

## Delineating the social valuation network in adolescents

Poornima Kumar,<sup>1,2</sup> Angela Pisoni,<sup>3</sup> Erin Bondy,<sup>4</sup> Rebecca Kremens,<sup>1</sup> Paris Singleton,<sup>5</sup> Diego A. Pizzagalli,<sup>1,2,6,†</sup> and Randy P. Auerbach<sup>7,8,†</sup>

<sup>1</sup>Center for Depression, Anxiety and Stress Research, McLean Hospital, Belmont, MA, 02478, USA, <sup>2</sup>Department of Psychiatry, Harvard Medical School, Boston, MA, 02115, USA, <sup>3</sup>Department of Psychology & Neuroscience, Duke University, Durham, NC, 27708, USA, <sup>4</sup>Department of Psychological & Brain Sciences, Washington University, St. Louis, MO, 63105, USA, <sup>5</sup>Department of Psychiatry & Behavioral Sciences, Northwestern University, Chicago, IL, 60611, USA, <sup>6</sup>McLean Imaging Center, McLean Hospital, Belmont, MA, 02478, USA, <sup>7</sup>Department of Psychiatry, Columbia University, New York, NY, 10032, USA, and <sup>8</sup>Division of Clinical Developmental Neuroscience, Sackler Institute, New York, NY, 10032, USA

Correspondence should be addressed to Poornima Kumar, 115 Mill Street, Belmont, MA 02478, USA. E-mail: pkumar@mclean.harvard.edu; Randy P. Auerbach, 1051 Riverside Drive, Pardes 2407, New York, NY 10032, USA. E-mail: rpa2009@cumc.columbia.edu.

†Made equal senior contributions.

### Abstract

Adolescents strive for peer approval, and an increased sensitivity to peers' opinions is normative. However, among vulnerable adolescents, peer evaluation can be detrimental, contributing to affective disorders. It is, therefore, critical to improve our understanding of neural underpinnings of peer evaluation. Prior research has investigated averaged neural responses to peer acceptance or rejection, neglecting to probe trial-by-trial computations that mirror real-time updating of daily activities. In non-social decision-making, a common neural valuation system centered on the medial prefrontal cortex (mPFC) has emerged, which evaluates different reward types on a common scale to guide choices. However, it is unclear whether the mPFC also tracks complex social scenarios involving peer feedback. To address this gap, we acquired fMRI data from 55 healthy adolescents during the Chatroom Task, which probes peer evaluation, and implemented a computational approach to characterize trial-by-trial social value, thereby allowing us to interrogate the neural correlates of social value. Consistent with our hypothesis, social value signals were encoded in the mPFC. Interestingly, analyses also revealed a wider social-specific valuation network including the precuneus and amygdala. Understanding how adolescents make social decisions and neural markers associated with it, may, ultimately, help us clarify promising targets for intervention.

**Key words:** social value; peer evaluation; medial prefrontal cortex; amygdala; precuneus

### Introduction

Adolescence is characterized by greater reliance on peer relationships and more autonomy from parents (Brown, 2013). Although this is developmentally normative, the increased exposure to peer rejection, for some, may lead to the onset of mental

disorders (including depression) and an increased risk of suicidal behaviors (Platt *et al.*, 2013; Stewart *et al.*, 2018). Adolescence also is a critical period for brain development (Spielberg *et al.*, 2014), and thus, understanding the neural mechanisms that characterize social processes—particularly when adolescents

Received: 28 March 2019; Revised: 15 August 2019; Accepted: 2 October 2019

© The Author(s) 2020. Published by Oxford University Press.

This is an Open Access article distributed under the terms of the Creative Commons Attribution NonCommercial-NoDerivs licence (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial reproduction and distribution of the work, in any medium, provided the original work is not altered or transformed in any way, and that the work properly cited. For commercial re-use, please contact journals.permissions@oup.com

are accepted or rejected by peers—may elucidate potential targets to guide future preventative interventions.

A widely used experimental paradigm to probe neural correlates of peer evaluation is the Chatroom Task (Guyer *et al.*, 2008; Guyer *et al.*, 2009; Guyer *et al.*, 2012). This ecologically valid task delivers peer feedback (i.e. acceptance versus rejection) within a simulated social context. Neuroimaging studies using this task have identified a wide network of brain regions engaged during processing of peer feedback that are relevant to depression and anxiety disorders, including the striatum, insula, amygdala and medial and ventrolateral prefrontal cortex (VLPFC; Guyer *et al.*, 2008; Guyer *et al.*, 2012; Lau *et al.*, 2012). Specifically, among healthy adolescents, the striatum, thalamus and VLPFC were recruited more strongly during peer acceptance compared to rejection, whereas the amygdala, mPFC and insula were more strongly recruited during peer rejection relative to acceptance (Guyer *et al.*, 2008; Guyer *et al.*, 2012). Interestingly, relative to healthy adolescents, anxious and depressed adolescents showed increased amygdala, insula and mPFC activation, and mPFC–amygdala coupling during peer rejection (Guyer *et al.*, 2009; Lau *et al.*, 2012; Silk *et al.*, 2014; Spielberg *et al.*, 2014).

Although these studies have provided important insights, these analyses have relied on averaged neural responses to peer acceptance and rejection across trials, neglecting to probe critical trial-by-trial computations. A trial-level approach is important and can potentially provide more fine-grained information that sheds light on computational processes relevant to affective disorders. This is critical as, in daily life, we continuously update our preferences based on expected and unexpected outcomes. For example, if a peer acts in an untoward way, the reflexive response would be to update the value of this peer (e.g. act in a more cautious manner during the subsequent encounter). In this context, social processing involves continuously updating the value associated with social stimuli based on the discrepancy between the expected and predicted social outcomes (e.g. whether or not the person you expected to like reciprocated your feelings). As the Chatroom Task reliably probes brain regions involved with social computation, there is an opportunity to elucidate regions implicated in this social valuation process.

During this task, participants initially select same-aged peers to chat with later in the study (i.e. *Initial Value*). After a brief delay typically spanning 1–2 weeks, participants rate their expectation of peers' interest in chatting with them (i.e. *Expected Value*) and later receive explicit feedback from peers—they are either accepted or rejected—and then rate their subjective feeling after receiving the outcome (i.e. *Social Outcome*). We expected that the discrepancy between the *Expected Value* and *Social Outcome* would lead to a social prediction error, which may then be used to update their *Initial Value* of the peer to obtain an updated *Social Value* for this peer. Utilizing this computational framework allows the computation of an individual's social value on a trial-by-trial basis after every outcome and the identification of brain regions that compute and encode this value. This may, ultimately, improve our understanding of social processes in the context of peer evaluation.

It has been proposed that social decisions may draw on a similar reinforcement learning framework as utilized during non-social decision making (Ruff & Fehr, 2014). In this context, it has been proposed that a common neural valuation network exists (Levy & Glimcher, 2012; Ruff & Fehr, 2014), which evaluates different reward types on a common scale to guide choices (Levy & Glimcher, 2012; Lehner *et al.*, 2017). The medial prefrontal cortex (mPFC) forms the core of this network and is consistently shown to encode subjective value for different types of simple

social (e.g. smile, praise) and non-social rewards [e.g. money, juice (Levy & Glimcher, 2012; Lin *et al.*, 2012)]. However, real-life social scenarios involve the integration of many potentially rewarding and aversive stimuli, and it is unclear whether there is a common neural valuation system that tracks these complex social scenarios (e.g. peer feedback). To address this gap, the study objective was to interrogate the neural correlates of social value during the Chatroom Task in healthy adolescents using a computational approach, involving trial-by-trial modulation of social value. Building on prior studies (Levy & Glimcher, 2012; Lin *et al.*, 2012), we hypothesized that the mPFC would encode social value across healthy adolescents during the Chatroom Task.

## Materials and methods

### Participants

Seventy healthy adolescents (45 females, 25 males) aged 12–14 years were recruited from the greater Boston area through online advertisements, posted flyers and direct mailings. Inclusion criteria included English fluency and right-handedness. Exclusion criteria included lifetime diagnosis of any psychopathology, mental retardation, organic brain syndrome, head injury resulting in loss of consciousness for 5 min or seizures. After exclusion due to motion and other structural abnormalities (see Results), the final sample considered for analyses included 55 adolescents (38 females, 17 males; age:  $13 \pm 0.82$ ).

### Procedure

The Partners Institutional Review Board provided approval for the study. Adolescents assented, and a legal guardian provided informed written consent. Procedures were completed over two laboratory visits. In the first visit, adolescents were administered a diagnostic interview using the Kiddie-Schedule for Affective Disorders and Schizophrenia (K-SADS-PL; Kaufman *et al.*, 1997). K-SADS is a semi-structured interview assessing lifetime DSM-IV disorders in youth. In addition, participants completed the Phase 1 of the Chatroom Task. During the second visit, which occurred within 1–2 weeks (mean =  $8.5 \pm 6.9$  days), participants completed Phase 2 of the Chatroom Task outside of the scanner, and Phase 3 was completed while functional magnetic resonance imaging (fMRI) data were acquired. High-resolution structural MRI data also were also acquired to aid registration of functional images to MNI space. Participants were remunerated \$80 (\$40 for Day 1 and \$40 for Day 2) for their participation.

### Chatroom task

The Chatroom Task (Guyer *et al.*, 2008, 2009; Figure 1) was designed to simulate differential response to peer feedback (i.e. acceptance versus rejection). E-Prime (Psychological Software Tools, Pittsburgh, PA) software was used to present stimuli and record responses. This task was divided into three phases. In Phase 1, participants were led to believe they were participating in a nationwide study of how adolescents interact in online chatrooms. First, they created an online profile (i.e. indicating likes and dislikes) and then photographs of the participants were taken. Next, they viewed photographs of 60 same-aged female/male adolescents (corresponding to the gender of the participant) and selected 30 adolescents they were 'interested' and 30 adolescents they were 'not interested' in chatting with online following a neuroimaging scan 1–2 weeks later [Note: this

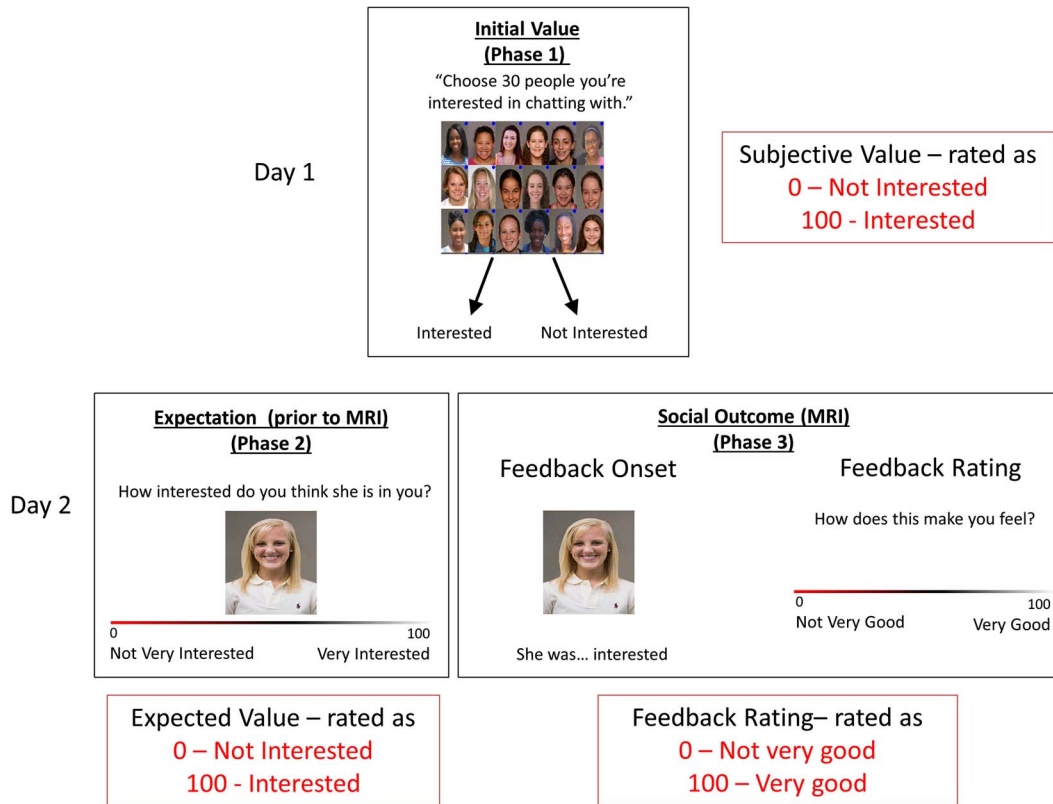


Figure 1. Task design of Chatroom Task, showing Phases 1, 2 and 3—Phases 1 and 2 took place outside the scanner, whereas Phase 3 occurred during the fMRI acquisition.

was a categorical decision between not interested and interested options]. Participants were informed that female/male peers (corresponding to the gender of the participant) from collaborating institutions would review their profiles and indicate whether they were interested (i.e. peer acceptance) or not interested (i.e. peer rejection) in chatting online. Participants viewed pictures but not profiles of other adolescents. Photographs were equated on contrast and luminescence. Approximately 70% of photos were Caucasian and 30% were not Caucasian (i.e. Black, Hispanic, Asian, Mixed Race). Participants rated each photograph once.

Phase 2 and 3 occurred 1–2 weeks after completing Phase 1. For Phase 2, participants were shown the photographs they previously classified as 'interested' and 'not interested' and asked to rate, 'How interested do you think s/he is in you?' on a visual analogue scale ranging from 0 (not very interested) to 100 (very interested) prior to the fMRI acquisition. Phase 3 of the Chatroom Task was completed in the scanner, during which participants received peer feedback from the 60 female/male adolescents allegedly participating in the nationwide study while fMRI data were acquired. During each trial (Figure 2), a participant viewed the photograph of a 'participating female/male adolescent' (1300 ms), and a photograph caption displaying 'interested' or 'not interested' was used to remind a participant about their prior selection. Then, a jittered fixation cross (1300–7600 ms) was presented, which was followed by the peer feedback superimposed under the photograph (2600 ms). After the feedback, a jittered fixation cross (1300–5200 ms) was displayed, and next a participant received a prompt, 'How does this make you feel?' and was instructed to provide a rating on a visual analogue scale ranging from 0 (very bad) to 100 (very good). Feedback was provided in pseudorandom order with no more than three trials of the same feedback type provided consec-

utively. Unbeknownst to the participants, feedback was fixed, as all participants received the same number of acceptance (30 interested trials) and rejection (30 not interested trials) trials. Participants utilized the button box to rate their feedback on a visual analogue scale presented on the presentation computer. After completing the Chatroom Task, participants were debriefed.

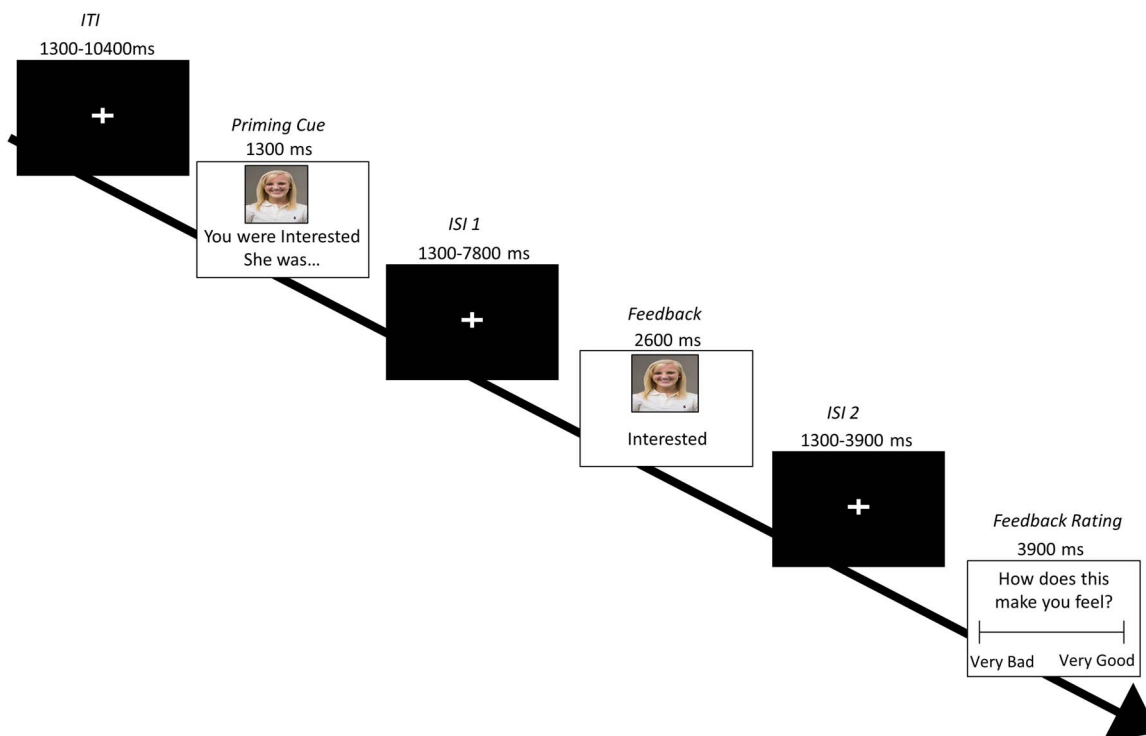
### Computational model of social value

Learning occurs when there is a discrepancy between expected and actual outcome, leading to a prediction error (PE). The value of the stimuli is then updated using this PE, explained by the following equation:

$$V_{\text{new}} = V_{\text{initial}} + \text{PE};$$

$$\text{where PE} = [\text{Social Outcome (O)} - \text{Expected Value (EV)}].$$

Computation of social value is straightforward in our paradigm, as all participants specify each of their subjective ratings. This provides the opportunity to compute social value and investigate brain regions that encode this value. First, participants' initial selection on whether they will be interested in chatting with the peers was represented as  $V_{\text{initial}}$  (Initial Value), with 'not interested' coded as 0 and 'interested' coded as 100 (i.e. Phase 1). Next, during Phase 2, participants rated their expectation on how interested peers would be in chatting with them on a visual analogue scale ranging from 0 (not very interested) to 100 (very interested), which reflected their Expected Value (EV). Finally, when participants were in the scanner, they



**Figure 2.** Trial design of Chatroom Task—A single trial design of the Phase 3 of the Chatroom Task during the fMRI acquisition.

received explicit feedback and rated how this feedback made them feel on a visual analogue scale ranging from 0 (*very bad*) to 100 (*very good*), which represented the *Social Outcome* ( $O$ ; modulated by individuals' social sensitivity; i.e. Phase 3). Average Subjective ratings and model derived Social Value during the task are reported in [Supplementary Table S1](#).

### Imaging data acquisition

Functional MRI data were acquired at the McLean Imaging Center on a Siemens Tim Trio 3 Tesla MR scanner using a 32-channel head coil. For functional scans, data were acquired in an interleaved fashion using T2\*-weighted gradient echo planer images (EPIs), with the following parameters TR/TE: 1300/32.2 ms; FOV: 212 mm; echo spacing=0.69 ms; matrix:  $64 \times 64$ ; 72 slices; in-plane resolution: 2 mm; flip angle =  $66^\circ$ ; voxels  $2 \times 2 \times 2$  mm; multiband factor = 8. A multiecho MPRAGE T1 structural image was acquired with the following parameters: TR: 2200 ms; TE1/TE2/TE3/TE4: 1.54/3.36/5.18/7 ms; voxel size:  $1.2 \times 1.2 \times 1.2$  mm; 144 slices. A field map was also acquired to correct for distortions with the following parameters: TR: 1000 ms; TE1/TE2: 10/12.46 ms; voxel size:  $3.5 \times 1.8 \times 2.5$  mm; 51 slices.

### Imaging data pre-processing

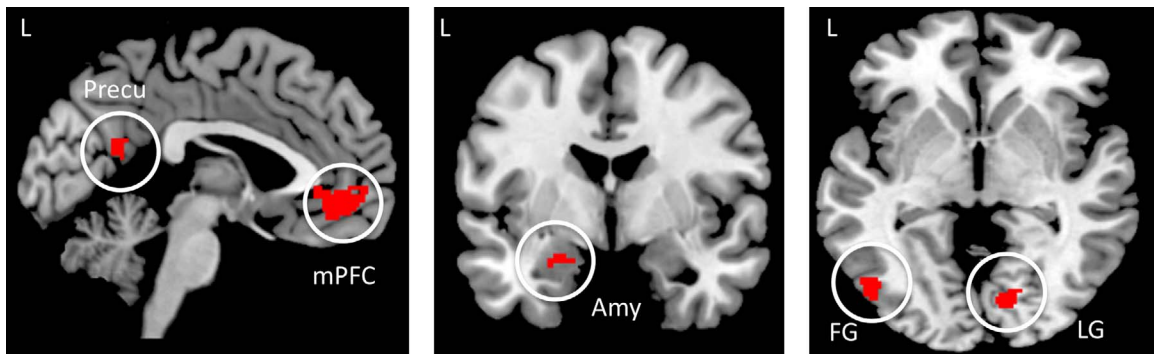
Functional MRI data were preprocessed and analyzed using Statistical Parametric Mapping software (SPM12; <http://www.fil.ion.ucl.ac.uk/spm>). Based on visual inspection of hardware-related artifacts in the raw images, two participants were excluded due to poor quality and were not processed further. For the remaining 68 participants' scans, distortion correction was applied using field maps acquired in the task session. Functional images were then realigned to the mean image of the series, corrected

for motion and slice timing-related artifacts, co-registered with the anatomical image, normalized to the  $2 \times 2 \times 2$  mm MNI template and smoothed with a 4 mm Gaussian kernel. A two-step procedure was utilized to account for motion correction. First, participants who had extensive movement ( $>4$  mm or  $4^\circ$  rotation from the reference first volume) throughout the task were excluded ( $n=5$ ). Second, for participants who had extensive movement only in the later part of the task, to increase the study power, only the first portion of these trials that was devoid of extensive movement were included and the latter part was excluded (e.g. first 60%, 72%, 99%, 42%, 90% trials from the entire task were included for 5 of the 63 adolescents). Then, the Artifact Detection Toolbox (ART) was used to identify outlier scans in global signal ( $>\pm 9$  SD) and movement ( $>2$  mm of movement or  $2^\circ$  of rotation from the previous volume). Participants with more than 7% trials excluded by ART were excluded from the analyses ( $n=8$ ). These outlier trials identified by ART were distributed throughout the task, unlike the extensive movement observed only in the first part of the task of the above participants. Mean percent of trials removed by ART for the remaining participants was  $2.25 \pm 1.7\%$ . The final sample included 55 adolescents (17 males and 38 females).

### Statistical analyses

First-level general linear model included six unmodulated regressors, corresponding to onset times of each event (cue, anticipation, feedback, post-feedback ISI and feedback rating) with a boxcar function spanning the entire duration of each event. To investigate brain regions that encoded the trial-by-trial computations of social value signals during the Chatroom Task, we parametrically modulated model-derived social values ( $V_{\text{new}}$ ) with a post-feedback ISI unmodulated regressor and convolved with a hemodynamic response function. The





**Figure 3.** Whole brain results—Brain activity correlated with social value derived from the computational model across all individuals. Precu—precuneus cortex, mPFC—medial prefrontal cortex, Amy—Amygdala, FG—fusiform gyrus, LG—lingual gyrus. Clusters are  $P < 0.05$  family-wise error corrected, with an initial cluster forming threshold of  $P < 0.001$ .

**Table 1.** Summary of brain regions encoding social value modeled at (A) ISI2 (post-feedback) and (B) feedback rating onset times. MNI peak coordinates and cluster size are reported.  $P < 0.05$  family-wise error (FWE) cluster corrected, with an initial cluster forming threshold of  $P = 0.001$

Brain region	Cluster size	MNI (x,y,z)	Z score	Cluster P (FWE)
<b>A. Social value modeled just after feedback</b>				
mPFC	458	-2, 44, -6	5.36	<0.001
Precuneus cortex	168	-6, -56, 8	4.16	<0.001
Fusiform gyrus	132	-48, -76, -4	3.96	<0.001
Lingual gyrus	62	12, -78, -4	4.37	0.035
Amygdala	61	-14, -6, -20	4.99	0.037
<b>B. Social value modeled at the time of feedback rating</b>				
Lingual gyrus	69	10, -78, -2	4.96	0.025

covariates of no interest included inter-trial interval, ART regressors, six motion realignment parameters and a constant term modeling the baseline of unchanged neural activation. For each participant, the linear coefficients of social value regressor were compared to 0 and the resulting contrast images were taken to conduct one sample t test to identify brain regions that encode social value. To test the temporal specificity of these social value signals, we parametrically modulated model-derived social values ( $V_{\text{new}}$ ) with a feedback rating unmodulated regressor in a separate general linear model.

## Results

### Sample characteristics

The final sample for the fMRI analyses included 55 adolescents (38 females, 17 males), aged 12–14 years ( $13.00 \pm 0.82$ ). Participants endorsed the following races: 85.5% White, 5.5% Asian, 3.6% Black or African American and 5.5% multiple races. The family's income distribution included the following: 54.5% = more than \$100 000, 18.2% = \$75 000 to \$100 000, 9.1% = \$50 000 to \$75 000 and 18.2% = not reported. These are summarized in [Supplementary Table S2](#).

### Chatroom behavioral data

To determine whether the task manipulation was believable, at the end of the session, the experimenter asked a series of questions that participants rated on a scale from 1 to 10 (higher scores reflect more positive responses for questions 1 and 2, but more negative responses for questions 3, 4 and 5; all were significantly different than zero,  $P < 0.001$ ): (1) 'How interested were you in this task?' ( $6.46 \pm 2.23$ ); (2) 'How happy were you when

someone expressed interest in chatting with you?' ( $7.78 \pm 1.76$ ); (3) 'How upset were you when someone rejected you?' ( $4.4 \pm 1.97$ ); (4) 'How angry were you when someone rejected you?' ( $2.9 \pm 1.82$ ); and (5) 'How nervous did you feel while waiting for the other person to make their choice?' ( $4.25 \pm 2.49$ ). Outlier criterion was defined as  $\pm 3$  SD on any item response; no participant data were removed based on these criteria. Collectively, these ratings indicate that the task elicited the intended effects, and all participants were effectively deceived by the task manipulation.

### Whole brain analyses

Consistent with our hypothesis, we observed social value signals encoded in the mPFC (peak voxel: -2, 44, -6;  $z = 5.36$ ; cluster size: 458). In addition, social value signals were observed in regions associated with social processing, including the left amygdala (peak voxel: -14, -6, -20;  $z = 4.99$ ; cluster size: 61) and left precuneus (peak voxel: -6, -56, 8;  $z = 4.16$ ; cluster size: 168). Two other regions that encoded social value were the right lingual gyrus (peak voxel: 12, -78, -4;  $z = 4.37$ ; cluster size: 62) and left fusiform gyrus (peak voxel: -48, -76, -4;  $z = 3.96$ ; cluster size: 132). All clusters were  $P < 0.05$  FWE cluster-corrected (with initial cluster forming threshold of  $P < 0.001$ ; [Figure 3](#); [Table 1, A](#)).

**Temporal specificity of social value signals.** To test the temporal specificity of social value signals, we modeled them at the time of feedback rating in a separate general linear model. However, we did not find value signals to be encoded in any of the regions except the lingual gyrus (peak voxel: 10, -78, -2;  $z = 4.96$ ; cluster size: 69; [Table 1, B](#)) during feedback rating. This suggests that the computation of social value occurs immediately after the feedback outcome.

**Exploratory analysis evaluating sex differences in social value encoding.** Mounting evidence suggests that females perceive and process social information differently than males (Pavlova, 2017; Proverbio, 2017). To explore sex differences, we extracted beta weights from the five clusters (mPFC, precuneus, amygdala, lingual and fusiform gyri). Social value encoding in the fusiform and lingual gyri did not differ between boys and girls. However, in regions specific to social computation (mPFC, precuneus and left amygdala), girls exhibited greater social value encoding than boys (all  $P < 0.05$ ; mPFC— $t(53) = 2.55$ ;  $P = 0.014$ ;  $d_s = 0.74$ , amygdala— $t(53) = 2.79$ ;  $P = 0.007$ ;  $d_s = 0.81$ , precuneus— $t(53) = 2.22$ ;  $P = 0.03$ ;  $d_s = 0.65$ ).

## Discussion

Navigating peer relationships is critical during adolescence. In this study, we investigated the neural correlates of the social valuation network in healthy adolescents using an ecologically valid peer evaluation paradigm. Unlike prior studies in this area (Guyer et al., 2012; Lau et al., 2012), trial-by-trial social values were calculated based on the individuals' selection of peers, expectation of peers' interest in chatting with them and their subjective feeling after the outcome that signaled peers' interests in them. Consistent with the 'common neural currency' theory (Levy & Glimcher, 2012), and our hypothesis, whole-brain analyses revealed that these social value signals were encoded in the mPFC across all individuals. Interestingly, our analyses also revealed a wider social-specific valuation network that included the precuneus cortex and amygdala.

Prior studies that have utilized this paradigm have investigated the average neural activation during peer acceptance and rejection, but have not capitalized on the trial-by-trial computations that occur during peer evaluation [Note: Average neural responses to peer acceptance vs rejection were consistent with prior research (Guyer et al., 2012), thereby validating the task, see [Supplementary Table S3](#)]. In addition, most studies often focus only on 'interested peers' trials, thereby neglecting a potentially valuable component of the task. Using a computational framework, we were able to identify brain regions that track social value parameters, providing insight into the neurobiology of social choice behavior. In addition, it enabled us to compare complex social behavior with other social and non-social decision-making.

There is a robust consensus that the mPFC plays a critical role in the dynamic computation of values associated with both primary (e.g. food) and secondary (e.g. monetary) non-social stimuli (Bartra et al., 2013; Clithero & Rangel, 2013). However, whether the valuation of social outcomes or social rewards relies on the mPFC is a subject of ongoing investigations. There is some support for the involvement of the mPFC in processing socially relevant information. For instance, representation of the self and others (Krienen et al., 2010), cooperative human partners (McCabe et al., 2001) and mentalizing (Amodio & Frith, 2006) recruit the mPFC. Similarly, lesion studies in non-human primates have shown that this region is critical for establishing social interest in other individual macaques (Rudebeck et al., 2006). Complementing these findings, mPFC activation has been found to correlate with individuals' propensity to pay more money to view an attractive face (Smith et al., 2010). Partially supporting a shared valuation system, self-reported ratings of facial attractiveness were encoded in the mPFC, suggesting that the subjective reward value of social stimuli may be coded similarly to primary and secondary rewards (O'Doherty et al., 2003). This would suggest that the brain maps these different

reward types on a common scale to guide choices (Hare et al., 2010; Peters & Büchel, 2010; Levy & Glimcher, 2012; Ruff & Fehr, 2014; Lehner et al., 2017). Consistent with this assumption, recent meta-analyses have highlighted overlapping value encoding for both simple social (e.g. attractiveness, praise, smile) and non-social rewards (e.g. money, juice) in the mPFC (Chase, Kumar, Eickhoff, & Dombrovski, 2015; Clithero & Rangel, 2013; Levy & Glimcher, 2012; Lin et al., 2012). Moreover, findings have extended to more complex social rewards, including during collaborative decision-making (Fareri et al., 2015) and intention to trust a partner during economic exchange games (King-Casas et al., 2005). Our results add to this body of research, suggesting that updating of social value associated with peer evaluations also recruits the mPFC. Even though our task did not have a learning component, our results suggest that computation of these social values might drive behavioral change during social decision-making recruiting regions similar to the non-social reinforcement learning circuitry.

Apart from the mPFC, social value signals also were encoded in other socially relevant brain regions including the amygdala and precuneus cortex. It is possible that during social decision-making, the mPFC communicates with higher level social processing regions to encode social perception. Even though we did not hypothesize social value to be encoded in the amygdala and precuneus, it is not surprising that these regions encode social value, considering their involvement in processing social stimuli (Vijayakumar et al., 2017). In addition, aberrant (increased) amygdala function to social feedback has been associated with both adult and adolescent anxiety and depressive disorders (Guyer et al., 2008; Lau et al., 2012; Spielberg et al., 2014; Kumar et al., 2017). In contrast, the precuneus is thought to support mentalizing processes, facilitating an individual's ability to comprehend or interpret other people's thoughts, feelings and intentions (Frith & Frith, 2003; Hyatt et al., 2015). The precuneus also might contribute to self-referential processing (Whitfield-Gabrieli et al., 2011) and, similar to our findings, has been implicated in social rejection and exclusion (Vijayakumar et al., 2017). Further supporting the idea that these regions contribute to computation of subjective value for social rewards, Smith et al. (2013) showed that connectivity between the mPFC and a network of regions including the amygdala and precuneus predicted individual differences in valuation to social rewards. Interestingly, these regions represent dominant hubs of the default mode network (DMN), which are thought to be activated largely at 'rest'. However, the DMN also was active during tasks that require participants to understand and interact with others, and interpreting self and others' emotional status, suggesting a substantial overlap between the brain regions typically involved in social cognitive processes and the default system (Whitfield-Gabrieli et al., 2011). Other brain region that was observed to encode these social value signals was the fusiform gyrus. Although reward-related responses in the fusiform gyrus have been identified (Chase et al., 2015; Kumar et al., 2018), this study argued that these signals may reflect attentional processing rather than reward processing *per se* (Arsenault et al., 2013).

Mounting evidence suggests that females perceive and process social information differently than males (Pavlova, 2017; Proverbio, 2017). In addition, central for our study, girls have been shown to exhibit increased sensitivity to social rejection (Stroud et al., 2017). Consistent with this finding, we found girls to have an increased social value signaling in the mPFC, amygdala and precuneus. This was observed despite girls and boys perceiving peer feedback similarly (boys and girls did not differ in the task

manipulation questionnaire scores that rated on their subjective feelings during the task). This is interesting, as some studies have demonstrated increased sensitivity to the interpersonal stressors in girls, but achievement stressors in boys (Stroud et al., 2017). Whether sex-specific neural responses to peer evaluation might index differential risk for adolescent depression is an important question for future studies. Specifically, previous research has shown increased neural responses to peer rejection to be associated with both current adolescent depression (Silk et al., 2014) and future risk for depressive symptoms. The present results suggest that girls are more attuned to social evaluation, giving more importance to social feedback when compared with boys, and recruit more strongly regions critically implicated in computation of social value (mPFC, precuneus and left amygdala). It is possible that this increased social value encoding in girls might be a risk factor of future depression if efficient adaptation of these events is not achieved. However, caution is warranted, as these analyses were exploratory in nature and included uneven groups. It is, therefore, crucial for future research to investigate the longitudinal neural markers of peer evaluation in girls and boys and identify interventions to overcome the negative effects of these interpersonal stressors.

### Limitations

Four limitations warrant attention. First, the modest ethnic distribution within this sample limits the generalizability of the findings. Second, the age range was restricted to 12 to 14 years old in order to reduce putative age-related effects. However, this restricted range may also limit the generalizability of these findings to younger or older youth. Third, the percent of excluded participants (21%) on the basis of gross motion is slightly higher compared to other studies. However, this is not surprising, as head motion is a significant concern for pediatric compared to adult imaging, and age is shown to inversely correlate with head motion (Satterthwaite et al., 2012). Last, our task design allowed us to probe value computations occurring at every trial (even though a given trial does not influence the next one) and thereby identify brain regions that encode these computations. It does not, however, allow us to probe how computations in one trial might influence future responses in subsequent trials. However, we believe that our approach paves the way for future studies utilizing computational models on tasks that explicitly compute and predict trial-by-trial social values.

### Conclusions

Our findings highlight a common neural currency valuation region (mPFC) that is involved in social decision-making, along with a social-specific core (amygdala and precuneus). Social rewards can provide gateways towards learning about others, building personal social networks, and establishing close relationships. Understanding how we make social decisions and neural markers associated with it will help us navigate promising avenues for intervention.

### Conflict of interest

Over the past 3 years, D.A.P. has received consulting fees from Akili Interactive Labs, BlackThorn Therapeutics, Boehringer Ingelheim, Compass and Takeda and an honorarium from Alkermes, for activities unrelated to the current research. No other authors report any conflicts of interest.

### Supplementary data

Supplementary data are available at SCAN online.

### Acknowledgments

Support also was provided through the Klingenstein Third Generation Foundation (RPA), Dana Foundation (DAP, RPA) and Tommy Fuss Fund (RPA, DAP). P.K. (R21MH105775), D.A.P. (R37MH068376, 5R01MH108602) and RPA (R21MH112330, U01MH108168) were partially supported by funds from the National Institute of Mental Health. P.K. was also partially supported by NARSAD's Young Investigator Award. The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health.

### References

- Amodio, D.M., Frith, C.D. (2006). Meeting of minds: the medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, 7, 268–77.
- Arsenault, J.T., Nelissen, K., Jarraya, B., et al. (2013). Dopaminergic reward signals selectively decrease fMRI activity in primate visual cortex. *Neuron*, 77(6), 1174–86.
- Bartra, O., McGuire, J.T., Kable, J.W. (2013). The valuation system: a coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. *NeuroImage*, 76, 412–27.
- Brown, B.B. (2013). Adolescents' relationships with peers. In: Lerner, R., Steinberg, L., editors. *Handbook of Adolescent Psychology*, 2nd edn, New York, NY: Wiley.
- Chase, H.W., Kumar, P., Eickhoff, S.B., et al. (2015). Reinforcement learning models and their neural correlates: an activation likelihood estimation meta-analysis. *Cognitive, Affective, & Behavioral Neuroscience*, 15, 435–59.
- Cliethero, J.A., Rangel, A. (2013). Informatic parcellation of the network involved in the computation of subjective value. *Social Cognitive and Affective Neuroscience*, 9, 1289–302.
- Fareri, D.S., Chang, L.J., Delgado, M.R. (2015). Computational substrates of social value in interpersonal collaboration. *Journal of Neuroscience*, 35, 8170–80.
- Frith, U., Frith, C.D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 358, 459–73.
- Guyer, A.E., Lau, J.Y.F., McClure-Tone, E.B., et al. (2008). Amygdala and ventrolateral prefrontal cortex function during anticipated peer evaluation in pediatric social anxiety. *Archives of General Psychiatry*, 65, 1303–12.
- Guyer, A.E., McClure-Tone, E.B., Shiffrin, N.D., et al. (2009). Probing the neural correlates of anticipated peer evaluation in adolescence. *Child Development*, 80, 1000–15.
- Guyer, A.E., Choate, V.R., Pine, D.S., et al. (2012). Neural circuitry underlying affective response to peer feedback in adolescence. *Social Cognitive and Affective Neuroscience*, 7, 81–92.
- Hare, T.A., Camerer, C.F., Knoepfle, D.T., et al. (2010). Value computations in ventral medial prefrontal cortex during charitable decision making incorporate input from regions involved in social cognition. *Journal of Neuroscience*, 30, 583–90.
- Hyatt, C.J., Calhoun, V.D., Pearlson, G.D., et al. (2015). Specific default mode subnetworks support mentalizing as revealed through opposing network recruitment by social and semantic fMRI tasks. *Human Brain Mapping*, 36, 3047–63.

- Kaufman, J., Birmaher, B., Brent, D., et al. (1997). Schedule for affective disorders and schizophrenia for school-age children-present and lifetime version (K-SADS-PL): initial reliability and validity data. *Journal of the American Academy of Child and Adolescent Psychiatry*, **36**, 980–8.
- King-Casas, B., Tomlin, D., Anen, C., et al. (2005). Getting to know you: reputation and trust in a two-person economic exchange. *Science*, **308**, 78–83.
- Krienen, F.M., Tu, P.-C., Buckner, R.L. (2010). Clan mentality: evidence that the medial prefrontal cortex responds to close others. *Journal of Neuroscience*, **30**, 13906–15.
- Kumar, P., Waiter, G.D., Dubois, M., et al. (2017). Increased neural response to social rejection in major depression. *Depression and Anxiety*, **34**, 1049–56.
- Kumar, P., Goer, F., Murray, L., et al. (2018). Impaired reward prediction error encoding and striatal-midbrain connectivity in depression. *Neuropsychopharmacology*, **43**, 1581–8.
- Lau, J.Y.F., Guyer, A.E., Tone, E.B., et al. (2012). Neural responses to peer rejection in anxious adolescents: contributions from the amygdala-hippocampal complex. *International Journal of Behavioral Development*, **36**, 36–44.
- Lehner, R., Balsters, J.H., Herger, A., et al. (2017). Monetary, food, and social rewards induce similar Pavlovian-to-instrumental transfer effects. *Frontiers in Behavioral Neuroscience*, **10**, 1–12.
- Levy, D.J., Glimcher, P.W. (2012). The root of all value: a neural common currency for choice. *Current Opinion in Neurobiology*, **22**, 1027–38.
- Lin, A., Adolphs, R., Rangel, A. (2012). Social and monetary reward learning engage overlapping neural substrates. *Social Cognitive and Affective Neuroscience*, **7**, 274–81.
- McCabe, K., Houser, D., Ryan, L., et al. (2001). A functional imaging study of cooperation in two-person reciprocal exchange. *Proceedings of the National Academy of Sciences*, **98**, 11832–5.
- O’Doherty, J.P., Dayan, P., Friston, K., et al. (2003). Temporal difference models and reward-related learning in the human brain. *Neuron*, **38**, 329–37.
- Pavlova, M.A. (2017). Sex and gender affect the social brain: beyond simplicity. *Journal of Neuroscience Research*, **95**, 235–50.
- Peters, J., Büchel, C. (2010). Neural representations of subjective reward value. *Behavioural Brain Research*, **213**, 135–41.
- Platt, B., Kadosh, K.C., Lau, J.Y.F. (2013). The role of peer rejection in adolescent depression. *Depression and Anxiety*, **30**, 809–21.
- Proverbio, A.M. (2017). Sex differences in social cognition: the case of face processing. *Journal of Neuroscience Research*, **95**, 222–34.
- Rudebeck, P.H., Buckley, M.J., Walton, M.E., et al. (2006). A role for the macaque anterior. *Policy Studies*, **313**, 2005–7.
- Ruff, C.C., Fehr, E. (2014). The neurobiology of rewards and values in social decision making. *Nature Reviews Neuroscience*, **15**, 549–62.
- Satterthwaite, T.D., Wolf, D.H., Loughhead, J., et al. (2012). Impact of in-scanner head motion on multiple measures of functional connectivity: relevance for studies of neurodevelopment in youth. *NeuroImage*, **60**, 623–32.
- Silk, J.S., Siegle, G.J., Lee, K.H., et al. (2014). Increased neural response to peer rejection associated with adolescent depression and pubertal development. *Social Cognitive and Affective Neuroscience*, **9**, 1798–807.
- Smith, D.V., Hayden, B.Y., Truong, T.-K., et al. (2010). Distinct value signals in anterior and posterior ventromedial prefrontal cortex. *Journal of Neuroscience*, **30**, 2490–5.
- Smith, D.V., Clithero, J.A., Boltuck, S.E., et al. (2013). Functional connectivity with ventromedial prefrontal cortex reflects subjective value for social rewards. *Social Cognitive and Affective Neuroscience*, **9**, 2017–25.
- Spielberg, J.M., Jarcho, J.M., Dahl, R.E., et al. (2014). Anticipation of peer evaluation in anxious adolescents: divergence in neural activation and maturation. *Social Cognitive and Affective Neuroscience*, **10**, 1084–91.
- Stewart, J.G., Valeri, L., Esposito, E.C., et al. (2018). Peer victimization and suicidal thoughts and behaviors in depressed adolescents. *Journal of Abnormal Child Psychology*, **46**, 581–96.
- Stroud, L.R., Papandonatos, G.D., D’Angelo, C.M., et al. (2017). Sex differences in biological response to peer rejection and performance challenge across development: a pilot study. *Physiology and Behavior*, **169**, 224–33.
- Vijayakumar, N., Cheng, T.W., Pfeifer, J.H. (2017). Neural correlates of social exclusion across ages: a coordinate-based meta-analysis of functional MRI studies. *NeuroImage*, **153**, 359–68.
- Whitfield-Gabrieli, S., Moran, J.M., Nieto-Castañón, A., et al. (2011). Associations and dissociations between default and self-reference networks in the human brain. *NeuroImage*, **55**, 225–32.