive to the salience of stimuli (Horvitz, 2000), the opposite directions of activation of these structures (amygdala vs ventral striatum) as a function of social context suggests that these structures fulfill unique roles in the coding of information about social context rather than processing salience solely.

In contrast, the role of the right DLPFC region that emerged in our results is less clear. The literature reporting activation in this area is various, though typically linking activity in this area with working memory and executive control processes (Duncan and Owen, 2000; Kane and Engle, 2002; Hillary et al., 2006). Nevertheless, other studies have suggested the involvement of the DLPFC in the processing of several aspects of social stimuli. For instance, the DLPFC has been found to be preferentially active when viewing a superiorly ranked player (in terms of performance) in a noncompetitive game, as opposed to an inferior player (Zink et al., 2008), even though the hierarchy information was technically irrelevant to the game. Also, activity in the DLPFC was found to be positively correlated with increases in compliance with social norms, in a paradigm where subjects were subject to social punishment (Spitzer et al., 2007). Common to these two studies is the presence of a potential threat stimulus (i.e. the higher ranked player, and the social punisher), which would be in line with the ‘social other’ in the social trials of our study. From a different perspective, several studies have shown a link between the activity in the DLPFC and risk-taking behavior: while repetitive transcranial magnetic stimulation in the DLPFC—which momentarily disrupts activity in the region—increases risk-taking behavior (van’t Wout et al., 2005; Knoch et al., 2006), transcranial direct current stimulation—which upregulates activity in the region—suppresses risk-taking behavior (Fecteau et al., 2007; Fecteau et al., 2007). One possible interpretation, though not corroborated by behavioral evidence, is that the ‘social other’ indeed induced a decrease in risk-taking behavior in the social trials. Nevertheless, because this finding was not predicted in our a priori hypotheses, these interpretations should be considered purely speculative until further investigation.

In summary, we propose that amygdala come on line whenever an unfamiliar ‘social other’ is detected, and provide an alarm signal to facilitate adaptive behavior. This alarm signal may be reflected as a reduced engagement of the ventral striatum, known to mediate motivation for action, and approach behavior.

There are several limitations to this study. First, the emotions elicited by the social context were not examined systematically. A more in-depth debriefing would be valuable to examine more thoroughly feelings towards the other player. Another limitation of this study is that cognitive operations such as weighting relative gains, or tracking the other player’s selection strategy during task performance could have influenced the findings. However, the lack of differences in the players’ strategies and reaction times between the social and nonsocial contexts might support the absence of significant effects of these factors. In addition, brain regions typically involved in error monitoring, such as the dorsal anterior cingulate cortex (Bush et al., 2002), or computations, such as parietal cortex (Dehaene et al., 1999) were not activated in the social vs nonsocial comparison, also arguing against an effect of weighting one’s own outcomes against other’s outcomes. However, it will be important in future studies to monitor these factors through task manipulation. Finally, we did not examine sex differences because of the restricted sample size. This is a critical factor to include in future work, given the literature on sex-related differences in social cognition (Bennett et al., 2005). One caveat of this study is the fact that the MRLsubjects were aware that subjects outside the scanner were able to see their choices. This knowledge could have led to a possible confound involving responses to the situation of being observed. Though the effects of such a confound cannot be completely discarded, they were minimized by the fact that choices were observable in both social and nonsocial trials, and potentially removed in the direct comparison of social with nonsocial choices. Nevertheless, this issue is an interesting question in itself that deserves further consideration. Another caveat is the generalizability of the present findings to other cultural groups. Indeed, it would be interesting to confirm that these findings are not restricted to Asian college students. Given that the universality of the neural bases of ‘theory of mind’ across populations of different cultural backgrounds remains to be confirmed (Kobayashi et al., 2006, 2007), it is wise not to assume that the neural correlates of other social cognitive processes are universal until further evidence is obtained.

Of note, because there is evidence that loss-aversion affects brain activity (Dreher, 2007; Tom et al., 2007), we performed additional analyses to examine whether there was an effect of individual loss-aversion in the results. Individual loss-aversion scores (percent of time the subject chose the low bet when a high and a low bets were presented, across the social and nonsocial trials) were computed, and indeed individual differences were considerable: scores were normally distributed and ranged between 80% and 10% (mean loss...
aversion: 47.4% ± 17.4). However, analyses of covariation did not reveal any contribution of this factor on behavioral performance (reaction time) or brain responses (BOLD signal) (data available upon request). Because the present study was not designed to examine such individual differences, these results are presented only for completeness.

Despite these limitations, the findings indicate a clear influence of social context on the neural correlates of decision making (Ernst and Paulus, 2005) and social information processing networks (Nelson et al., 2005). The findings cannot be attributed solely to a nonspecific effect of salience of the social context since the pattern of activation includes both greater and lower regional activation in social vs non-social trials. This study suggests a number of directions for future research, as well as testable hypotheses. A critical component will be the assessment of psychopathologies manifesting core social deficits, such as social phobia, autism and psychopathy. Another research direction is the evaluation of neurodevelopmental changes in the interaction between social context and decision making, which is so critical in adolescence.

REFERENCES

Adolphs, R. (2003). Cognitive neuroscience of human social behaviour. Nature Reviews Neuroscience, 4(3), 165–78.
Adolphs, R., Baron-Cohen, S., Tranel, D. (2002). Impaired recognition of social emotions following amygdala damage. Journal of Cognitive Neuroscience, 14(8), 1264–74.
Aiello, J.R., Douthitt, E.A. (2001). Social facilitation from Triplet to electronic performance monitoring. Group Dynamics, 5(3), 163–80.
Amaral, D.G. (2003). The amygdala, social behavior, and danger detection. Annals of the New York Academy of Sciences, 1000, 337–47.
Ammodio, D.M., Frith, C.D. (2006). Meeting of minds: the medial frontal cortex and social cognition. Nature Reviews Neuroscience, 7(4), 268–77.
Bennett, S., Farrington, D.P., Huesmann, L.R. (2005). Explaining gender differences in crime and violence: the importance of social cognitive skills. Aggression and Violent Behavior, 10(3), 263–88.
Breiter, H.C., Aharon, I., Kahneman, D., Dale, A., Shizgal, P. (2001). Functional imaging of neural responses to expectancy and experience of monetary gains and losses. Neuron, 30(2), 619–39.
Bush, G., Vogt, B.A., Holmes, J., et al. (2002). Dorsal anterior cingulate cortex: a role in reward-based decision making. Proceedings of the National Academy of Sciences of the United States of America, 99(1), 523–8.
Clark, L., Cools, R., Robbins, T.W. (2004). The neuropsychology of ventral prefrontal cortex: decision-making and reversal learning. Brain and Cognition, 55(1), 41–53.
Damasio, A.R. (1996). The somatic marker hypothesis and the possible functions of the prefrontal cortex. Philosophical Transactions of the Royal Society of London Series B Biological Sciences, 351(1346), 1413–20.
Davis, M., Whalen, P.J. (2001). The amygdala: vigilance and emotion. Molecular Psychiatry, 6(1), 13–34.
Dehaene, S., Spelke, E., Pinel, P., Stanescu, R., Tsivkin, S. (1999). Sources of mathematical thinking: behavioral and brain-imaging evidence. Science, 284(5416), 970–4.
Delgado, M.R., Nystrom, L.E., Fissell, C., Noll, D.C., Fiez, J.A. (2000). Tracking the hemodynamic responses to reward and punishment in the striatum. Journal of Neurophysiology, 84(6), 3072–7.
Depue, R.A., Morrone-Strupinsky, J.V. (2005). A neurobehavioral model of affiliative bonding: implications for conceptualizing a human trait of affiliation. The Behavioral and Brain Sciences, 28(3), 313–50 discussion 350–95.

Di Chiara, G. (1999). Drug addiction as dopamine-dependent associative learning disorder. European Journal of Pharmacology, 375(1–3), 13–30.
Di Ciano, P., Cardinal, R.N., Cowell, R.A., Little, S.J., Everitt, B.J. (2001). Differential involvement of NMDA, AMPA/kainate, and dopamine receptors in the nucleus accumbens core in the acquisition and performance of pavlovian approach behavior. The Journal of Neuroscience, 21(23), 9471–7.
Dreher, J.C. (2007). Sensitivity of the brain to loss aversion during risky gambles. Trends in Cognitive Sciences, 11(7), 270–2.
Duncan, J., Owen, A.M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. Trends in Neurosciences, 23(10), 475–83.
Duvernoy, H.M., editor. (1999). The Human Brain – Surface, Blood Supply, and Three-Dimensional Sectional Anatomy, 2nd edn, NewYork and Vienna: Springer.
Ernst, M., Fudge, J. (in press). Adolescence: on the neural path to adulthood. Anatomy, connectivity of the nodes of the triadic model. In: Potenza, M., Grant, J., editors. Young Adult Mental Health, Oxford University Press.
Ernst, M., Paulus, M.P. (2005). Neurobiology of decision making: a selective review from a neurocognitive and clinical perspective. Biological Psychiatry, 58(8), 597–604.
Ernst, M., Pine, D.S., Hardin, M. (2006). Triadic model of the neurobiology of motivated behavior in adolescence. Psychological Medicine, 36(3), 299–312.
Eshel, N., Nelson, E.E., Blair, R.J., Pine, D.S., Ernst, M. (2007). Neural substrates of choice selection in adults and adolescents: development of the ventrolateral prefrontal and anterior cingulate cortices. Neuropsychologia, 45(6), 1270–9.
Fectue, S., Knoch, D., Fregoni, F., Sultani, N., Boggio, P., Pascual-Leone, A. (2007). Diminishing risk-taking behavior by modulating activity in the prefrontal cortex: a direct current stimulation study. Journal of Neurosciences, 27(46), 12500–5.
Fectue, S., Pascual-Leone, A., Zald, D.H., et al. (2007). Activation of prefrontal cortex by transcranial direct current stimulation reduces appetite for risk during ambiguous decision making. Journal of Neurosciences, 27(23), 6212–8.
Flessbach, K., Weber, B., Trautner, P., et al. (2007). Social comparison affects reward-related brain activity in the human ventral striatum. Science, 318(5854), 1305–8.
Fox, N.A., Henderson, H.A., Marshall, P.J., Nichols, K.E., Ghera, M.M. (2005). Behavioral inhibition: linking biology and behavior within a developmental framework. Annual Review of Psychology, 56, 235–62.
Frith, C.D., Frith, U. (2006). How we predict what other people are going to do. Brain Research, 1070(1), 36–46.
Gobbini, M.I., Hazby, J.V. (2006). Neural response to the visual familiarity of faces. Brain Research Bulletin, 71(1–3), 76–82.
Gusnard, D.A., Akbudak, E., Shulman, G.L., Raichle, M.E. (2001). Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. Proceedings of the National Academy of Sciences of the United States of America, 98(7), 4259–64.
Hariri, A.R., Mattay, V.S., Tessitore, A., et al. (2002). Serotonin transporter genetic variation and the response of the human amygdala. Science, 297(5580), 400–3.
Hariri, A.R., Weinberger, D.R. (2003). Imaging genomics. British Medical Bulletin, 65, 259–70.
Hillary, F.G., Genova, H.M., Chiaravalloti, N.D., Rypma, B., DeLuca, J. (2006). Prefrontal modulation of working memory performance in brain injury and disease. Human Brain Mapping, 27(11), 837–47.
Holland, P.C., Gallagher, M. (1999). Amygdala circuitry in attentional and representational processes. Trends in Cognitive Sciences, 3(2), 65–73.
Horvitz, J.C. (2000). Mesolimbocortical and nigrostriatal dopamine responses to salient non-reward events. Neuroscience, 96(4), 651–6.
Insel, T.R. (2003). Is social attachment an addictive disorder? Physiology and Behavior, 79(3), 351–7.
Izuma, K., Saito, D.N., Sadato, N. (2008). Processing of social and monetary rewards in the human striatum. Neuron, 58(2), 284–94.
Kane, M.J., Engle, R.W. (2002). The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: an individual-differences perspective. Psychonomic Bulletin and Review, 9(4), 637–71.

Knoch, D., Gianotti, L.R., Pasqual-Leone, A., et al. (2006). Disruption of right prefrontal cortex by low-frequency repetitive transcranial magnetic stimulation induces risk-taking behavior. Journal of Neurosciences, 26(24), 6469–72.

Knutson, B., Adams, C.M., Fong, G.W., Hommer, D. (2001). Anticipation of increasing monetary reward selectively recruits nucleus accumbens. Journal of Neurosciences, 21(16), RC159.

Kobayashi, C., Glover, G.H., Temple, E. (2006). Cultural and linguistic influence on neural bases of 'Theory of Mind': an fMRI study with Japanese bilinguals. Brain and Language, 98(2), 210–20.

Kobayashi, C., Glover, G.H., Temple, E. (2007). Cultural and linguistic effects on neural bases of 'Theory of Mind' in American and Japanese children. Brain Research, 1164, 95–107.

LeDoux, J.E. (2000). Emotion circuits in the brain. Annual Review of Neuroscience, 23, 155–84.

Lee, D. (2008). Game theory and neural basis of social decision making. Nature Neuroscience, 11(4), 404–9.

Missoni, R. (2003). The defense system of fear: behavior and neurocircuitry. Neuropsychologie Clinique, 33(2), 55–66.

Mogenson, G.J., Yang, C.R. (1991). The contribution of basal forebrain to limbic-motor integration and the mediation of motivation to action. Advances in Experimental Medicine and Biology, 295, 267–90.

Nelson, E.E., Leibenluft, E., McClure, E.B., Pine, D.S. (2005). The social re-orientation of adolescence: a neuroscience perspective on the process and its relation to psychopathology. Psychological Medicine, 35(2), 163–74.

Northoff, G., Heinzel, A., de Greck, M., Bernpolh, F., Dobrowolny, H., Panksepp, J. (2006). Self-referential processing in our brain – a meta-analysis of imaging studies on the self. Neuroimage, 31(1), 440–57.

Penny, W.D., Holmes, A.P., Friston, K.J. (2003). Random effects analysis. In: Frackowiak, R.S.J., Friston, K.J., Frith, C. et al. editors. Human Brain Function, 2nd edn, London: Academic Press.

Price, J.L., Carmichael, S.T., Drevets, W.C. (1996). Networks related to the orbital and medial prefrontal cortex: a substrate for emotional behavior? Progress in Brain Research, 107, 523–36.

Rilling, K.J., Sanfey, A.G., Aronson, J.A., Nystrom, L.E., Cohen, J.D. (2004). Opposing BOLD responses to reciprocated and unreciprocated altruism in putative reward pathways. Neuroreport, 15(16), 2539–43.

Rogers, R.D., Everitt, B.J., Baladachino, A., et al. (1999). Dissociable deficits in the decision-making cognition of chronic amphetamine abusers, opiate abusers, patients with focal damage to prefrontal cortex, and tryptophan-depleted normal volunteers: evidence for monoaminergic mechanisms. Neuropsychopharmacology, 20(4), 322–39.

Satpute, A.B., Lieberman, M.D. (2006). Integrating automatic and controlled processes into neurocognitive models of social cognition. Brain Research, 1079(1), 86–97.

Schmitz, T.W., Kawahara-Baccus, T.N., Johnson, S.C. (2004). Metacognitive evaluation, self-relevance, and the right prefrontal cortex. Neuronimage, 22(2), 941–7.

Schwartz, C.E., Wright, C.L., Shin, L.M., Kagan, J., Rauch, S.L. (2003). Inhibited and uninhibited infants ‘grown up’: adult amygdalar response to novelty. Science, 300(5627), 1952–3.

Siegal, M., Varley, R. (2002). Neural systems involved in ‘theory of mind’. Nature Reviews Neuroscience, 3(6), 463–71.

Spitzer, M., Fischbacher, U., Herrnberger, B., Gron, G., Fehr, E. (2007). The neural signature of social norm compliance. Neuron, 56(1), 185–96.

Talairach, J., Tournoux, P. (1988). Co-Planar Stereotaxic Atlas of the Human Brain: 3-Dimensional Proportional System: An Approach to Cerebral Imaging. New York: Thieme Medical Publishers.

Tom, S.M., Fox, C.R., Trepel, C., Poldrack, R.A. (2007). The neural basis of loss aversion in decision-making under risk. Science, 315(5811), 515–8.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., et al. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. Neuroimage, 15, 273–89.

van’t Wout, M., Kahn, R.S., Sanfey, A.G., Aleman, A. (2005). Repetitive transcranial magnetic stimulation over the right dorsolateral prefrontal cortex affects strategic decision-making. Neuroreport, 16(16), 1849–52.

Wilkinson, D., Halligan, P. (2004). The relevance of behavioural measures for functional-imaging studies of cognition. Nature Reviews Neuroscience, 5(1), 67–73.

Wise, R.A., Rompre, P.P. (1989). Brain dopamine and reward. Annual Review of Psychology, 40, 191–225.

Worsley, K.J., Marrett, S., Neelin, P., Vandal, A.C., Friston, K.J., Evans, A.C. (1996). A unified statistical approach for determining significant signals in images of cerebral activation. Human Brain Mapping, 4(1), 58–73.

Zajonc, R.B. (1965). Social facilitation. Science, 149, 269–74.

Zald, D.H. (2003). The human amygdala and the emotional evaluation of sensory stimuli. Brain Research Brain Research Reviews, 41(1), 88–123.

Zink, C.F., Tong, Y., Chen, Q., Bassett, D.S., Stein, J.L., Meyer-Lindenberg, A. (2008). Know your place: neural processing of social hierarchy in humans. Neuron, 58(2), 273–83.