Behavioral and Neural Properties of Social Reinforcemen Learning

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Social learning is critical for engaging in complex interactions with other individuals. Learning from positive social exchanges, s acceptance from peers, may be similar to basic reinforcement learning. We formally test this hypothesis by developing a novel p that is based on work in nonhuman primates and human imaging studies of reinforcement learning. The probability of receiving p social reinforcement from three distinct peers was parametrically manipulated while brain activity was recorded in healthy adult event-related functional magnetic resonance imaging. Over the course of the experiment, participants responded more quickly to peers who provided more frequent positive social reinforcement, and rated them as more likeable. Modeling trial-by-trial leas showed ventral striatum and orbital frontal cortex activity correlated positively with forming expectations about receiving social forcement. Rostral anterior cingulate cortex activity tracked positively with modulations of expected value of the cues (peers). To the findings across three levels of analysisÑsocial preferences, response latencies, and modeling neural responsesÑare consist reinforcement learning theory and nonhuman primate electrophysiological studies of reward. This work highlights the fundar influence of acceptance by oneÕs peers in altering subsequent behavior.

Introduction

Successfully navigating our social environment depends on learning from positive and negative encounters with others and shaping future behavior toward those individuals. Psychologists have proposed that positive social exchanges are fundamentally rewarding for humans (Bandura and Walters, 1963; Baumeister and Leary, 1995; Steinberg, 2008), suggesting that learning from social interactions may draw on basic reinforcement learning mechanisms. The present study was designed to test this hypothesis by building on reinforcement learning studies in nonhuman primates and human imaging studies (Schultz et al., 1997; Fiorillo et al., 2003; McClure et al., 2003; D'Ardenne et al., 2008).

Reinforcement learning from primary (e.g., food) and secondary (e.g., money) reinforcers has been shown to engage specific neural circuitry. In its simplest form, it is explained by the classic Rescorla–Wagner model (Rescorla and Wagner, 1972). According to this model, learning to associate arbitrary cues with greatest probability of providing social acceptance to the participant. We applied a simple Rescorla–Wagner rule in behavioral and functional imaging analyses to target the neural bases of these behavioral changes, hypothesizing that the ventral striatum and OFC would code prediction error signals (Schultz et al., 1997; O'Doherty, 2007). Thus, the current study elucidates neurobiological mechanisms for key learning processes during social exchanges that shape behavior through positive interactions.

Materials and Methods

Р . Forty-six adults (aged 18-28 years; 22 females) participated in the experiment. Thirty-six completed the task during functional magnetic resonance imaging (fMRI) (aged 18-28 years; all right-handed; 19 females). Three individuals in the fMRI group were excluded due to insufficient number of correct trials in any condition (=2; 1 male) or noncompliance with the task (= 1, male). Participants reported no history of neurological and/or psychiatric disorders in a standard screening or on the Structured Clinical Interview for DSM-IV Axis I Disorders (SCID) (First et al., 2007) and imagingparticipants reported no contraindications for an MRI. Two participants did not complete the SCID due to time constraints. All participants provided written consent approved by the Institutional Review Board at Weill Cornell Medical College and were debriefed and compensated following their participation.

E _______. The experiment was conducted during two separate sessions. The first session introduced the cover story, leading participants to believe they would receive actual social feedback during a task that would be completed on the second visit. Participants were shown up to five photographs of gender- and ethnicity-matched peers. They then selected three with whom they would like to interact, and rated the three peers for how likeable and attractive they looked on a scale from 1 (not very) to 10 (very). Participants also completed a personal survey where they listed information about themselves (birthday; hometown; and favorite music, TV shows, books, guoi5z9siandexianda1 37leryË(agz9si3(agz9si3(agz9si3(nked)-16gz9snvpfy(looked)-169snvpf-160hy(First)-

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probability and time (pre-interaction, post-interaction) on likeability ratings $(F_{(2,78)} = 5.48, < 0.01; Fig. 2). P$ analyses indicated that post-task ratings decreased linearly with decreasing interaction probability, such that peers who interacted less with the participant were rated as less likeable (linear terrais)= 7.17, < 0.02). Whereas pre-task likeability ratings were equivalent for all three peers (s> 0.48), after the task the Frequent ($_{\rm (39)}=-2.26,\ <0.03)$ and Con tinuous ($_{\rm (39)}=-2.68,\ <0.02)$ peers were rated as more likeable than the rarely reinforcing peer, though there was not a significant difference in likeability ratings after the task between the Frequent and Continuous peers ($_{39)} = -0.69$, > 0.49). Attractiveness ratings were not significantly modulated by task conditions (main effects of reinforcement probability, time, and interaction s > 0.09).

Participants responded correctly to 95.63% of trials (SD 3.54%). Response accuracy was not significantly modulated by the task conditions (main effects of reinforcement probability, Imaging time, and interactions:s > 0.29).

As indexed by the prediction error parametric regressor, predic-Response latencies to the cue varied as participants learned the error signals () were positively associated with activity in reinforcement contingency outcomes associated with each peer, the rostral anterior cingulate cortex, ventral striatum, anterior as indicated by a significant interaction between probability of sula, and OFC (Table 1; Fig. 3). The parametric values in the general linear model encompassed positive and negative predicreinforcement and time ($E_{2,84}$) = 3.98, < 0.03; Fig. 2). *P*

tests showed that, whereas there was no difference in reaction errors, demonstrating that the BOLD fluctuations in these regions tracked learning signals reflecting reinforcement expecduring the late trials for the Frequent reinforcement condition tancies. Together, these findings delineate an orbital frontostria- $(_{(42)} = 2.49, < 0.02)$, compared with the Rare reinforcement tal circuit showing significantly greater activity associated with condition. There was a trend for responses to be faster in the positive social reinforcement. Continuous reinforcement condition $(_{42}) = 2.01, < 0.06)$ than in the Rare reinforcement condition. Overall, participants_E

were faster during the late versus early triats $f_{2} = 15.21$, < We also examined regions of the brain that positively correlated with 0.01) and there was no main effect of probability of social reintearning to distinguish the faces of the peers based on their differenforcement when collapsing across time $(E_4) = 1.43$, > 0.25). tial rates of positive social reinforcement (learned cue value). Specif-

To further test for the effects of learning, we compared reagcally, group analysis of the cue phase of trials that tracked positively tion times for Rare and Continuous reinforcement before and with modulations of expected value identified greater activity in after reinforcement contingencies were reversed at the end of the rostral anterior cingulate cortex with larger expected value (Fig. experiment. Evidence that participants had implicitly learned the). No other regions survived whole-brain correction. No regions contingencies was further supported by the interaction betweewithin the frontostriatal circuitry of interest demonstrated negative time (sixth run vs reversal) and reinforcement probability (rarelycorrelations with expected value (i.e., brain regions sensitive to lower reinforcing vs continuously reinforcing) on reaction times expected values) at corrected thresholding. $(F_{(1,42)} = 10.15, < 0.01; Fig. 2C)P$ tests showed a signif

icant reaction time speeding when the Rare condition switched tDiscussion

delivering Continuous reinforcement $(4_{2}) = 3.13$, < 0.01). Repeated social exchanges shape our behavior toward others. In There were no main effects of reinforcement probability $(F_{ij} =$ this experiment, we examined how different probabilities of pos-2.77, = 0.1) or time ($F_{1,42}$) = 1.35, > 0.25). There was also no itive interaction from distinct peers rapidly influence social learndifference in the Frequent condition (unchanged during reversaling. Within a reinforcement learning framework, we developed a reaction times between the last run and the reversal $r_{\mu\mu}$ (= novel social paradigm and demonstrated that the neural systems -1.48, > 0.15). engaged while forming social expectations are similar to those

Additionally, we examined how reaction times (RT) changednvolved in basic reward learning. This overlap in neural circuitry based on feedback from the preceding trial as another index and function is consistent with prediction error-related learning how the reinforcement contingencies altered behavior. We found and with our hypothesis that positive social interactions can serve that participants were faster on the subsequent trial after not secondary reinforcers, taking on the attributes of primary rereceiving positive reinforcement (mearscore RT:-0.01, SD:

0.13) versus when they had received positive reinforcement (mean -score RT: 0.07, SD: 0.1_{42} = 2.86, < 0.01).

provide positive social reinforcement. This finding is similar to studies that demonstrate improved performance on a trial that follows receiving punishment (Hester et al., 2010) or choosing to make a bet more often after losing money than after winning money (Liu et al., 2007), though the present study did not assess strategic behavior directly. Together, the behavioral findings demonstrate that participants learned the reinforcement contingencies and thus provide an objective index of social learning.

The changes in likeability ratings and response latencies did not appear to be conscious behavioral choices. The majority (93%) of participants were unable to articulate the reinforcement patterns,

suggesting little if any explicit awareness of the reinforcement contingencies. These findings demonstrate that social preferences and actions can be influenced after only brief encounters with peers and without conscious awareness. Such rapid changes highlight the influence of positive social interactions on effectively altering subsequent behavior.

The neural correlates of these behavioral changes draw upon the same neural circuitry as that implicated in reinforcement learning (Alexander et al., 1986; Haber and Knutson, 2010). Prediction error (δ) learning engaged the ventral striatum and or bital frontal cortex, similar to previous studies using single-cell recordings (Schultz et al., 1997; Fiorillo et al., 2003; Sul et al., 2010) and human imaging studies with primary reinforcers such as juice (McClure et al., 2003; O'Doherty et al., 2003; D'Ardenne

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ment outcomes. Specifically, one peer always provided positive social reinforcement, another one frequently provided positive social reinforcement, and the third rarely provided positive social reinforcement. Ratings of likeability changed from the beginning to the end of the experiment, with less reinforcing peers becoming less likeabile, and more reinforcing peers yielding higher ratings of likeability by the end of the task. By asking participants to make a simple button response during the cue presentation, we tested whether speeding of response latencies (action tendencies) indexed learned associations between a given peer and their probability of providing positive social reinforcement. As expected due to the simplicity of the task, accuracy was at ceiling and there were no statistical differences in accuracy for the three peers.

In the current study, we observed faster responses to peers who provided positive social reinforcement more often, similar to studies where participants responded more quickly to cues that reliably predicted receiving a primary or secondary reward (O'Doherty et al., 2006; Spicer et al., 2007). Measuring differences in reaction times to cues to index learning differs from reinforcement studies that use modulated choice behavior as an indicator of learning (Tanaka et al., 2004; Daw and Doya, 2006; Schönberg et al., 2007). Choice tasks index changes in explicit preferences or a participant's strategy in maximizing reinforcement, while in the current study, changes in responses are thought to index differences in approach behaviors that are based on learning from a prior history of social feedback. In addition, participants showed faster reaction times after trials that did not

about investors' decisions (King-Casas et al., 2005; Phan et References

2010). Our results complement these studies by demonstrating Aexander GE, DeLong MR, Strick PL (1986) Parallel organization of functionally segregated circuits linking basal ganglia and cortex. Annu Rev neural mechanism for how prior positive interactions with others shape our expectations for future interactions. Given the in-Bandura A, Walters RH (1963) Social learning and personality develop-

creased sensitivity in the ventral striatumappetitive stimuli ment. New York: Holt, Rinehart and Winston.

during adolescence (Galvan et al., 2050 merville et al., 2011), Baumeister RF, Leary MR (1995) The need to belong: desire for interperas well as the greater influence of peers during adolescencesonal attachments as a fundamental human motivation. Psychol Bull (Spear, 2000; Gardner and Steinberg, 2005), this work clearly 117:497-529.

raises the question of how peer interaction differentially impacts modulates human brain response to reward. J Neurosci 21:2793–2798. learning and behavior across development and how this may be to the Mark M, Nystrom LE, Fissell K, Carter CS, Cohen JD (1999) Conflict differentially represented in the brain. Accordingly, it would be monitoring versus selection-for-action in anterior cingulate cortex. Nainteresting to explore whether adolescents show increased sensi-ture 402:179-181.

Botvinick MM, Cohen JD, Carter CS (2004) Conflict monitoring and antetivity during social learning relative to children and adults. rior cingulate cortex: an update. Trends Cogn Sci 8:539-546. The expected values to the cues corresponded with Bray S, O'Doherty J (2007) Neural coding of reward-prediction error sig-greater activity in the rostral anterior cingulate cortex. Previous and during classical conditioning with attractive faces. I Neurophysio nals during classical conditioning with attractive faces. J Neurophysiol

studies have shown the rostral anterior cingulate cortex/medial 97:3036-3045. prefrontal cortex is sensitive to cues that predict reward receiptox RW (1996) AFNI: Software for analysis and visualization of functional (Tanaka et al., 2004; Knutson et al., 2005; Palminteri et al., 2009)

and may play a role in general learning about the value of information and using this information for future decisions (Rushworth and Behrens, 2008). Lesion studies in nonhuman primates have shown this region is important for establishing patterns of social interest in other individual male or female macaques (Rudebeck et al., 2006). Human imaging studies have shown this region is sensitive when choosing to approach peers relative to celebrities (Güroglu et al., 2008) and when engaging in a series of actions during live relative to recorded interactions (Redcay et al., 2010). Given these studies examining social value in the anterior cingulate cortex, and the extensive literature showing a general sensitivity of this region in monitoring response conflict (Botvinick et al., 1999, 2004), our findings suggest that learning social cue values drives changes in behavior that may differ or conflict with the cognitive demands of the situation (e.g., task demands). Over the course of the experiment, this conflict may increase as behavior is modulated in response to changing expected values. Although the current study did not find that the orbital frontostriatal circuit was sensitive to expected values, the findings in the anterior cingulate cortex may suggest a role for this region in processing behavioral tendencies toward learned social cues. These findings thus offer insight into the neural processing of quick social decisions.

Concl sions

Our findings provide direct evidence for how brief, positive, social interactions can significantly shape social learning across three discrete measures: social preferences, behavioral actions, and neural activity. After short interactions with others, social preferences and actions can be altered, highlighting the significance of social acceptance in biasing behavior. Moreover, we show that formal computational models of reinforcement learning apply to secondary reinforcement learning in the social domain. We demonstrate that the neural circuitry involved in forming prediction error signals about receiving social reinforcement, including the ventral striatum and orbital frontal cortex, overlaps with circuitry that subserves learning about other types of rewards (e.g., food or money). Overall, the findings suggest that similar mechanisms underlie basic reinforcement learning and our ability to rapidly and flexibly update our expectations during interactions with others, which enables us to effectively navigate the social environment.

- Li J, Daw ND (2011) Signals in human striatum are appropriate for policy update rather than value prediction. J Neurosci 31:5504–5511.
- Li J, Delgado MR, Phelps EA (2011) How instructed knowledge modulates the neural systems of reward learning. Proc Natl Acad Sci U S A 108:55–60.
- Lin A, Adolphs R, Rangel A (2011) Social and monetary reward learning engage overlapping neural substrates. Soc Cogn Affect Neurosci. Advance online publication. Retrieved March 22, 2011. doi:10.1093/scan/nsr006.
- Liu X, Powell DK, Wang H, Gold BT, Corbly CR, Joseph JE (2007) Functional dissociation in frontal and striatal areas for processing of positive and negative reward information. J Neurosci 27:4587–4597.

McClure SM, Berns GS, Montague PR (2003) Temporal prediction errors in