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The amygdalostriatal and corticostriatal effective connectivity in anticipation and evaluation of facial attractiveness

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ABSTRACT

Decision-making consists of several stages of information processing, including an anticipation stage and an outcome evaluation stage. Previous studies showed that the ventral striatum (VS) is pivotal to both stages, bridging motivation and action, and it works in concert with the ventral medial prefrontal cortex (vmPFC) and the amygdala. However, evidence concerning how the VS works together with the vmPFC and the amygdala came mainly from neuropathology and animal studies; little is known about the dynamics of this network in the functioning human brain. Here we used fMRI combined with dynamic causal modeling (DCM) to investigate the information flow along amygdalostriatal and corticostriatal pathways in a facial attractiveness guessing task. Specifically, we asked participants to guess whether a blurred photo of female face was attractive and to wait for a few seconds ("anticipation stage") until an unblurred photo of feedback face, which was either attractive or unattractive, was presented ("outcome evaluation stage"). At the anticipation stage, the bilateral amygdala and VS showed higher activation for the "attractive" than for the "unattractive" guess. At the outcome evaluation stage, the vmPFC and the bilateral VS were more activated by feedback faces whose attractiveness was congruent with the initial guess than by incongruent faces; however, this effect was only significant for attractive faces, not for unattractive ones. DCM showed that at the anticipation stage, the choice-related information entered the amygdalostriatal pathway through the amygdala and was projected to the VS. At the evaluation stage, the outcome-related information entered the corticostriatal pathway through the vmPFC. Bidirectional connectivities existed between the vmPFC and VS, with the VS-to-vmPFC connectivity weakened by unattractive faces. These findings advanced our understanding of the reward circuitry by demonstrating the pattern of information flow along the amygdalostriatal and corticostriatal pathways at different stages of decision-making.

1. Introduction

Organisms seek to maximize its reward and minimize its punishment, a tendency called behavioral optimization (Diekhof, Kapsb, Falkaib, & Gruberb, 2012). Behavioral optimization depends on the neural capacity to represent reward-related information and to use this information to guide decision-making. Psychological and neurobiological investigation of decision-making conceptualizes it as consisting of action selection, anticipation and evaluation of outcome, and updating of value representation (Knutson & Greer, 2008; Platt, 2003). Neuroimaging research in the past decade has identified three functionally related brain structures that probably form the core network for reward processing and decision-making, i.e., the ventral striatum (VS), the ventral medial prefrontal cortex (vmPFC), and the amygdala (Balleine & Killcross, 2006; Rangel, Camerer, & Montague, 2008; Schoenbaum, Roesch, Stalnaker, & Takahashi, 2009).

The VS is pivotal to reward processing, reinforcement learning, and goal-directed behavior (Delgado, Li, Schiller, & Phelps, 2008; Diekhof et al., 2012; Haber & Knutson, 2010; O'Doherty et al., 2003; Schultz, 1998; Sesack & Grace, 2010) and it functions at different stages of decision-making (Platt, 2003). For instance, anticipation of both primary (e.g., pleasant taste or unpleasant electrical stimulation) and secondary (e.g., money) reinforcer elicits VS activation (Knutson & Greer, 2008). At the outcome evaluation stage, the VS is found to encode the prediction error signal, i.e., the discrepancy between the prediction and the actual outcome (Bayer & Glimcher, 2005; Hare, O'Doherty, Camerer, Schultz, & Rangel, 2008; Li et al.,

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2011; Schultz, 1998). The vmPFC and the adjacent parts of the medial orbitofrontal cortex (mOFC) are consistently implicated in representing abstract value of choices and outcomes (FitzGerald, Seymour, & Dolan, 2009; Kim, Shimojo, & O'Doherty, 2010; Knutson, Fong, Adams, Varner, & Hommer, 2001; Knutson, Fong, Bennett, Adams, & Homme, 2003; O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001; for reviews, see Kringelbach, 2005; O'Doherty, 2004; Schoenbaum, Roesch, Stalnaker, & Takahashi, 2009).

The vmPFC and VS are structurally and functionally connected. Anatomical studies on non-human primates showed that tracers injected in the vmPFC labeled the fibers that terminate in the nucleus accumbens (NAcc), a limited area within the VS (Haber, Kunishio, Mizobuchi, & Lynd-Balta, 1995). Instead of directly innervating the prefrontal cortex, the efferent projections from VS primarily target the pallidum and midbrain. The latter structures in turn project back to the prefrontal cortex, including the vmPFC (Hedreen & DeLong, 1991). Neuroimaging techniques, such as the diffusion tensor imaging (DTI) and resting state MRI, have also demonstrated the frontostriatal structural connectivity in humans (Cauda et al., 2011; Di Martino et al., 2008). Functionally, studies on drug addiction provide evidence for the interplay between the vmPFC and the VS (Goldstein & Volkow, 2002; Kalivas & Volkow, 2005), suggesting that the prefrontal-to-NAcc glutamate projection may substantiate the transmission from the value of the reinforcer (e.g., cues of drug) represented in the prefrontal cortex to the craving sensation generated in the striatum. However, little is known about the role of this functional interplay in decision-making in healthy population.

The amygdala, although typically envisaged as the center of fear conditioning and negative emotions (LeDoux, 2000; Morris et al., 1996; Phelps & LeDoux, 2005), has been demonstrated to play specific roles in reward processing and appetitive learning (Li, Schiller, Schoenbaum, Phelps, & Daw 2011; Paton, Belova, Morrison, & Salzman, 2006; for reviews, see Baxter & Murray, 2002; Seymour & Dolan, 2008), in both human (Gottfried, O'Doherty, & Dolan, 2002; O'Doherty et al., 2002) and non-human animals (Shabel & Janak, 2009). It was proposed that the amygdala signals the biological salience of potential actions or outcomes, rather than encodes fear-related information alone (Balleine & Killcross, 2006). A recent model-based fMRI study confirmed this hypothesis by demonstrating the computational role of amygdala in reinforcement learning (Li et al., 2011). The authors found that the amygdala represents the importance of the prediction error signal, generated in the VS, to the organism's goal and thus determines the extent to which the organism learns from it. Indeed, the amygdala has strong unidirectional anatomical projection to the VS. While both the dorsal striatum and VS receive input from the cortex, thalamus, and brainstem, the VS alone receives a dense projection from the amygdala and hippocampus (Friedman, Aggleton, & Saunders, 2002; Fudge & Haber, 2000; Russchen & Price, 1984). Russchen and Price (1984), for example, found that the striatum was labeled from injections of anterograde tracer into the amygdaloid complex. It has also been demonstrated that the amygdalostriatal interaction is critical for goal-directed behaviors in rodent (Di Ciano & Everitt, 2004; Setlow, Holland, & Gallagher, 2002). In Setlow et al. (2002), rats with contralaterally placed unilateral lesions of basolateral amygdala complex and nucleus accumbens (part of the VS) failed to acquire second-order conditioned responses in an appetitive Pavlovian learning task. Since contralaterally placed unilateral lesions effectively disconnected the amygdala and the VS functionally, this finding demonstrated that these two structures form a functionally connected system critical for processing information concerning learned motivational value. However, given that evidence for the functional interplay between the amygdala and the VS came mainly from non-human animal studies, it is important to demonstrate directly the functional connectivity between the two structures in human decision-making.

In this study, we used fMRI and dynamic causal modeling (DCM) to investigate the patterns of effective connectivities of the amygdalostriatal and the corticostriatal pathways at different stages of decision-making in human. We asked participants to guess whether a blurred photo of female face was attractive and to wait for a few seconds ("anticipation stage") until an unblurred photo of feedback face, which was either attractive or unattractive, was presented ("outcome evaluation stage"; Fig. 1). Attractive faces are rewarding and can drive the neural activation of the brain areas related to reward processing (e.g., the VS and the vmPFC) in the observers (Aharon et al., 2001; Chatterjee, Thomas, Smith, & Aguirre, 2009; Cloutier, Heatherton, Whalen, & Kelley, 2008; Ishai, 2007; Senior, 2003; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007). Thus, our experimental setup allowed us to disassociate: (1) the neural activations related to anticipation from the those related to the evaluation of feedback faces and (2) the "cognitive" reward (Elliott, Frith, & Dolan, 1997; Poldrack, Prabhakaran, Seger, & Gabrieli, 1999) of feedback (correct vs. wrong in the guessing task) from the intrinsic rewarding value (or biological salience) of the feedback (attractive vs. unattractive faces). Based on existing evidence concerning the functions of the amygdalostriatal and corticostriatal pathways in decision-making, we tested two specific hypotheses: (1) at the anticipation stage, the choice-related anticipatory information would be projected from the amygdala to the VS and (2) at the outcome evaluation stage, the outcome-related information would be projected from the vmPFC to the VS and the strength of this projection would be modulated by the attractiveness of feedback faces.

2. Materials and methods

2.1. Participants

Eighteen undergraduate students (nine female; mean age 21 years, ranging from 18 to 22 years) participated in the experiment. Participants reported no abnormal neurological history, had normal or corrected-to-normal vision, and participants were strongly right-handed. The study was carried out in accordance with the Declaration of Helsinki and was approved by the Ethics Committee of the Department of Psychology, Peking University.

2.2. Stimuli

One hundred and ninety-two grayscale photos of Asian female faces were selected from the photo pools of Peking University and the Institute of Psychology, Chinese Academy of Sciences, and were rated by twenty participants who did not participate in the scanning. A 7-point scale was used for each rating, with "1" indicating unattractive, "4" indicating not sure and "7" indicating attractive. The 96 attractive faces selected were consistently rated as attractive (with scores more than five) while the 96 unattractive faces selected were consistently rated as unattractive (with scores less than three). Faces met the following criteria: eye gaze forward, head position forward, neutral or mildly positive facial expression, and unfamiliar to the participants. We did not include male faces because participants in the pretest showed large variation in their attractiveness rating for male faces. Stimuli were adjusted to be of approximately equal size and luminance and centered in a 200×200 pixel frame with a dark background.

Another ten faces were Gaussian-blurred with Photoshop™ and were used as uninformative blurred faces for the anticipation stage. The attractiveness rating of these faces was between 3 and 5 on the 7-point scale. Unknown to the participants, the blurred face in each trial was not the same one as the feedback face. The purpose of this manipulation was to exclude the potential