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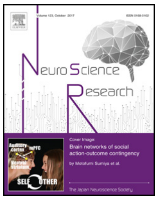

Brain networks of social action-outcome contingency: The role of the ventral striatum in integrating signals from the sensory cortex and medial prefrontal cortex

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ABSTRACT

Social interactions can be facilitated by action-outcome contingency, in which self-actions result in relevant responses from others. Research has indicated that the striatal reward system plays a role in generating action-outcome contingency signals. However, the neural mechanisms wherein signals regarding self-action and others' responses are integrated to generate the contingency signal remain poorly understood. We conducted a functional MRI study to test the hypothesis that brain activity representing the self modulates connectivity between the striatal reward system and sensory regions involved in the processing of others' responses. We employed a contingency task in which participants made the listener laugh by telling jokes. Participants reported more pleasure when greater laughter followed their own jokes than those of another. Self-relevant listener's responses produced stronger activation in the medial prefrontal cortex (mPFC). Laughter was associated with activity in the auditory cortex. The ventral striatum exhibited stronger activation when participants made listeners laugh than when another did. In physio-physiological interaction analyses, the ventral striatum showed interaction effects for signals extracted from the mPFC and auditory cortex. These results support the hypothesis that the mPFC, which is implicated in self-related processing, gates sensory input associated with others' responses during value processing in the ventral striatum.

1. Introduction

Social interactions play a critical role in the development of social and cognitive skills (Goldstein et al., 2003; Kuhl et al., 2003; Csibra and Gergely, 2006; Meltzoff et al., 2009; van de Pol et al., 2010). Social interactions can be facilitated by action-outcome contingency (Jones and Gerard, 1967), in which one's own actions result in relevant responses from others. Social action-outcome contingency can lead to longer interactions that are associated with positive responses (e.g., smiling in children) (Matarazzo et al., 1964; Legerstee and Varghese, 2001; Soussignan et al., 2006; Gratch et al., 2006) and enhance improvements in motor skills (Dobkin et al., 2010; Sugawara et al., 2012).

Previous neuroimaging studies have highlighted the role of the striatal reward system in action outcome-contingency (O'Doherty et al., 2004; Tricomi et al., 2004; Zink et al., 2004; Tanaka et al., 2008; Schilbach et al., 2010; Li and Daw, 2011; FitzGerald et al., 2014). For instance, Zink et al. (2004) postulated that action-outcome contingency is related to the saliency of the reward. In their functional magnetic resonance imaging (fMRI) study, saliency of a monetary reward was manipulated according to whether its receipt depended on the correct detection of a target (active task) or was completely independent of such detection (passive task). Significant caudate and nucleus accumbens (NAcc) activation occurred following the active compared to passive task. The action-outcome

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contingency signal is also generated when the outcome is a social reward, such as successful joint attention (Schilbach et al., 2010). This action-outcome contingency signal is considered critical for instrumental learning, which may be used to update expected values of an action (O'Doherty et al., 2004; Hare et al., 2008), action preferences (Li and Daw, 2011), or reflect the success of the action that leads to the desirability of repeating it in the future (FitzGerald et al., 2014). In the present study, we focused our investigation on one basic question related to action-outcome contingency signals: How is this signal generated in the striatal reward system? The action-outcome contingency signal is dependent upon two types of signals: a signal representing the individual's own action and a signal associated with the outcome of that action. However, as these signals have not been evaluated separately in previous studies, the mechanisms wherein signals associated with self-actions and their outcomes are integrated in order to generate an action-outcome contingency signal are not well understood.

Although the nature of the self-concept is inherently complex, previous neuroimaging studies have suggested that activity in a distributed set of brain regions associated with information processing is altered by the presence of self-related information (Northoff et al., 2006; Uddin et al., 2007; Sugiura, 2013 for review). Among these regions, the medial prefrontal cortex (mPFC) is consistently reported and thus proposed as a critical node of self-related processing. For instance, a recent meta-analysis revealed that a part of the mPFC was more frequently activated by self-related judgments than other-related judgments (Denny et al., 2012). The mPFC is sensitive to social signals directed at the self (e.g., hearing one's own name compared to a different name) (Kampe et al., 2003). Sui and Humphreys (2015) proposed that self-reference increases the coupling between brain regions that are assigned to different stages of information processing. For instance, their previous study demonstrated that participants respond to shapes associated with themselves faster than those associated with others in judging the correctness of learned associations, and that this effect is associated with coupling between brain regions involving the mPFC (Sui et al., 2013). Given that the relationship between the sensory cortex and striatum is associated with the reward value of the sensory input (Salimpoor et al., 2013), it is possible that signals from components of the self-related network, such as the mPFC, may modulate the input of sensory signals of the outcome to value processing in order to generate action-outcome contingency signals.

In the present study, we conducted an fMRI analysis involving 39 healthy adult volunteers. We employed a task in which the participant attempted to make a listener laugh by telling funny jokes. In this task, the utterance was regarded as the action, and the laughter was regarded as the outcome. Two factors were manipulated: the speaker of the joke and the listener's response. We evaluated brain activity when the participant heard the listener's response to an uttered joke. We hypothesized that the mPFC reflects self-related activity associated with the effect of the speaker, whereas activity in the auditory cortex reflects the processing of laughter. Moreover, we hypothesized that self-related activity in the mPFC modulates the functional connectivity between the auditory cortex and striatum for the value processing of the outcome.

2. Materials and methods

2.1. Participants

Thirty-nine healthy individuals aged 19–29 years (20 men and 19 women; mean age = 21.2 years; standard deviation [SD] = 1.8 years) participated in the study. We analyzed data from 38 participants [19 men and 19 women, aged 19–29 years, mean ± SD age = 21.15 ± 1.79 years], after excluding one participant from the analysis due to excessive head motion (over 2 mm in each run). All participants were native Japanese speakers and right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). No participants had a history of symptoms requiring neurological, psychological, or other medical care. All participants provided written informed consent. The study was approved by the ethical committee of the National Institute for Physiological Sciences of Japan. All methods were carried out in accordance with the approved guidelines.

2.2. Experimental design

Participants completed two tasks: the pseudo-interactive joke task and the supplementary gambling task. The gambling task was conducted after the pseudo-interactive joke task and was used to confirm overlapping activity in the striatum between the two tasks (see Supplementary methods for details). In total, the experiment lasted 2.5 h.

2.3. Pseudo-interactive joke task

In this task, one of the two actors (SELF or OTHER) uttered a joke (speaker), and a listener made a response after the utterance. There were three listener responses (Group laughter, Single laughter, and No laughter). Accordingly, this task contained six conditions: SELF_Group (i.e., the self-utterance of a joke followed by group laughter), SELF_Single, SELF_No, OTHER_Group, OTHER_Single, and OTHER_No.

2.4. Stimuli

2.4.1. Selection of jokes

We initially prepared 528 jokes from a Japanese TV show program (IPPON GRAND PRIX; Fuji Television Network, Inc., Tokyo, Japan). We then conducted two rating tests with a 7-point Likert scale; the 176 jokes with the highest ratings were chosen by 11 volunteers (7 men and 4 women, aged 26–36 years, mean ± SD age = 29.36 ± 3.55 years), and the 120 funniest jokes among these 176 jokes were further selected by another 33 volunteers (22 men and 11 women, aged 21–39 years, mean ± SD age = 25.72 ± 4.26 years). Finally, we chose 90 of these 120 jokes in which the number of mora in the punchline was matched (mean ± SD = 16.57 ± 7.84 years). We also chose eight jokes among the unchosen jokes for use in practice trials.

2.4.2. Auditory stimuli

The listeners' responses and jokes uttered by participants of the OTHER group were developed as follows. We used two types of laughter as listener responses: One type represented laughter from multiple individuals (Group laughter), and the other type represented laughter from a single person (Single laughter). We selected sound files available on the internet (SONICWIRE, http://sonicwire.com/) and edited them such that the laughs were clear, gender-ambiguous, and matched in length (3.3 s) (Adobe Audition 3.0, Adobe Systems Inc., San Jose, CA, USA). The sound pressure levels were adjusted such that the participants could hear the responses comfortably during the scanning. Three experimenters confirmed that they felt subjective pleasure when these stimuli were presented after they uttered the punchline of a joke. In addition to the Group and Single laughter stimuli, we prepared a stimulus that had the same length of silence with no laugh (No laughter). We recorded the sound of an experimenter (SO) uttering jokes and edited the recorded sound with the same procedure as laughter, such that its duration ranged from 3 to 6 s.