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

Hongbo Yu [a], Zhiheng Zhou [a], Xiaolin Zhou [a,b,c,d,*]

[a] Center for Brain and Cognitive Sciences and Department of Psychology, Peking University, Beijing 100871, China
[b] Key Laboratory of Machine Perception (Ministry of Education), Peking University, Beijing 100871, China
[c] Key Laboratory of Computational Linguistics (Ministry of Education), Peking University, Beijing 100871, China
[d] PKU-IDG/McGovern Institute for Brain Research, Peking University, Beijing 100871, China

a r t i c l e i n f o

Article history:
Accepted 30 April 2013
Available online xxxx

Keywords:
Ventral striatum
Amygdala
Ventral medial prefrontal cortex
fMRI
Effective connectivity
Facial attractiveness

a b s t r a c t

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 pun-

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 unidirec-

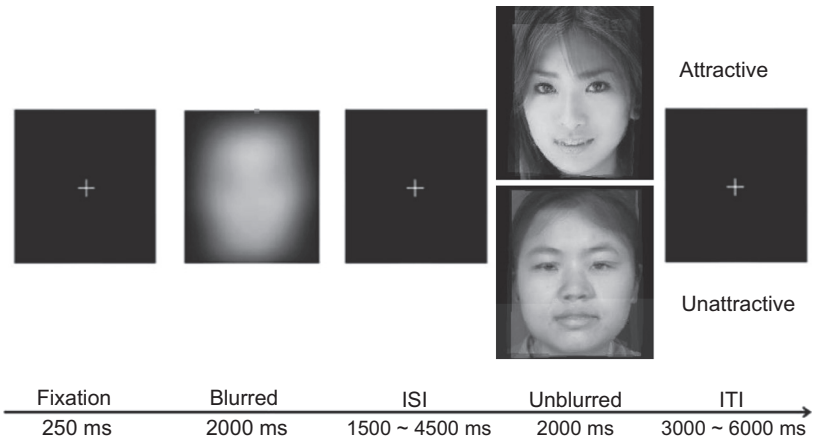


Fig. 1. Sequence of events in a single trial. For purposes of illustration, the attractive and the unattractive faces in the figure were morphed from several faces used in the experiment.

influence of the blurred faces on the perceptual processing of the subsequent feedback faces as well as to make sure that about half of the trials would constitute "correct" trials.

2.3. Procedures

Stimuli were presented at a viewing distance of about 60 cm through an LCD projector onto a rear projection screen located behind the participant's head. Participants viewed the screen through an angled mirror on the head-coil. The task was administered using Presentation software (http://nbs.neuro-bs.com/) to control the presentation and timing of stimuli.

A similar experiment procedure was adopted here as in our previous study (Zhang, Li, Qian, & Zhou, 2012). At the start of each trial, a white fixation cross was presented for 250 ms against a black screen. Next, one of the ten blurred photos was presented for 2000 ms at the center of the screen, during which the participant made a guess as to whether the blurred face was attractive or unattractive by pressing a button with the right index or ring finger. The mapping between responses and fingers was counterbalanced across participants. The participant was told to press the button as soon as possible, and if the response was made after the blurred photo disappeared from the screen this trial was removed from the analysis. After the response, a fixation sign was presented again with a varying duration, ranging from 1500 to 4500 ms. Then an unblurred face was presented for 2000 ms. The participant was asked to watch it but do nothing. The unblurred face served as an (implicit) feedback from which the participant was able to infer whether he had made a right guess. The inter-trial interval (ITI) was jittered between 3000 ms and 6000 ms, during which a fixation cross was presented (Fig. 1).

The experiment was divided into two functional scanning sessions, each containing 96 trials and lasted about 17.2 min. The 96 attractive faces and 96 unattractive faces were randomly and equally presented in each session. The order of feedback was pseudo-randomized so that no more than four attractive or unattractive faces were presented consecutively. Before scanning, participants were familiarized with the task by practicing in a training session for about 20 trials.

2.4. MRI data acquisition

A Siemens 3T Trio scanner with a standard head coil at the Beijing MRI Center for Brain Research was used to obtain T2*-weighted echo-planar images (EPI) with blood oxygenation level-dependent (BOLD) contrast (matrix, 64×64, in-plane resolution, 3×3). Thirty-two transversal slices of 4 mm thickness that covered the whole brain were acquired according to an interleaved order with a 1 mm gap (repetition time = 2000 ms, echo time = 30 ms, field of view = 200×200, and flip angle = 90°).

2.5. fMRI data preprocessing

The obtained fMRI data were preprocessed and analyzed using Statistical Parametric Mapping software SPM8 (Wellcome Trust Department of Cognitive Neurology, London, UK). The first five volumes of each session were discarded to allow stabilization of magnetization. Images were realigned to the sixth volume of the first session for head motion correction. Then the mean EPI image of each participant was computed and spatially normalized to the MNI single subject template using the 'unified segmentation' function in SPM8. This algorithm is based on a probabilistic framework that enables image registration, tissue classification, and bias correction to be combined within the same generative model. The resulting parameters of a discrete cosine transform, which define the deformation field necessary to move individual data into the space of the MNI tissue probability maps, were then combined with the deformation field transforming between the latter and the MNI single subject template. The ensuing deformation was subsequently applied to individual EPI volumes. All images were thus transformed into standard MNI space and re-sampled to $2\text{ mm} \times 2\text{ mm} \times 2\text{ mm}$ voxel size. The data were then smoothed with a Gaussian kernel of 8 mm full-width half-maximum to accommodate inter-subject anatomical variability. Different ways of re-sampling and spatial smoothing do not change the pattern of brain activations. A temporal high-pass filter with a cutoff frequency of 1/128 Hz was used to remove low-frequency drifts in an fMRI time series.

2.6. Basic fMRI data analyses

Statistical analyses based on the general linear model (GLM) were performed first at the participant level and then at the group level. At the participant-level, events for response and outcome delivery were modeled with a delta function convolved with a canonical hemodynamic response function (HRF) (Friston et al., 1998). The first-order temporal derivatives were included (Henson, Price, Rugg, Turner, & Friston, 2002). Six critical regressors were defined: two corresponded to the anticipation phase (guess attractive vs. guess unattractive) and the others corresponded to the four possible combinations of outcome evaluation (attractiveness × congruency). The six rigid body parameters were also included to correct for the head motion artifact. For the group level analysis, we first calculated the simple main effects for each of

the six critical regressors for each participant. The six first-level individual contrast images were then fed into a flexible factorial test across participants in the second-level design matrix.

Contrasts corresponding to anticipation and the outcome evaluation were defined: ''Guess_Attractive > Guess_Unattractive'', ''Attractive_Outcome > Unattractive_Outcome'', ''Congruent_Outcome > Incongruent_Outcome'', and the reversed contrasts of the above ones. Statistical analyses were conducted both at the whole-brain and predefined region of interest (ROI). For the whole-brain analysis, clusters that survived $p < 0.001$ (uncorrected) at peak voxel level and p (FWE) < 0.05 at cluster level were reported (Table 1). *A priori* ROI activations were tested for significance by using small-volume correction (SVC) within a 10 mm-radius sphere with a peak threshold of p (FWE) < 0.05 and an extent threshold of 100 mm^3 ($\approx$12 voxels). Beta estimates corresponding to the six critical regressors were extracted from and averaged across the 27 voxels around the peak voxel indentified by the whole-brain contrasts. ROI activation timecourse was based on percent signal change and was extracted using MarsBaR (Brett, Anton, Valabregue, & Poline, 2002) from a 6 mm-radius sphere around the peak voxel revealed by contrast.wi0''Guess_Atdent6H2-32.5(r4-1790.5244.-17.5(peak8(Dynamic-1.308timaus.308825(modeli.7(corr(100

"unattractive" guesses ($M = 82$, $SD = 18$; $t(17) = 3.13$, $p < 0.01$, two tailed). A post-experiment test showed that participants all agreed with the facial attractiveness categorization of the unblurred faces derived from the pretest. At the feedback stage, the distribution of trials for the four conditions was as follows: attractive-congruent, 26.7%, attractive-incongruent, 21.8%, unattractive-congruent, 21.0%, and unattractive-incongruent, 27.7%.

3.2. Neuroimaging results

3.2.1. Neural activations related to anticipation and outcome evaluation

The "Guess_Attractive > Guess_Unattractive" revealed activa-

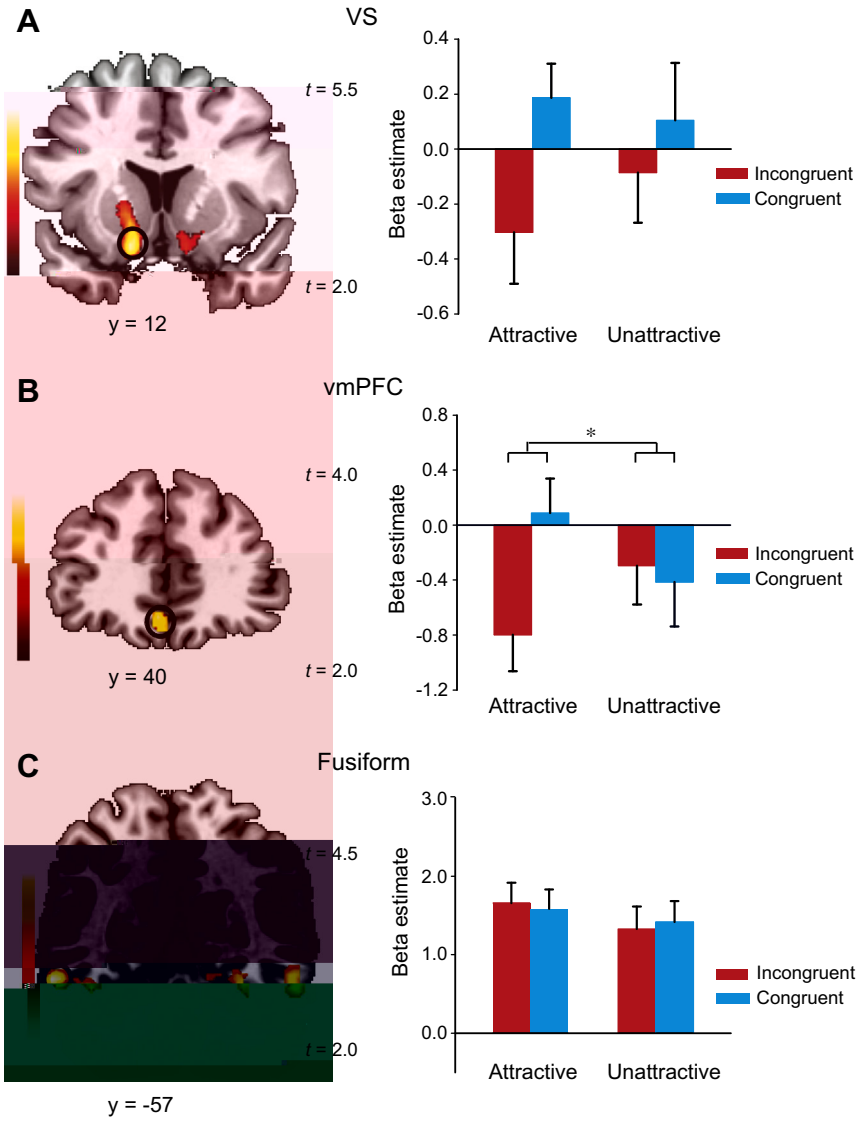


Fig. 3. Brain activation map corresponding to the feedback stage. At the whole-brain level, the attractive feedback faces compared with the unattractive faces activated the bilateral fusiform and occipital areas (A) and the congruent feedback compared with the incongruent feedback activated the bilateral ventral striatum (VS) and the ventral medial prefrontal cortex (vmPFC) (B and C). The parameter estimates extracted from the activation foci (4-mm sphere) were plotted on the right. *: Significant congruency-by-attractiveness interaction at $p < 0.05$. Error bars indicate SEM.

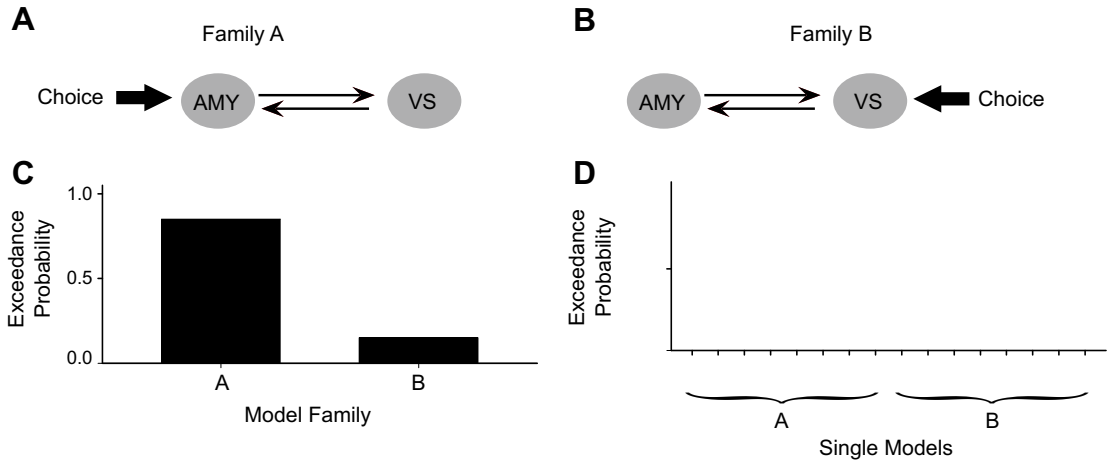
of attractive faces ($t(17) = -2.27$, $p < 0.05$). Second, the intrinsic connectivity from the amygdala to the VS was significantly larger than 0 ($t(17) = 3.01$, $p < 0.01$) and also larger than the intrinsic connectivity from the VS to the amygdala ($t(17) = 3.00$, $p < 0.01$). Third, although the modulatory effects of "Guess_Attractive" (0.11 ± 0.24; $t(17) = 1.91$, $p = 0.07$ uncorrected) and "Guess_Unattractive" (0.03 ± 0.07; $t(17) = 2.07$, $p = 0.05$ uncorrected) on the amygdala-to-VS intrinsic connectivity were marginally significant when tested separately, the combined modulatory effect of these two conditions was significantly larger than zero (0.07 ± 0.14; $t(17) = 2.24$, $p < 0.05$). These results indicated that the choice-related information is first represented in the amygdala and is projected to the vmPFC and that this functional connectivity could be enhanced by the act of choice.

3.3. Functional interplay between VS and vmPFC during outcome evaluation

For the outcome evaluation stage, the model family in which the vmOFC served as information input (Family B) had an exceedance probability (0.98) far greater than the exceedance probability of the alternative model family (0.02). The estimated DCM parameters of the average model of the winning Family B (Fig. 5 and Table 5) highlighted two main findings. (1) There existed bidirectional intrinsic connectivities between the VS and the vmPFC. (2) Unattractive faces reduced the effective connectivity from the VS to the vmPFC (see Table 5).

4. Discussion

In this study, we used fMRI and DCM to investigate the pattern of effective connectivities of the amygdalostriatal and corticostriatal pathways in different stages of decision-making, i.e., anticipation and outcome evaluation. We asked participants to guess whether a blurred photo of female face was attractive (anticipation stage) and then presented them with an unblurred photo of either an attractive or an unattractive face (outcome evaluation stage). We found that at the anticipation stage, anticipating unattractive faces reduced the neural activation in the bilateral amygdala and the VS. Moreover, there existed intrinsic connectivity from the amygdala to the VS and this connectivity could be en-



hanced by the act of choice. At the outcome evaluation stage, the VS and the vmPFC were more activated by outcomes that were congruent with the initial guess as compared with those that were incongruent. This congruency effect was further modulated by the attractiveness of the feedback faces such that it was present mainly for the attractive faces, not for the unattractive ones. DCM analysis demonstrated that outcome-related information entered the corticostriatal pathway through the vmPFC. There existed bidirectional intrinsic connectivities between the VS and the vmPFC, but unattractive feedback faces could decrease the effective connectivity from the VS to the vmPFC.

4.1. The effective connectivity from the amygdala to the VS at the anticipation stage

We found that anticipation of unattractive faces reduced the activity of the amygdala and the VS compared with anticipation of attractive faces. We also found significant intrinsic connectivity from the amygdala to the VS but not the other way around, fitting well with the anatomical evidence from rodent which demonstrated the unidirectional projection from the amygdala to the striatum (Friedman et al., 2002; Fudge & Haber, 2000). Taken together, we argue that when anticipating unattractive faces the

amygdala decreases the activity in the VS through the unidirectional projection. Given the amygdala's role in signaling biological salience (

Table 5
Model parameters estimated based on model Family B (corticostriatal).

Parameter	Mean ± *SD* (Hz)
Intrinsic connectivity	
VS → vmOFC	0.10 ± 0.15**
vmOFC → VS	0.30 ± 0.25***
Modulation (on VS → vmOFC)	
Congruent_Attractive	−0.02 ± 0.04
Incongruent_Attractive	−0.01 ± 0.10
Attractive	−0.01 ± 0.07
Congruent_Unattractive	−0.02 ± 0.05
Incongruent_Unattractive	−0.03 ± 0.05
Unattractive	−0.03 ± 0.04**
Driving input	
Incongruent_Attractive	−0.23 ± 0.40*
Incongruent_Unattractive	−0.07 ± 0.33
Congruent_Attractive	0.04 ± 0.29
Congruent_Unattractive	0.03 ± 0.36

Corrected for multiple comparison following Bonferroni's procedure.
* $p < 0.1$.
** $p < 0.05$.
*** $p < 0.01$.

2005). These studies suggested that the knowledge of "success" in doing something is itself rewarding and can drive the activity in the VS. Taken together, we may argue that whether positive feedbacks, as compared with negative feedbacks, can elicit stronger activity in the VS is highly context-dependent.

The vmPFC is consistently implicated in encoding reward magnitude rather than prediction error (Hare et al., 2008). Our finding that the vmPFC was more activated by congruent as compared with incongruent outcomes is in line with the previous studies using similar tasks (Elliott et al., 1997; Poldrack et al., 1999; Schnider et al., 2005) and confirms our suggestion that the knowledge of having made a correct response, relative to the knowledge of making a mistake, is of higher subjective value to the participants in the present setup. We did not observe a main effect of attractiveness in the vmPFC, inconsistent with some previous studies (Cloutier et al., 2008; Ishai, 2007; Winston et al., 2007). However, these studies also highlighted the flexibility of vmPFC in encoding subjective value: while attractive female faces, as compared with unattractive female faces, activated the vmPFC of male or homosexual female observers, such differential effect was absent for female or homosexual male observers (Cloutier et al., 2008; Ishai, 2007; Winston et al., 2007). In our study, while both male and female participants were recruited, only female faces were presented as stimuli. Therefore, at the group level, the main effect of attractiveness for the male and for the female participants could have been canceled out. On the other hand, the feedback congruency, as a function of the attractiveness of the presented faces, did not differ between male and female participants, and thus the effect of congruency showed up in the vmPFC at the group level.

4.3. The effective connectivity between the vmPFC and the VS at the evaluation stage

Confirming our hypothesis, we found that the outcome information entered the reward processing network through the vmPFC. The vmPFC receives inputs from sensory cortices (Bar, 2009) and calculates the reward values (Kringelbach, 2005; Schoenbaum et al., 2009). The intrinsic connectivity from the vmPFC to the VS, which is supported by anatomical evidence (Haber, Fudge, & McFarland, 2000), may reflect the dynamic process by which visual, and perhaps aesthetic (Winston et al., 2007), properties of the feedback faces were conveyed to the VS. In the VS, the valence of the feedback faces (attractive vs. unattractive) was compared with expectation or initial guess, by which the congruency-related signal was generated (Schultz, 1998). This congruency-related information may be projected back to the vmPFC, perhaps via the mediation of the thalamus (Haber & Knutson, 2010), to update the hedonic responses or experienced value of the outcomes.

We further found that this back projection was reduced by unattractive faces, suggesting a modulatory effect of outcome salience on the transmission of congruency-related information from the VS to the vmPFC. The scheme we sketched above was in accordance with a recently proposed theory concerning the circuits for reward processing (Der-Avakian & Markou, 2012) and it echoes an intracranial EEG study of the functional interaction between the VS and the medial frontal cortex in reward processing (Cohen et al., 2009; also see Cohen, Heller, & Ranganath, 2005). The authors recorded electrophysiological activity directly from the NAcc from 5 patients undergoing deep brain stimulation and asked them to perform a reward-learning task in which they first learned stimulus-outcome associations, and then chose from among the learned stimuli to win as much monetary incentive as possible. They observed a dynamic relationship between the medial frontal cortex and the NAcc: the medial frontal cortex activity initially preceded the NAcc activity in time, but then the NAcc activity became preceding the medial frontal cortex activity (Cohen et al., 2009). This pattern of serial activation is consistent with our suggestion of the bidirectional effective connectivities between the VS and the vmPFC.

To conclude, our analyses of effective connectivity fit into a larger picture of the functions of the VS in decision-making and goal-directed behaviors, which proposes that the VS serves as an interface between value and action, integrating reinforcement signals to bias reward-seeking behavior (Haber & Knutson, 2010; Sesack & Grace, 2010). Specifically, at the anticipation stage, the VS receives choice-related anticipatory, salience-related information (Knutson & Greer, 2008) from the amygdala and adjusts its own activity according to such information. At the outcome evaluation stage, the VS receives feedback-related information from the vmPFC and compares it with expectation. This congruency-related information may be projected back to the vmPFC (Haber & Knutson, 2010) to update the hedonic responses or experienced value of the outcome. Moreover, the strength of this connectivity is modulated by the salience of the outcome. This study extended previous understanding of the functions of the reward circuitry by demonstrating the pattern of information flow along the amygdalostriatal and corticostriatal pathways at different stages of decision-making.

Acknowledgments

This study was supported by National Basic Research Program of China (973 Program: 2010CB833904) and by grants from the Natural Science Foundation of China (30110972 and 91232708). We thank Mr. Philip Blue and two anonymous reviewers for their constructive comments on an earlier version of the manuscript.

References

Abler, B., Walter, H., Erk, S., Kammerer, H., & Spitzer, M. (2006). Prediction error as a linear function of reward probability is coded in human nucleus accumbens. *Neuroimage, 31*, 790–795.
Aharon, I., Etcoff, N., Ariely, D., Chabris, C. F., O'Connor, E., & Breiter, H. C. (2001). Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron, 32*, 537–551.
Balleine, B. W., & Killcross, S. (2006). Parallel incentive processing: An integrated view of amygdala function. *Trends in Neurosciences, 29*, 272–279.
Bar, M. (2009). The proactive brain: memory for predictions. *Transactions of the Royal Society of London Series B, Biological Sciences, 364*, 1235–1243.

Baxter, M. G., & Murray, E. A. (2002). The amygdala and reward. *Nature Reviews Neuroscience, 3*, 563–573.

Bayer, H. M., & Glimcher, P. W. (2005). Midbrain dopamine neurons encode a quantitative reward prediction error signal. *Neuron, 47*, 129–141.

Brett, M., Anton, J., Valabregue, R., & Poline, J. (2002). Region of interest analysis using an SPM toolbox. In *Presented at the 8th international conference on functional mapping of the human brain*, Sendai, Japan, June 2–6, 2002. Available on CD-ROM in Neuroimage, Vol 16, No 2.

Bzdok, D., Langner, R., Caspers, S., Kurth, F., Habel, U., Zilles, K., et al. (2011). ALE meta-analysis on facial judgments of trustworthiness and attractiveness. *Brain Structure and Function, 215*, 209–223.

Cauda, F., Cavanna, A. E., D'agata, F., Sacco, K., Duca, S., & Geminiani, G. C. (2011). Functional connectivity and coactivation of the nucleus accumbens: A combined functional connectivity and structure-based meta-analysis. *Journal of Cognitive Neuroscience, 23*, 2864–2877.

Chatterjee, A., Thomas, A., Smith, S. E., & Aguirre, G. K. (2009). The neural response to facial attractiveness. *Neuropsychology, 23*, 135–143.

Cloutier, J., Heatherton, T. F., Whalen, P. J., & Kelley, W. M. (2008). Are attractive people rewarding? Sex differences in the neural substrates of facial attractiveness. *Journal of Cognitive Neuroscience, 20*, 941–951.

Cohen, M. X., Axmacher, N., Lenartz, D., Elger, C. E., Sturm, V., & Schlaepfer, T. E. (2009). Neuroelectric signatures of reward learning and decision-making in the human nucleus accumbens. *Neuropsychopharmacology, 34*, 1649–1658.

Cohen, M. X., Heller, A. S., & Ranganath, C. (2005). Functional connectivity with anterior cingulate and orbitofrontal cortices during decision-making. *Brain Research. Cognitive Brain Research, 23*, 61–70.

Delgado, M. R., Li, J., Schiller, D., & Phelps, E. A. (2008). The role of the striatum in aversive learning and aversive prediction errors. *Philosophical Transactions of the Royal Society B, 363*, 3787–3800.

Der-Avakian, A., & Markou, A. (2012). The neurobiology of anhedonia and other reward-related deficits. *Trends in Neurosciences, 35*, 35–78.

Di Ciano, P., & Everitt, B. (2004). Direct interactions between the basolateral amygdala and nucleus accumbens core underlie cocaine-seeking behavior by rats. *Journal of Neuroscience, 24*, 7167–7173.

Di Martino, A., Scheres, A., Margulies, D. S., Kelly, A. M. C., Uddin, L. Q., Shehzad, Z., et al. (2008). Functional connectivity of human striatum: A resting state fMRI study. *Cerebral Cortex, 18*, 2735–2747.

Diekhof, E. K., Kapsb, L., Falkaib, P., & Gruberb, O. (2012). The role of the human ventral striatum and the medial orbitofrontal cortex in the representation of reward magnitude – An activation likelihood estimation meta-analysis of neuroimaging studies of passive reward expectancy and outcome processing. *Neuropsychologia, 50*, 1252–1266.

Elliott, R., Frith, C. D., & Dolan, R. J. (1997). Differential neural response to positive and negative feedback in planning and guessing tasks. *Neuropsychologia, 35*, 1395–1404.

FitzGerald, T. H., Seymour, B., & Dolan, R. J. (2009). The role of human orbitofrontal cortex in value comparison for incommensurable objects. *Journal of Neuroscience, 29*, 8388–8395.

Friedman, D. P., Aggleton, J. P., & Saunders, R. C. (2002). Comparison of hippocampal, amygdala, and perirhinal projections to the nucleus accumbens: Combined anterograde and retrograde tracing study in the Macaque brain. *Journal of Comparative Neurology, 450*, 345–365.

Friston, K., Fletcher, P., Josephs, O., Holmes, A., Rugg, M. D., & Turner, R. (1998). Event-related fMRI: Characterizing differential responses. *Neuroimage, 7*, 30–40.

Friston, K., Harrison, L., & Penny, W. (2003). Dynamic causal modelling. *Neuroimage, 19*, 1273–1302.

Fudge, J. L., & Haber, S. N. (2000). The central nucleus of the amygdala projection to dopamine subpopulations in primates. *Neuroscience, 97*, 479–494.

Goldstein, R. Z., & Volkow, N. D. (2002). Drug addiction and its underlying neurobiological basis: Neuroimaging evidence for the involvement of the frontal cortex. *American Journal of Psychiatry, 159*, 1642–1652.

Gottfried, J. A., O'Doherty, J., & Dolan, R. (2002). Appetitive and aversive olfactory learning in humans studied using event-related functional magnetic resonance imaging. *Journal of Neuroscience, 22*, 10829–10837.

Haber, S., Fudge, J. L., & McFarland, N. R. (2000). Striatonigrostriatal pathways in primates form an ascending spiral from the shell to the dorsolateral striatum. *Journal of Neuroscience, 20*, 2369–2382.

Haber, S., & Knutson, B. (2010). The reward circuit: linking primate anatomy and human imaging. *Neuropsychopharmacology, 35*(1), 4–26.

Haber, S., & McFarland, N. R. (1999). The concept of the ventral striatum in nonhuman primates. *Annals of the New York Academy of Sciences, 877*, 33–48.

Haber, S., Kunishio, K., Mizobuchi, M., & Lynd-Balta, E. (1995). The orbital and medial prefrontal circuit through the primate basal ganglia. *Journal of Neuroscience, 15*, 4851–4867.

Hare, T. A., O'Doherty, J., Camerer, C. F., Schultz, W., & Rangel, A. (2008). Dissociating the role of the orbitofrontal cortex and the striatum in the computation of goal values and prediction errors. *Journal of Neuroscience, 28*, 5623–5630.

Hedreen, J. C., & DeLong, M. R. (1991). Organization of striatopallidal, striatonigal, and nigrostriatal projections in the Macaque. *Journal of Comparative Neurology, 304*, 569–595.

Henson, R. N. A., Price, C. J., Rugg, M. D., Turner, R., & Friston, K. J. (2002). Detecting latency differences in event-related BOLD responses: Application to words versus nonwords and initial versus repeated face presentations. *Neuroimage, 15*, 83–97.

Ishai, A. (2007). Sex, beauty and the orbitofrontal cortex. *International Journal of Psychophysiology, 63*, 181–185.

Kalivas, P. C., & Volkow, N. D. (2005). The neural basis of addiction: A pathology of motivation and choice. *American Journal of Psychiatry, 162*, 1403–1413.

Kim, H., Shimojo, S., & O'Doherty, J. P. (2010). Overlapping responses for the expectation of juice and money rewards in human ventromedial prefrontal cortex. *Cerebral Cortex, 21*, 769–776.

Knutson, B., Fong, G. W., Adams, C. M., Varner, J. L., & Hommer, D. (2001). Dissociation of reward anticipation and outcome with event-related fMRI. *NeuroReport, 12*, 3683–3687.

Knutson, B., Fong, G. W., Bennett, S. M., Adams, C. M., & Homme, D. (2003). A region of mesial prefrontal cortex tracks monetarily rewarding outcomes: Characterization with rapid event-related fMRI. *Neuroimage, 18*, 263–272.

Knutson, B., & Greer, S. (2008). Anticipatory affect: Neural correlates and consequences for choice. *Philosophical Transactions of the Royal Society B, 363*, 3771–3786.

Kringelbach, M. L. (2005). The human orbitofrontal cortex: Linking reward to hedonic experience. *Nature Reviews Neuroscience, 6*, 691–702.

LeDoux, J. E. (2000). Emotion circuits in the brain. *Annual Review of Neuroscience, 23*, 155–184.

Li, J., Schiller, D., Schoenbaum, G., Phelps, E., & Daw, N. D. (2011). Differential roles of human striatum and amygdala in associative learning. *Nature Neuroscience, 14*, 1250–1252.

Liberzon, I., Phan, K. L., Decker, L. R., & Taylor, S. F. (2003). Extended amygdala and emotional salience: A PET activation study of positive and negative affect. *Neuropsychopharmacology, 28*, 726–733.

Morris, J. S., Frith, C. D., Perrett, D. I., Rowland, D., Young, A. W., Calder, A. J., et al. (1996). A differential neural response in the human amygdala to fearful and happy facial expressions. *Nature, 383*, 812–815.

O'Doherty, J. P. (2004). Reward representations and reward-related learning in the human brain: Insights from neuroimaging. *Current Opinion in Neurobiology, 14*, 769–776.

O'Doherty, J. P., Dayan, P., Friston, K., Critchley, H., & Dolan, R. J. (2003). Temporal difference models and reward-related learning in the human brain. *Neuron, 38*, 329–337.

O'Doherty, J. P., Deichmann, R., Critchley, H., & Dolan, R. (2002). Neural responses during anticipation of a primary taste reward. *Neuron, 33*, 815–826.

O'Doherty, J. P., Kringelbach, M. L., Rolls, E. T., Hornak, J., & Andrews, C. (2001). Abstract reward and punishment representations in the human orbitofrontal cortex. *Nature Neuroscience, 4*, 95–102.

Paton, J. J., Belova, M. A., Morrison, S. E., & Salzman, C. D. (2006). The primate amygdala represents the positive and negative value of visual stimuli during learning. *Nature, 439*, 865–870.

Penny, W. D., Stephan, K. E., Daunizeau, J., Rosa, M. J., Friston, K. J., Schofield, T. M., et al. (2010). Comparing families of dynamic causal models. *PLoS Computational Biology, 6*, e1000709.

Penny, W. D., Stephan, K. E., Mechelli, A., & Friston, K. J. (2004). Comparing dynamic causal models. *Neuroimage, 22*, 1157–1172.

Phelps, E. A., & LeDoux, J. E. (2005). Contributions of the amygdala to emotion processing: From animal models to human behavior. *Neuron, 48*, 175–187.

Platt, M. L. (2003). Neural correlates of decisions. *Current Opinion in Neurobiology, 12*, 141–148.

Poldrack, R. A., Prabhakaran, V., Seger, C. A., & Gabrieli, J. D. (1999). Striatal activation during acquisition of a cognitive skill. *Neuropsychology, 13*, 564–574.

Rangel, A., Camerer, C., & Montague, P. R. (2008). A framework for studying the neurobiology of value-based decision making. *Nature Reviews Neuroscience, 9*, 545–555.

Russchen, F. T., & Price, J. L. (1984). Amygdalostriatal projections in the rat. Topographical organization and fiber morphology shown using the lectin PHA-L as an anterograde tracer. *Neuroscience Letters, 47*, 15–22.

Schnider, A., Treyer, V., & Buck, A. (2005). The human orbitofrontal cortex monitors outcomes even when no reward is at stake. *Neuropsychologia, 43*, 316–323.

Schoenbaum, G., Roesch, M. R., Stalnaker, T. A., & Takahashi, Y. K. (2009). A new perspective on the role of the orbitofrontal cortex in adaptive behaviour. *Nature Reviews Neuroscience, 10*, 885–892.

Schultz, W. (1998). Predictive reward signal of dopamine neurons. *Journal of Neurophysiology, 80*, 1–27.

Senior, C. (2003). Beauty in the brain of the beholder. *Neuron, 38*(4), 525–528.

Sesack, S. R., & Grace, A. A. (2010). Cortico-basal ganglia reward network: Microcircuitry. *Neuropsychopharmacology, 35*, 27–47.

Setlow, B., Holland, P. C., & Gallagher, M. (2002). Disconnection of the basolateral amygdala complex and nucleus accumbens impairs appetitive pavlovian second-order conditioned responses. *Behavioral Neuroscience, 116*, 267–275.

Seymour, B., & Dolan, R. (2008). Emotion, decision making, and the amygdala. *Neuron, 58*, 662–671.

Shabel, S. J., & Janak, P. H. (2009). Substantial similarity in amygdala neuronal activity during conditioned appetitive and aversive emotional arousal. *Proceedings of the National Academy of Sciences of the United States of America, 106*, 15031–15036.

Stephan, K. E., Penny, W. D., Daunizeau, J., Moran, R. J., & Friston, K. J. (2009). Bayesian model selection for group studies. *Neuroimage, 46*, 1004–1017.

Stephan, K. E., Penny, W. D., Moran, R. J., den Ouden, H. E. M., Daunizeau, J., & Friston, K. J. (2010). Ten simple rules for dynamic causal modeling. *Neuroimage, 49*, 3099–3109.

Winston, J. S., O'Doherty, J., Kilner, J. M., Perrett, D. I., & Dolan, R. J. (2007). Brain systems for assessing facial attractiveness. *Neuropsychologia, 45*, 195–206.

Zhang, Y., Li, X., Qian, X., & Zhou, X. (2012). Brain responses in evaluating feedback stimuli with a social dimension. *Frontiers in Human Neuroscience, 6*, 24.