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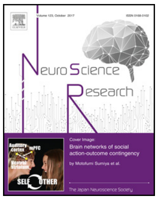

# Brain networks of social action-outcome contingency: The role of the ventral striatum in integrating signals from the sensory cortex and medial prefrontal cortex

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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.

#### 2.4.3. Pairing jokes with listener responses

The 90 funniest jokes were categorized into six sets (15 jokes in each set) such that the mean rating of funniness was matched between them. Each set was pseudo-randomly chosen for each task condition.

### 2.5. Stimulus presentation

Participants lay in the MR scanner with their ears plugged and tight but comfortable foam padding placed around each participant's head. We used Presentation software (Neurobehavioral Systems, Albany, CA, USA) (RRID: SCR_002521) to present visual and auditory stimuli and record button responses. Visual stimuli were projected with a liquid-crystal display projector (CP-SX12000J; Hitachi Ltd., Tokyo, Japan) onto a half-transparent screen. Participants viewed stimuli via a mirror placed above the head coil. The viewing angle was large enough for participants to observe stimuli (13.1° [horizontal] × 10.5° [vertical] at maximum). Participants listened to auditory stimuli through ceramic headphones (KIYOHARA-KOUGAKU, Tokyo, Japan). Participants' utterances were recorded with an opto-microphone system (KOBATEL Corporation, Kanagawa, Japan). Behavioral responses were collected via an optical button box (HHSC–1 × 4; Current Designs Inc., Philadelphia, PA, USA).

### 2.6. Cover story

Participants were instructed to read the punchline of jokes aloud in one condition, whereas they were asked to listen to the punchline of jokes that were played by a computer in the other condition. Participants were encouraged to read the punchline in a funny way. Before the experiment, participants met an individual whose gender was the same as their own; they were told that this individual would be listening to the jokes in another room and evaluating the funniness of the jokes by pressing buttons corresponding to one of the three auditory responses. The participants were told that this listener was different from the reader of the joke in the OTHER condition. Although the listener's response was pre-determined (as described in the section on stimuli), participants were told that the listener evaluated the funniness of the joke. We confirmed that all participants believed that another real person evaluated the uttered jokes.

### 2.7. Task schedule

Participants conducted three runs, each of which lasted for 810 s (810 vol per run). Each run consisted of 30 trials lasting for 25 s (750 s). Each of the six conditions was presented five times in each run. We inserted a 35-s baseline before the first trial and a 25-s baseline after the last trial (750 + 60 = 810 s). Fig. 1 shows the task schedule of each trial. Each trial consisted of five phases: Preparation, Speaker's Action, Listener's Response, Rating, and Rest (Fig. 1).

#### 2.7.1. Preparation phase

The setup and punchline of a joke were visually presented on the screen. Four seconds after the appearance of the joke, the setup was read aloud by an experimenter's voice (the same voice as in the OTHER condition). This phase took between 7 and 10 s in total, depending on the length of the joke.

#### 2.7.2. Speaker's Action phase

One of the two frame colors was superimposed on the visual stimuli. When a red frame appeared, the participant was asked to read the punchline aloud (SELF condition). Conversely, when a blue frame was presented, the participant was asked to listen to the punchline that was read aloud by the OTHER (OTHER condition). This phase took 3 s–6 s depending on the length of the joke.

#### 2.7.3. Listener's Response phase

One of the three levels of laughter was presented while a star mark was visually presented for 4 s (Group laughter/Single laughter/No laughter). In the Group or Single laughter conditions, participants heard 3.3 s of laughter 0.5 s after the star mark appeared. No sound was presented in the No laughter condition.

#### 2.7.4. Rating phase

Participants reported the degree of subjective pleasure using a 7-point Likert scale (1 = no pleasure, 7 = very pleasurable). Participants pressed two buttons with their right index and middle fingers to choose their subjective pleasure rating. The initial position of choice was pseudo-randomized on the rating scale.

#### 2.7.5. Rest phase

Finally, we inserted a resting period such that the duration of each trial was 25 s. The duration of this phase varied from 1 to 7 s.

### 2.8. Data acquisition

We used a 3T whole-body scanner (Verio; Siemens Erlangen, Germany) with a 32-element phased-array head coil. In order to obtain T2*-weighted (functional) images, we employed a multiband echo-planar imaging (EPI) sequence that collected multiple EPI slices simultaneously and reduced the volume repetition time (TR) (Moeller et al., 2010). We utilized the following sequences to cover the whole brain: TR = 1 s; echo time (TE) = 30 ms; flip angle (FA) = 80°; field-of-view (FOV) = 192 × 192 mm; in-plane resolution = 2 mm × 2 mm; 60 2-mm axial slices with 0.5 mm slice gap; and multiband factor = 6. Between the functional runs, we obtained anatomical T1-weighted scans that covered the whole brain (voxel size = 1 mm × 1 mm × 1 mm). We used an MP2RAGE (Magnetization Prepared 2 Rapid Acquisition Gradient Echoes) sequence that provided anatomical images with high contrast between gray and white matter (Marques et al., 2010).

### 2.9. Data processing

Image processing and statistical analyses were performed using the statistical Parametric Mapping (SPM8) package (Friston et al., 2007) (RRID: SCR_007037). The first 10 functional images were discarded in each run to allow the signal to reach a state of equilibrium. The remaining volumes were used for subsequent analyses. To correct for the participant's head motion, functional images from each run were realigned to the first image, and again realigned to the mean image after the first realignment. After the T1-weighted anatomical images were segmented into different tissue classes, each participant's T1-weighted anatomical image was co-registered with the mean image of all EPI images for each participant. The co-registered anatomical images were spatially normalized to the standard Montreal Neurological Institute (MNI) T1 brain template (ICBM 152) (Evans et al., 1993; Friston et al., 1995). Normalized fMRI images were filtered using a relatively small spatial smoothing kernel (4 mm at full-width half-maximum [FWHM]) to accurately determine the location of the regions in the basal ganglia (e.g., the ventral striatum) at the group level (Sacchet and Knutson, 2012).

### 2.10. Statistical analysis

Behavioral data were analyzed with SPSS software (RRID: SCR_002865). Concerning fMRI data analysis, linear contrasts between conditions were calculated for individual participants and

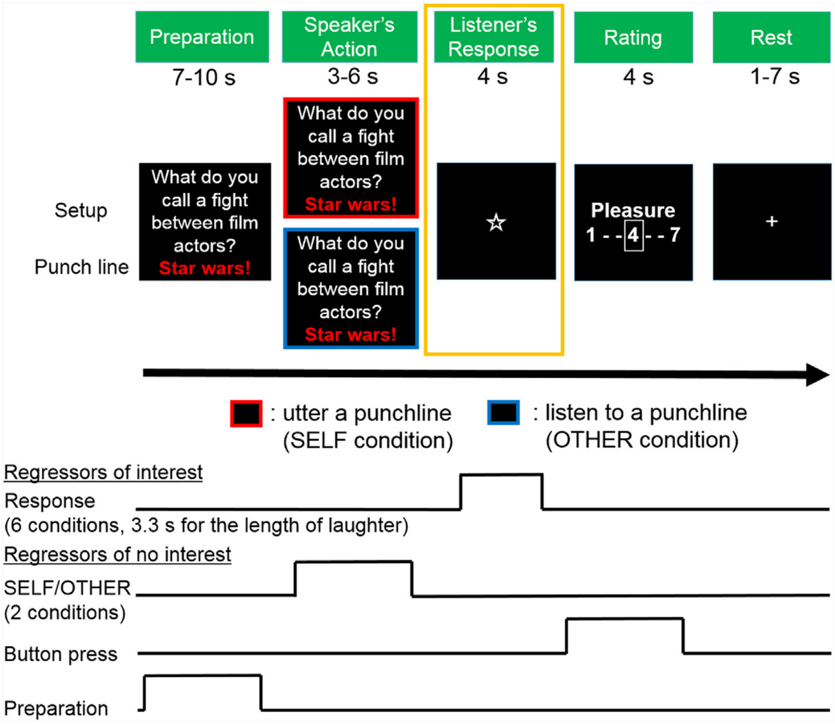

**Fig. 1.** Sequence of events in the pseudo-interactive joke task.
Each trial consisted of five phases: preparation, speaker's action, listener's response, rating, and rest. In the preparation phase, the participant observed and listened to the setup of a joke. Two conditions were prepared in the action phase: When the frame of the screen turned red, the participant uttered the punchline of the joke (SELF condition), whereas when the frame of the screen turned blue, the participant listened to the punchline, which was read aloud by the OTHER (OTHER condition). Each punchline was new and presented only once. In the response phase, the participant heard one of three responses from the listener: laughter of people (Group laughter), laughter of a single individual (Single laughter), or silence (No laughter). The participant then rated his or her pleasantness by pressing buttons in the rating phase. Activities during the task were modeled with boxcar functions for each phase except the rest condition. The regressors shown were convolved with the canonical hemodynamic response function. We focused our analysis on the listener's response phase (yellow frame).

incorporated into a random-effects model to make inferences at a population level (Holmes and Friston, 1998).

### 2.10.1. Initial individual analysis

After preprocessing, task-related activation was evaluated using a general linear model (Friston et al., 1994; Worsley and Friston, 1995). The design matrix contained regressors of three fMRI runs. Each run included six regressors of interest (2 Speakers × 3 Listener's Responses) that were modeled at the onsets of listener's responses. The duration of each regressor was 3.3 s, corresponding to the duration of the auditory response (Fig. 1). In addition, each run also included the following five regressors: one regressor for the Preparation phase, two regressors for the Speaker's Action phase (SELF or OTHER), one regressor for the Rating phase, and one regressor for the button press. We confirmed weak correlations between regressors of the Speaker's Action phase and regressors of the Listener's Response phases (mean r value = 0.24, ranging from 0.23 to 0.25). The blood-oxygen-level dependent (BOLD) signal for all the tasks was modeled with boxcar functions convolved with a canonical hemodynamic response function characterized by two gamma functions, one modeling the peak and one modeling the undershoot. Six regressors of rigid-body head motion parameters (three displacements and three rotations) were included as regressors of no interest. We also applied a high-pass filter with a cut-off of 128 s to remove low-frequency signal components. Assuming a first-order autoregressive model, the serial autocorrelation was estimated from the pooled active voxels with the restricted maximum likelihood (ReML) procedure and used to whiten the data (Friston et al., 2002). No global scaling was performed. To calculate the estimated parameters, a least-squares estimation was performed on the whitened data. The weighted sum of the parameter estimates in the individual analyses constituted contrast images. The contrast images obtained from the individual analyses represented the normalized task-related increment of the MR signal of each participant.

### 2.10.2. Subsequent random-effects analysis

Contrast images from the individual analyses were used for the group analysis. We adopted a flexible factorial design to construct a single design matrix involving 2 × 3 task conditions in the Listener's Response phase. All conditions were modeled as within-subject (dependent) levels, and unequal variance among conditions was assumed. The estimates for the conditions were compared using linear contrasts. The resulting set of voxel values for each contrast constituted a statistical parametric map of the t-statistic (SPM {t}).

Given our hypotheses, we evaluated the following predefined contrasts. The effect of self-action was evaluated as [(SELF_Group + SELF_Single + SELF_No) – (OTHER_Group + OTHER_Single + OTHER_No)] (SELF minus OTHER). The effects of listeners' responses were evaluated as either [(SELF_Group + OTHER_Group) – (SELF_No + OTHER_No)] (Group minus No Laughter), [(SELF_Single + OTHER_Single) – (SELF_No + OTHER_No)] (Single minus No Laughter), or [(SELF_Group + OTHER_Group) – (SELF_Single + OTHER_Single)] (Group minus Single). Finally, action-outcome contingency effects were evaluated as [(SELF_Group – SELF_No) – (OTHER_Group – OTHER_No)], or [(SELF_Single – SELF_No) – (OTHER_Single – OTHER_No)]. The threshold for the SPM{t} was set at $t_{(222)} > 3.13$ (equivalent to $p < 0.001$ uncorrected). The statistical threshold for the spatial extent test on the clusters was set at $p < 0.05$ and

**Fig. 2.** Rating of subjective pleasure.
The ratings of subjective pleasure showed greater differences between different degrees of laughter in the SELF than OTHER condition. Two-way analysis of variance (ANOVA; Speaker × Listener's response) revealed a significant interaction ($p < 0.0001$). *Post hoc* pairwise comparisons with Bonferroni's correction revealed that the rating in the Group ($p < 0.0001$) and Single laughter ($p = 0.0001$) conditions was greater for the SELF than OTHER condition, whereas the rating for the OTHER was greater than that for the SELF in the No (No laughter) condition ($p < 0.0001$). Data are presented as the mean ± standard error of the mean (SEM) of 38 participants.

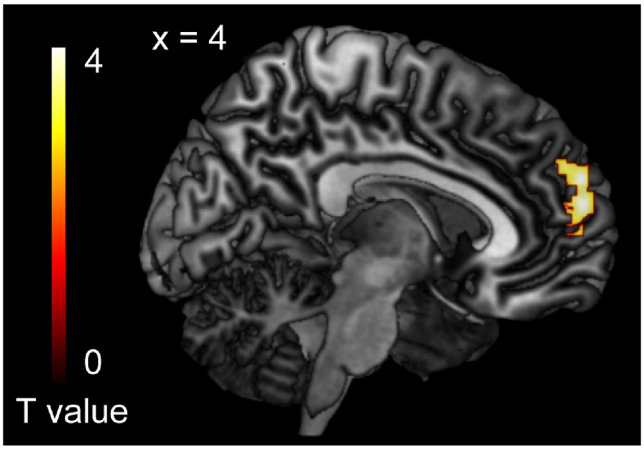

**Fig. 3.** The effect of self action (SELF minus OTHER).
The contrast for the main effect of Speaker [(SELF_No + SELF_Single + SELF_Group) − (OTHER_No + OTHER _Single + OTHER _Group)] revealed significant activation in the medial prefrontal cortex (mPFC) only. The size of the activation was thresholded at $p < 0.05$ and familywise-error (FWE) corrected for multiple comparisons over the whole brain, with the height threshold set at $p < 0.001$ (uncorrected). Activation is superimposed on a surface-rendered T1-weighted magnetic resonance image of an individual who did not participate in the study.

corrected for multiple comparisons [family-wise error (FWE)] over the whole brain (Friston et al., 1996).

We evaluated brain activation after excluding any activation outside the gray matter with the masking procedure. Brain regions were anatomically defined and labeled according to probabilistic atlases (Desikan et al., 2006; Shattuck et al., 2008). Furthermore, we used an atlas of the human brain (Mai et al., 2007) to confirm the structures in and around the ventral striatum.

#### 2.10.3. Physio-physiological interaction (PPI) analysis

We conducted physio-physiological interaction (PPI) analyses (Friston et al., 1997) in order to test the hypothesis that self-related activity in the mPFC modulates the functional connectivity between the auditory cortices (AC) and reward system.

We identified the top peak coordinates of activation depicted by each effect of the joke task: the mPFC by the effect of self action, and the AC by the effect of the listener's response. As we observed bilateral activation of the AC, the left and right hemispheres were defined as separate seed regions, which were defined by spheres (radius: 8 mm) centered on the peak coordinates of these regions. We extracted the time series of the signal from each seed region after excluding the effects of no interest with F contrasts.

We then calculated the PPI terms between the mPFC and the AC in the following four steps. First, the MR signal from each seed region was extracted as an eigenvariate time series. Second, the extracted MR signal was deconvolved with the canonical hemodynamic response function (HRF). The resulting time series represented an approximation of neural activity (Gitelman et al., 2003). Third, the neural time series of the two seed regions were detrended and multiplied (dot product) so that the resulting time series represented the interaction of neural activity between the two seed regions. In the present study, we calculated the interaction of neural activity between the mPFC and right AC, as well as that between the mPFC and left AC. Finally, the interaction time series was convolved with the HRF, representing an interaction variable at the hemodynamic level (PPI term).

For each participant, we constructed two design matrices; one for the mPFC and right AC and the other for the mPFC and left AC. Each design matrix involved nine regressors: the PPI term between the mPFC and AC in one hemisphere, two regressors representing the time-series of the MR signal of these seed regions, and six regressors representing head motion effects. In the group analysis, we conducted one-sample *t*-tests on the contrast images of the PPI terms obtained from these individual analyses. We applied the same statistical thresholds utilized for the analysis of brain activation ($P < 0.05$ FWE corrected at cluster level, with threshold at $t_{(37)} > 3.33$ corresponding to $p < 0.001$ uncorrected).

## 3. Results

### 3.1. Behavioral results

The participants rated subjective pleasure after the listener's response in each trial (Fig. 1). Greater laughter yielded greater pleasure in both the SELF and OTHER conditions, whereas the increment of the pleasure rating between the listener's responses was greater for the SELF than OTHER condition (Fig. 2). Two-way repeated-measures analysis of variance (ANOVA; 2 levels of Speaker × 3 levels of Listener's Response) of the pleasure rating revealed a significant main effect of Speaker ($F_{(1,37)} = 24.1$, $p < 0.0001$), a significant main effect of Listener's Response ($F_{(2,74)} = 99.5$, $p < 0.0001$), and a significant interaction ($F_{(2,74)} = 37.9$, $p < 0.0001$). *Post hoc* pairwise comparisons with Bonferroni's correction confirmed that all Listener's Responses differed significantly for the SELF (p values < 0.0001) but not for the OTHER condition (Group vs. Single, $p = 0.161$; Group vs. No, $p = 0.006$; Single vs. No, $p = 0.003$). Rating scores for the SELF were significantly greater than those for the OTHER in the Group Laughter ($p < 0.0001$) and Single Laughter conditions ($p = 0.0001$), whereas the rating in the No Laughter condition was significantly lower in the SELF than in the OTHER conditions ($p < 0.0001$).

### 3.2. Functional MRI results

#### 3.2.1. The effect of self action (SELF minus OTHER)

The contrast of SELF minus OTHER [(SELF_Group + SELF_Single + SELF_No) − (OTHER_Group + OTHER_Single + OTHER_No)] revealed significant activation only in the mPFC (Fig. 3). The peak coordinate was located at x = 4, y = 58, z = 16, corresponding to Brodmann area 10 (Lancaster et al., 2000; Table 1).

**Table 1**
The effect of self action (SELF minus OTHER).

| Spatial extent test | | MNI coordinates (mm) | | | t-value | Location | |
|---|---|---|---|---|---|---|---|
| Cluster size (mm$^3$) | $P_{\text{FWE-corr}}$ | x | y | z | | Side | Area |
| SELF minus OTHER [(SELF_No + SELF_Single + SELF_ Group) − (OTHER_No + OTHER_Single + OTHER_Group)] (Fig. 3) | | | | | | | |
| 1200 | < 0.01 | 4 | 58 | 16 | 4.03 | R | mPFC |

Activation was thresholded at $p < 0.05$ and familywise-error (FWE) corrected for multiple comparisons over the whole brain, with the height threshold set at $p < 0.001$ uncorrected. The terms x, y, and z represent the stereotaxic coordinates (mm). R, right hemisphere; mPFC, medial prefrontal cortex; MNI, Montreal Neurological Institute.

### 3.2.2. *The effects of the listener's response*

The contrast of Group minus No laughter [(SELF_Group + OTHER_Group) − (SELF_No + OTHER_No)] revealed regions of significant activation in the bilateral superior temporal gyrus, bilateral Heschl's gyrus, and bilateral cuneus, as well as the right middle temporal gyrus and right lingual gyrus (Supplemental Fig. S1 and Table 2).

The contrast of Single minus No laughter [(SELF_Single + OTHER_Single) − (SELF_No + OTHER_No)] revealed regions of significant activation in the bilateral superior temporal gyrus and bilateral Heschl's gyrus.

The contrast of Group minus Single laughter [(SELF_Single + OTHER_Single) − (SELF_No + OTHER_No)] revealed regions of significant activation in the bilateral mPFC, bilateral lingual gyrus, bilateral inferior frontal gyrus, bilateral lateral orbitofrontal cortex, right superior occipital gyrus right middle frontal gyrus, and left cuneus. No overlap of activation with the effect of self action was observed.

### 3.2.3. *The effect of action-outcome contingency*

The contrast of action-outcome contingency effect [(SELF_Group − OTHER_Group) − (SELF_No − OTHER_No)] revealed regions of significant activation in the ventral striatum (VS): the bilateral NAcc, bilateral ventral caudate nucleus, and right putamen (Fig. 4 and Table 3). Moreover, the same contrast revealed significant activation in the right lingual gyrus and right inferior occipital gyrus. At a more lenient threshold ($T > 3.13$ without FWE correction at the cluster level), we observed activation in the ventral mPFC ($x = -8$, $y = 54$, $z = -2$). The contrast of [(SELF_Single − OTHER_Single) − (SELF_No − OTHER_No) revealed no significant activation.

In order to further validate the action-outcome contingency effect (Kriegeskorte et al., 2009), we examined brain activity related to the amount obtained in the gambling task (Izuma et al., 2008). The premise in this analysis was that the VS is sensitive to reward, regardless of whether the reward is monetary or social (Izuma et al., 2008). This analysis on the gambling task revealed significant activation in brain regions including the bilateral NAcc (Supplemental Table S1). We defined regions of interest (ROI) of the VS according to the top peak coordinates in the gambling task. These ROIs exhibited action-outcome contingency effects not only between group and no laughter, but also between group and single laughter (Supplemental Fig. S2).

### 3.2.4. *Physio-physiological interaction (PPI) analyses*

We observed the action-outcome contingency effect in brain regions including the VS. In addition, the mPFC exhibited effects related to self action, whereas the effects of listener's response were associated with brain regions such as the AC. We then tested our prediction that the mPFC modulates functional connectivity between the sensory cortex and VS using PPI analyses (Friston et al., 1997). We defined seed regions as spheres of 8 mm in radius centered around the peak coordinates of each region: the mPFC ($x = 4$, $y = 58$, $z = 16$), right AC (in Heschl's gyrus [$x = 52$, $y = -12$, $z = 2$]), and left AC (in the superior temporal gyrus [$x = -48$, $y = -28$, $z = 8$]). The coordinates of the AC were chosen based on the contrast of Group minus No laughter, as its interaction with the effect of self-action [(SELF_Group − OTHER_Group) − (SELF_No − OTHER_No)] alone revealed significant activation in the VS.

PPI analysis with seeds in the mPFC and right AC revealed activity in the bilateral NAcc (Fig. 5). The same analysis revealed PPI effects in the following bilateral regions: the superior frontal gyrus, precentral gyrus, postcentral gyrus, middle occipital gyrus, lingual gyrus, inferior occipital gyrus, fusiform gyrus, inferior frontal gyrus, middle frontal gyrus, insula, Heschl's gyrus, superior temporal gyrus, and cerebellum. In addition, we also observed activity in the right anterior cingulate gyrus, right mPFC, left middle temporal gyrus, left superior occipital gyrus, and left hippocampus (Table 4). We also observed a significant correlation between the interaction term of subjective pleasure and PPI effect at the top peak coordinate of the left NAcc ($x = -6$, $y = 10$, $z = -14$, $r = 0.28$, $n = 38$, $p < 0.05$ one-tailed). We observed highly similar results when the mPFC and the left AC were used as seed regions (Table 5).

### 3.2.5. *Is the PPI effect in the ventral striatum observed using other sensory cortices as seed areas?*

In order to further validate the result of the PPI analysis, we conducted a supplementary analysis wherein the visual cortex, instead of the AC, was used as the seed region. We expected that the PPI effect in the VS would not be observed, as this sensory region would play non-essential roles in processing of listener's response. The seed region was defined based on the top peak of activation in the visual cortex that was depicted as the effect of listener's response ($x = -4$, $y = -96$, $z = 8$, Table 2). This analysis revealed PPI effects in the following bilateral regions: the mPFC, anterior cingulate gyrus, superior, middle, and inferior occipital gyrus, middle and inferior frontal gyrus, precentral gyrus, insula, fusiform gyrus, and cerebellum. In addition, we also observed activity in the right middle temporal gyrus, left postcentral gyrus, and left putamen. However, no significant effects were observed for the VS (data not shown).

## 4. Discussion

### 4.1. *Behavioral performance*

Subjective pleasure was greater for group and single laughter in the SELF condition than in the OTHER condition. In contrast, the absence of the listener's response in the SELF condition decreased subjective pleasure relative to the OTHER condition. This result indicates that action-outcome contingency increases subjective pleasure, consistent with previous findings that action-outcome contingency increases positive response to social interactions (e.g., degree of smile) and extends the duration of social interaction (Gratch et al., 2006; Soussignan et al., 2006).

### 4.2. *Functional implication of the mPFC*

As compared to self-irrelevant responses (i.e., response followed by another's utterance of the punchline), listening to self-relevant responses activated the mPFC that corresponds to Brodmann Area 10. This finding indicates that the mPFC plays a critical role in mon-

**Table 2**
The effect of listener's response.

| Spatial extent test | | MNI coordinates (mm) | | | t-value | Location | |
|---|---|---|---|---|---|---|---|
| Cluster size (mm$^3$) | $P_{FWE\text{-}corr}$ | x | y | z | | Side (Supplemental Fig. S1) | Area |
| Group minus No Laughter [(SELF_ Group − SELF_No) + (OTHER_ Group − OTHER_No)] | | | | | | | |
| 36,120 | <0.001 | 56 | −24 | 10 | 17.47 | R | Superior temporal gyrus |
| | | 62 | −56 | 6 | 4.09 | R | Middle temporal gyrus |
| | | 52 | −12 | 2 | 20.24 | R | Heschl's gyrus |
| 35,104 | <0.001 | −48 | −28 | 8 | 20.31 | L | Superior temporal gyrus |
| | | −52 | −20 | 6 | 19.82 | L | Heschl's gyrus |
| 25,784 | <0.001 | 6 | −86 | 36 | 4.49 | R | Cuneus |
| | | −4 | −96 | 8 | 5.31 | L | Cuneus |
| | | 20 | −58 | 6 | 4.88 | R | Lingual gyrus |
| Single minus No Laughter [(SELF_ Single − SELF_No) + (OTHER_Single − OTHER_No)] | | | | | | | |
| 34,144 | <0.001 | 56 | −24 | 10 | 17.71 | R | Superior temporal gyrus |
| | | 50 | −16 | 4 | 19.47 | R | Heschl's gyrus |
| 34,608 | <0.001 | −48 | −28 | 8 | 20.21 | L | Superior temporal gyrus |
| | | −42 | −26 | 4 | 20.54 | L | Heschl's gyrus |
| Group minus Single Laughter [(SELF_ Group − SELF_Single) + (OTHER_ Group − OTHER_Single)] | | | | | | | |
| 5304 | <0.001 | −14 | 44 | 48 | 5.82 | L | mPFC |
| 1504 | <0.01 | 12 | 50 | 38 | 5.13 | R | mPFC |
| 30,280 | <0.001 | 14 | −90 | 32 | 4.76 | R | Superior occipital gyrus |
| | | −12 | −76 | 12 | 4.92 | L | Lingual gyrus |
| | | −4 | −96 | 8 | 5.96 | L | Cuneus |
| | | 16 | −82 | 6 | 6.75 | R | Lingual gyrus |
| 13,104 | <0.001 | 14 | 42 | 10 | 4.42 | R | Middle frontal gyrus |
| | | −6 | 32 | −10 | 5.61 | L | mPFC |
| | | 2 | 42 | −10 | 4.85 | R | mPFC |
| 960 | <0.05 | −44 | 28 | 4 | 4.12 | L | Inferior frontal gyrus |
| | | −44 | 24 | −6 | 4.17 | L | Lateral orbitofrontal cortex |
| 1344 | <0.01 | 44 | 30 | −2 | 3.40 | R | Inferior frontal gyrus |
| | | 32 | 18 | −16 | 4.92 | R | Lateral orbitofrontal cortex |

Activation was thresholded at $p < 0.05$ and FWE corrected for multiple comparisons over the whole brain, with the height threshold set at $p < 0.001$ uncorrected. The terms x–z represent the stereotaxic coordinates (mm). R, right hemisphere; L, left hemisphere; MNI, Montreal Neurological Institute; mPFC: medial prefrontal cortex.

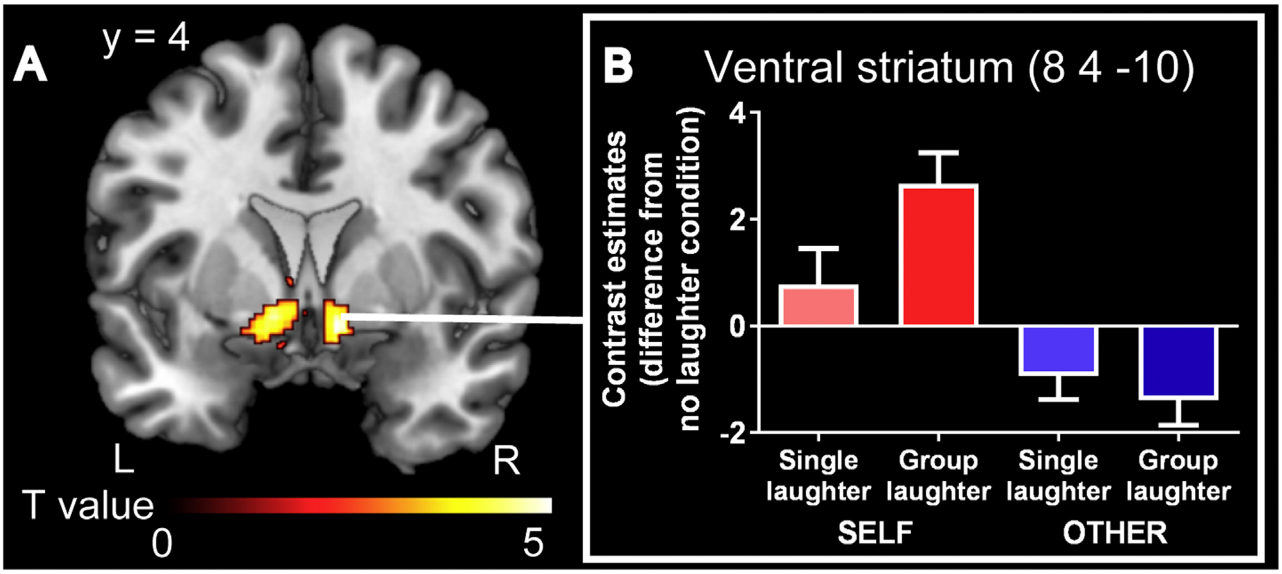

**Fig. 4.** The effect of action-outcome contingency.
**(A)** The contrast for the interaction effect [(SELF_Group − SELF_No) − (OTHER _Group − OTHER_No)] revealed significant activation in the ventral striatum (VS) only. The size of the activation was thresholded at $p < 0.05$ and family-wise error (FWE) corrected for multiple comparisons over the whole brain, with the height threshold set at $p < 0.001$ uncorrected. **(B)** Activation pattern in the top peak coordinate of the right VS (see Table 3 for details of coordinates). Data are presented as the mean ± standard error of the mean (SEM) of 38 participants.

itoring the outcome of self-action, consistent with the hypothesis that the mPFC is involved in the non-physical and abstract representation of the self in the context of social interaction (Uddin et al., 2007; Sugiura, 2013). To parsimoniously explain the involvement of the mPFC in a broad range of social tasks (Van Overwalle, 2009), Krueger et al. (2009) proposed that the mPFC represents event simulators (elators) that encompass a multi-modal representation of social event knowledge distributed throughout brain regions. Elators provide the underlying properties for social cognitive structures that are involved in planning and monitoring one's

**Table 3**
The effect of action-outcome contingency.

| Spatial extent test | | MNI coordinates (mm) | | | t-value | Location | |
|---|---|---|---|---|---|---|---|
| Cluster size (mm$^3$) | $P_{FWE\text{-}corr}$ | x | y | z | | Side | Area |
| [(SELF_ Group – SELF_No) – (OTHER_Group – OTHER_No)] (Fig. 4) | | | | | | | |
| 760 | <0.05 | 10 | 12 | −2 | 4.11 | R | Caudate nucleus |
| | | 18 | 10 | −8 | 3.65 | R | Putamen |
| | | 8 | 4 | −10 | 5.35 | R | NAcc |
| 1304 | <0.01 | −10 | 14 | −2 | 4.74 | L | Caudate nucleus |
| | | −10 | 8 | −8 | 4.65 | L | NAcc |
| 1696 | <0.01 | 14 | −72 | −8 | 4.25 | R | Lingual gyrus |
| | | 16 | −78 | −14 | 4.26 | R | Inferior occipital gyrus |
| [(SELF_ Single – SELF_No) – (OTHER_Single – OTHER_No)] | | | | | | | |
| No significant activation | | | | | | | |

Activation was thresholded at $p < 0.05$ and FWE corrected for multiple comparisons over the whole brain, with the height threshold set at $p < 0.001$ uncorrected. The terms x–z represent the stereotaxic coordinates (mm). R, right hemisphere; L, left hemisphere; NAcc, nucleus accumbens; MNI, Montreal Neurological Institute.

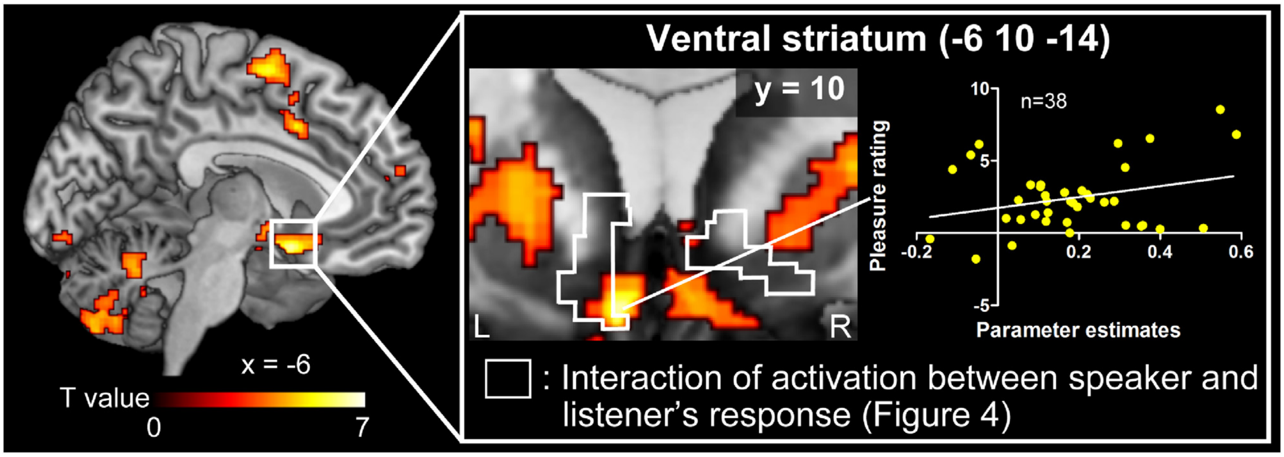

**Fig. 5.** Physio-physiological interaction (PPI) in the ventral striatum (VS).
**Left,** PPI activation with the medial prefrontal cortex (mPFC) and right auditory cortex as seed regions is shown. PPI activation overlapped with the interaction effect between Speaker and Listener's response (white lines, Fig. 4). The size of activation was thresholded at $P < 0.05$ and family-wise error (FWE) corrected for multiple comparisons over the whole brain, with the height threshold set at $p < 0.001$ uncorrected. Note that we also confirmed PPI activation in the VS even when the left auditory cortex was used as a seed region (see Table 5). **Right**, Coronal section of the VS and its adjacent structure. PPI activity at the top peak coordinate was significantly correlated with the interaction term of the rating of pleasure [(SELF_Group – SELF_NO) – (OTHER_Group – OTHER _No)] ($r = 0.28$, $p < 0.042$ one-tailed).

own behavior and understanding and predicting the behavior of others.

Previous studies have suggested the existence of a functional gradient along an axis from self to other within the mPFC (Mitchell et al., 2006; Denny et al., 2012; Sul et al., 2015; Wittmann et al., 2016), as well as an axis from executed to modeled choices (Nicolle et al., 2012). Our self-relevant activation appears to be extended in both directions in each functional gradient. Self-related processing is highly related to the processing of the other in social interactions (Cooley, 1902; Mead, 1934). In the present study, compared with the response to the other's utterance participants may have paid more attention to the listener's responses to their own actions in order to infer the mental state of the listener. Such processing of self-relevant responses from others is related to activation of the mPFC. This speculation is consistent with the framework that the mPFC is a part of the network involved in the awareness that the attention or intentionality of another person is directed at the self ("interpersonal self", Sugiura et al., 2013).

### 4.3. Action-outcome contingency effects in the striatum

Action-outcome contingency effects were observed in the VS. As these effects were revealed as interactions between the self-relevance and the listener's response, effects that are common in all conditions (e.g., pleasure rating) should be canceled out. This finding is consistent with those of previous studies that have highlighted the functional role of the VS in social action-outcome contingency (Pfeiffer et al., 2014; Schilbach et al., 2010). We observed no significant activation in more dorsal parts of the fronto-striatal circuits that have been associated with action-outcome contingency learning (Delgado et al., 2005; Seger and Cincotta, 2005). This may be due to the nature of our task, as the jokes were presented once and thus there was no opportunity for the participants to learn, for example, how to tell the joke in a funnier way for the listener (Seger and Cincotta, 2005).

### 4.4. Physio-physiological interaction in the ventral striatum

In the PPI analysis, we found that activity in the VS reflected an interaction of signals extracted from two regions: the mPFC, in which an effect of self-relevance was observed, and the AC, in which an effect of laughter was observed. This result indicates that the functional connectivity of the VS with a region that reflects one of two effects (self-action and listener's response) is modulated by the other (Fig. 6). As this PPI effect was positively correlated with

**Table 4**
Physio-physiological interaction (PPI) seeded on the right auditory cortex and mPFC.

| Spatial extent test | | MNI coordinates (mm) | | | t-value | Location | |
|---|---|---|---|---|---|---|---|
| Cluster size (mm$^3$) | $P_{FWE\text{-}corr}$ | x | y | z | | Side | Area |
| 5328 | <0.001 | 14 | 8 | 48 | 6.27 | R | Superior frontal gyrus |
| | | 6 | 14 | 36 | 5.73 | R | Anterior cingulate gyrus |
| 2072 | <0.001 | 56 | 0 | 40 | 4.26 | R | Precentral gyrus |
| | | 56 | −6 | 38 | 4.65 | R | Postcentral gyrus |
| 6664 | <0.001 | −12 | 10 | 38 | 5.68 | L | Superior frontal gyrus |
| | | −14 | 52 | 16 | 5.84 | L | Middle frontal gyrus |
| 29280 | <0.001 | −48 | −4 | 28 | 5.91 | L | Precentral gyrus |
| | | −50 | −10 | 20 | 5.67 | L | Postcentral gyrus |
| | | −36 | −32 | 12 | 6.54 | L | Middle temporal gyrus |
| | | −52 | −18 | 6 | 6.17 | L | Heschl's gyrus |
| | | −52 | −18 | −2 | 7.37 | L | Superior temporal gyrus |
| 1000 | <0.05 | 14 | 54 | 16 | 5.22 | R | mPFC |
| 16512 | <0.001 | −24 | −80 | 18 | 4.47 | L | Superior occipital gyrus |
| | | −24 | −94 | −6 | 5.92 | L | Lingual gyrus |
| | | −20 | −96 | −8 | 5.54 | L | Middle occipital gyrus |
| | | −26 | −88 | −14 | 6.27 | L | Inferior occipital gyrus |
| | | −44 | −64 | −16 | 5.09 | L | Fusiform gyrus |
| 9968 | <0.001 | 28 | −76 | 16 | 5.47 | R | Middle occipital gyrus |
| | | 14 | −90 | −8 | 5.58 | R | Lingual gyrus |
| | | 20 | −82 | −10 | 6.07 | R | Inferior occipital gyrus |
| | | 42 | −50 | −10 | 4.37 | R | Fusiform gyrus |
| 12480 | <0.001 | 36 | 22 | 14 | 6.00 | R | Inferior frontal gyrus |
| | | 28 | 28 | 8 | 6.71 | R | Middle frontal gyrus |
| | | 30 | 14 | 8 | 5.26 | R | Insula |
| | | −26 | 22 | 6 | 6.34 | L | Insula |
| | | −34 | 32 | 4 | 5.78 | L | Inferior frontal gyrus |
| | | 6 | 30 | −2 | 6.78 | R | mPFC |
| | | −20 | −10 | −10 | 5.35 | L | Hippocampus |
| | | −6 | 10 | −14 | 6.44 | L | NAcc |
| | | 6 | 8 | −16 | 5.39 | R | NAcc |
| 12480 | <0.001 | 50 | −22 | 4 | 6.81 | R | Heschl's gyrus |
| | | 56 | −6 | −2 | 7.06 | R | Superior temporal gyrus |
| 6072 | <0.001 | 4 | −56 | −32 | 5.76 | R | Cerebellum |
| | | −16 | −66 | −44 | 4.90 | L | Cerebellum |
| 3160 | <0.001 | 12 | −78 | −46 | 6.30 | R | Cerebellum |

Activation was thresholded at $p < 0.05$ FWE corrected for multiple comparisons over the whole brain, with the height threshold set at $p < 0.001$ uncorrected. The terms x–z represent the stereotaxic coordinates (mm). R, right hemisphere; L, left hemisphere. mPFC, medial prefrontal cortex; NAcc, nucleus accumbens; MNI, Montreal Neurological Institute.

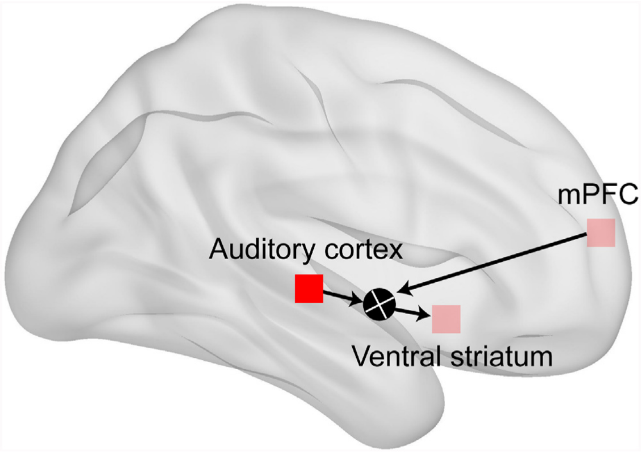

**Fig. 6.** Proposed model of the brain network underlying the social action-outcome contingency.
The top-down signal from the medial prefrontal cortex (mPFC) may modulate functional connectivity of the auditory cortex and ventral striatum (VS). This modulation may result in an interaction effect in the VS between sensory feedback from the other and signals associated with monitoring the outcome of self-action. Such interaction may underlie the subjective pleasure of social action-outcome contingency.

self-rated pleasure, the modulation of functional connectivity may be associated with representation of reward value.

Given that the PPI analysis does not allow one to formulate conclusions about clear-cut directionality (Staudinger et al., 2011), two possibilities may be considered. First, it is possible that the AC modulates functional connectivity between the mPFC and VS, as this functional connectivity is related to the level of self-esteem (Chavez and Heatherton, 2015). However, self-esteem was unlikely to change rapidly in our experiment. Rather, our result supports the hypothesis that the input of signals in the AC evoked by laughter to value processing in the VS is modulated by the signal from the mPFC. A previous fMRI study on the reward value of music showed that the VS and functional connectivity with the AC were correlated with the desirability of music after listening to an excerpt (Salimpoor et al., 2013). The authors concluded that interaction between the sensory cortices and reward circuitry plays a critical role in representing music-related rewards. FitzGerald et al. (2014) reported that selective attention modulates inputs to value processing. The authors manipulated selective attention via a task in which participants had to choose whether to accept or reject an offer indicated by visual and auditory stimuli. By manipulating which stimulus determined the value of the offer (relevance), the authors revealed that choice activity in the VS solely reflects the value of the currently relevant stimulus, indicating that selective attention modulates the impact of sensory stimuli on value processing in the VS. The present study revealed a similar gating effect of the VS, with three features distinct from those of FitzGerald et al. (2014): First, the preceding action (by self or others) gates the outcome input to value processing; second, outcome-related activity

**Table 5**
Physio-physiological interaction (PPI) analysis in the left auditory cortex and mPFC.

| Spatial extent test | | MNI coordinates (mm) | | | t-value | Location | |
|---|---|---|---|---|---|---|---|
| Cluster size ($mm^3$) | $P_{FWE\text{-}corr}$ | x | y | z | | Side | Area |
| 1176 | <0.001 | 18 | 36 | 44 | 6.16 | R | mPFC |
| 3088 | <0.001 | −18 | 22 | 44 | 5.83 | L | mPFC |
| | | −12 | 6 | 36 | 5.42 | L | Anterior cingulate gyrus |
| 2592 | <0.001 | 14 | 20 | 42 | 5.96 | R | Superior frontal gyrus |
| | | 6 | 12 | 32 | 4.23 | R | Anterior cingulate gyrus |
| 3024 | <0.001 | −38 | 0 | 38 | 3.49 | L | Middle frontal gyrus |
| | | −50 | −2 | 30 | 4.88 | L | Precentral gyrus |
| | | −52 | −8 | 20 | 4.51 | L | Postcentral gyrus |
| 3488 | <0.001 | −36 | −38 | 20 | 3.61 | L | Supramarginal gyrus |
| | | −34 | −30 | 12 | 4.49 | L | Middle temporal gyrus |
| | | −50 | −20 | 4 | 4.88 | L | Heschl's gyrus |
| | | −50 | −20 | −4 | 4.92 | L | Superior temporal gyrus |
| 1896 | <0.001 | −22 | −80 | 16 | 4.23 | L | Superior occipital gyrus |
| | | −30 | −76 | 14 | 4.80 | L | Middle occipital gyrus |
| 3304 | <0.001 | 14 | 52 | 16 | 7.54 | R | mPFC |
| | | 30 | 12 | 10 | 6.00 | R | Insula |
| | | 34 | 32 | 8 | 6.50 | R | Inferior frontal gyrus |
| | | 28 | 28 | 6 | 6.86 | R | Middle frontal gyrus |
| 1528 | <0.01 | −36 | 22 | 12 | 5.31 | L | Inferior frontal gyrus |
| | | −26 | 22 | 8 | 5.70 | L | Insula |
| | | −32 | 32 | 6 | 5.99 | L | Middle frontal gyrus |
| 3376 | <0.001 | 50 | −18 | 2 | 4.56 | R | Heschl's gyrus |
| | | 58 | −4 | 0 | 4.70 | R | Superior temporal gyrus |
| 8344 | <0.001 | −36 | −68 | 2 | 5.12 | L | Middle occipital gyrus |
| | | −30 | −78 | −6 | 5.37 | L | Inferior occipital gyrus |
| | | −44 | −64 | −16 | 4.36 | L | Fusiform gyrus |
| 4856 | <0.001 | 24 | −96 | −2 | 3.57 | R | Middle occipital gyrus |
| | | 20 | −80 | −10 | 6.38 | R | Inferior occipital gyrus |
| 1520 | <0.01 | 4 | 24 | −6 | 5.98 | R | mPFC |
| | | 8 | 8 | −14 | 5.15 | R | NAcc |
| 1224 | <0.01 | 4 | −2 | −2 | 4.50 | R | Lingual gyrus |
| | | −10 | 22 | −10 | 5.01 | L | mPFC |
| | | −8 | −4 | −12 | 4.21 | L | Brainstem |
| | | −8 | 16 | −12 | 4.83 | L | NAcc |
| 1576 | <0.01 | 4 | −66 | −38 | 3.35 | R | Cerebellum |
| | | −8 | −68 | −46 | 4.55 | L | Cerebellum |
| 1608 | <0.01 | 30 | −66 | −50 | 5.17 | R | Cerebellum |

Activation was thresholded at $p < 0.05$, FWE corrected for multiple comparisons over the whole brain, with the height threshold set at $p < 0.001$ uncorrected. The terms x–z represent the stereotaxic coordinates (mm). R, right hemisphere; L, left hemisphere. mPFC, medial prefrontal cortex; NAcc, nucleus accumbens; MNI, Montreal Neurological Institute.

in the "self" region (mPFC) can drive this gating; and, third, the signal transfer between the sensory cortices (i.e., the AC) and the VS is represented as the change in functional connectivity between the two regions. These features are consistent with frameworks proposed by Krueger et al. (2009) and by Sui and Humphreys (2015), highlighting the importance of self-reference in action-outcome contingency effect.

The PPI effect in the present study can be interpreted to indicate that the mPFC sends a source signal to the VS to change the gain of the neural response to inputs from the AC (Stephan et al., 2008). This gain-control mechanism may change the patterns of interactions between the VS and AC as well as activity in the VS itself. Given that activity in the VS and its connectivity with the mPFC and AC were correlated with subjective pleasure, the modulatory effect of the mPFC on the auditory cortico-striatal network may explain pleasant experiences through social action-outcome contingency.

We also observed the PPI effect in many other brain regions. However, if these regions are involved in social action-outcome contingency, activity in these regions should be associated with an interaction effect between Speaker and Listener's Response. Given that no such interaction was observed, the role of these regions in social action-outcome contingency remains to be elucidated.

### 4.5. Future directions

There are three limitations of note with regard to the present study. First, we designed our task such that the strength of the action-outcome contingency was pseudo-randomized. Future studies should confirm a link between the contingency effect and learning effects. Second, as the striatum is involved in non-social action-outcome contingency, social and non-social contingency effects should be compared in future studies. Third, PPI analysis has several limitations. For instance, PPI analysis does not allow one to formulate conclusions regarding clear-cut directionality among the mPFC, AC, and VS, and regarding whether the input of the mPFC and AC directly affects the signal in the VS. Future studies should incorporate effective connectivity analysis (e.g., Dynamic Caudal Modeling, Friston et al., 2003) and structural connectivity analysis to clarify the interactions among these regions in detail.

Despite these shortcomings, our findings may contribute to the understanding of neurodevelopmental disorders. For instance, individuals with autism spectrum disorders (ASD) exhibit impairments in social action-outcome contingency (Gergely, 2001; Nadel, 2002). Previous studies have provided only indirect evidence that the brain network underlying this contingency is atypical (Lombardo et al., 2010; Abrams et al., 2013). Thus, future studies should examine how ASD affects the brain network underlying the social action-outcome contingency in order to investigate the pathological origin of such disorders and develop effective early interventions.

## 5. Conclusion

In the present study, we observed interaction effects with regard to signals extracted from the mPFC and auditory cortex in the VS using a social action-outcome contingency task. These results indicate that social contingency involves the interaction of multiple brain regions beyond the striatal reward system. As the connectivity of the VS was associated with subjective pleasure, this distributed network may be responsible for the rewarding nature of social action-outcome contingency.

## Conflict of interest

The authors declare no competing financial interests.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.neures.2017.04.015.

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