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Being a leader in a rhythmic interaction activates reward-related brain regions

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ABSTRACT

Interpersonal rhythmic interaction is one of the fundamental behaviors that allow humans to socially interact with others. In this study, we provide novel neuroimaging evidence that being followed by other agents in such an interaction is pleasant for humans. Using functional magnetic resonance imaging, we measured the brain activity of 17 participants while they performed a virtual drum-hitting task, in one of the following conditions: a) alternating with a virtual agent that would always copy their hitting pace, or b) alternating with a virtual agent that would randomly hit the drum. The participants reported a significantly higher subjective feeling of being followed by the agent in the first condition. Moreover, almost all participants preferred the agent that followed their drum-hitting rhythm. The activity of the caudate nucleus, which is one of the reward-related brain structures, was found to be associated with the subjective feeling of being followed, suggesting that the sense of being the leader, in an interpersonal rhythmic interaction, creates a pleasant feeling.

1. Introduction

Interpersonal interaction is the basis of human social interaction. For example, imitating one's action and sharing attention with others (joint attention) are representative interpersonal, interactive behaviors. Indeed, many psychological studies have been conducted to analyze the behavioral characteristics of two individuals when they perform joint actions (see the review by Knoblich et al., 2011). In addition, recent neuroimaging studies have revealed the brain mechanisms that are involved when two individuals socially interact with each other (Saito et al., 2010; Kawasaki et al., 2013; Yun et al., 2012).

Apart from that, there is another line of research that suggests the existence of reward effects generated through social interaction. For example, it has been shown that the striatum (one of the reward-related brain regions) is activated when an action of a participant is imitated by others and when a participant's attention is shared by others (Schilbach et al., 2010; Decety et al., 2002), suggesting that the participant might feel pleasure in these situations (e.g., the chameleon effect; Chartrand and Bargh, 1999). In the neuroimaging literature, the striatum has been shown to increase its activity in response not only to primary rewards such as liquid or food (Berns et al., 2001; Sescousse et al., 2013) and sexual stimuli (Redouté et al., 2000; Sescousse et al., 2013), but also to monetary and social rewards (Elliott et al., 2000; Izuma et al., 2008; Wake and Izuma, 2017; Sescousse et al., 2013). Hence, the above results (Schilbach et al., 2010; Decety et al., 2002) indicate that the experience of being followed by others can be "rewarding" for the human brain, suggesting that humans feel pleasure in such situation. However, this observation has been made when a human interacts with another human; it is not clear if similar phenomena (brain activation in the reward-related brain system and subjective experience of pleasure) are also found when a human interacts with a

Abbreviations: EPI, echo-planar imaging; FWE, family-wise error; fMRI, functional magnetic resonance imaging; GLM, general linear model; MNI, Montreal Neurological Institute; PCA, principle component analysis; ROI, region of interest; VAS visual analogue scaleVMPFC, ventromedial prefrontal cortex.

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non-human virtual agent, especially when a human experiences being followed by a virtual agent.

In the present study, we thus measured brain activity in 17 healthy volunteers, with functional magnetic resonance imaging (fMRI), while they performed an alternating virtual drum-hitting task in one of the two following conditions: in the first one, a virtual agent hit the drum after the participant, by copying the time interval between the agent's hit and the participant's hit in the previous pair of hitting ("Copy agent" condition); in the second condition, a virtual agent hit the drum after the participant, randomly, that is, regardless of the time interval ("Random agent" condition). Thus, only in the Copy agent condition, the participant's hitting pace was replicated by the virtual agent.

The participants were asked to rate their subjective impression about the two virtual agents (i.e., the degree to which they felt that their hitting was followed by the agent [sense of being followed; in other words, sense of being a leader]) and the degree to which they felt that they followed the agent's hitting [sense of being a follower]). We expected that the participants would rate their impression of being followed higher in the Copy agent condition. Moreover, the participants were asked about the agent they preferred, and we expected that they would prefer the Copy agent.

We examined the brain regions that were more active in the Copy agent condition than in the Random agent condition. We also conducted a parametric modulation analysis to identify the brain regions in which the activity was modulated by the sense of being followed. We hypothesized that the Copy agent condition activates reward-related areas more than the Random agent condition, and that activity in the reward-related regions is modulated by the sense of being followed. In particular, we had a specific anatomical hypothesis for the striatum (caudate nucleus), which is associated with social reward processing (Izuma et al., 2008; Wake and Izuma, 2017), and thus, we set our region of interest (ROI) in the caudate nucleus.

2. Materials and methods

2.1. Participants

Seventeen right-handed, healthy adults (nine females and eight males, mean age, 22 ± 1.7 years, ranging from 20 to 25 years) participated in this study. None of the participants had a medical record of neurological or psychiatric disorders. The protocol used in this study was approved by the Ethics Committee of the National Institute of Information and Communications Technology. All participants provided written informed consent prior to the experiment. The experiment was carried out following the principles and guidelines of the Declaration of Helsinki (1975).

2.2. Experimental design

Each participant lay in the MRI scanner with their head immobilized by an elastic band and sponge cushions and with their ears plugged. An MRI-compatible, four-button response box (Current Designs Inc.) was placed under the right hand of the participant. Visual stimuli were projected onto a screen and viewed by the participants via a mirror mounted on the head coil. Each participant completed two experimental runs, each lasting 370 s. Each run was composed of 12 drum-hitting trials, each with a duration of 20 s (Fig. 1). Each trial was followed by a 10-s rating period, during which the participants evaluated their impression about the trial (see below). Each run also included a period of 5 s before the first trial and a period of 5 s after the last trial.

In each trial, the participants performed a virtual drum-hitting task, alternating with a virtual agent that was projected on the right side of the screen. We designed two different characters (Fig. 1, see below). An in-house computer program developed in Processing software (ver. 3, https://processing.org/) controlled the animation of each character, who hit the drum taking turns with the par-

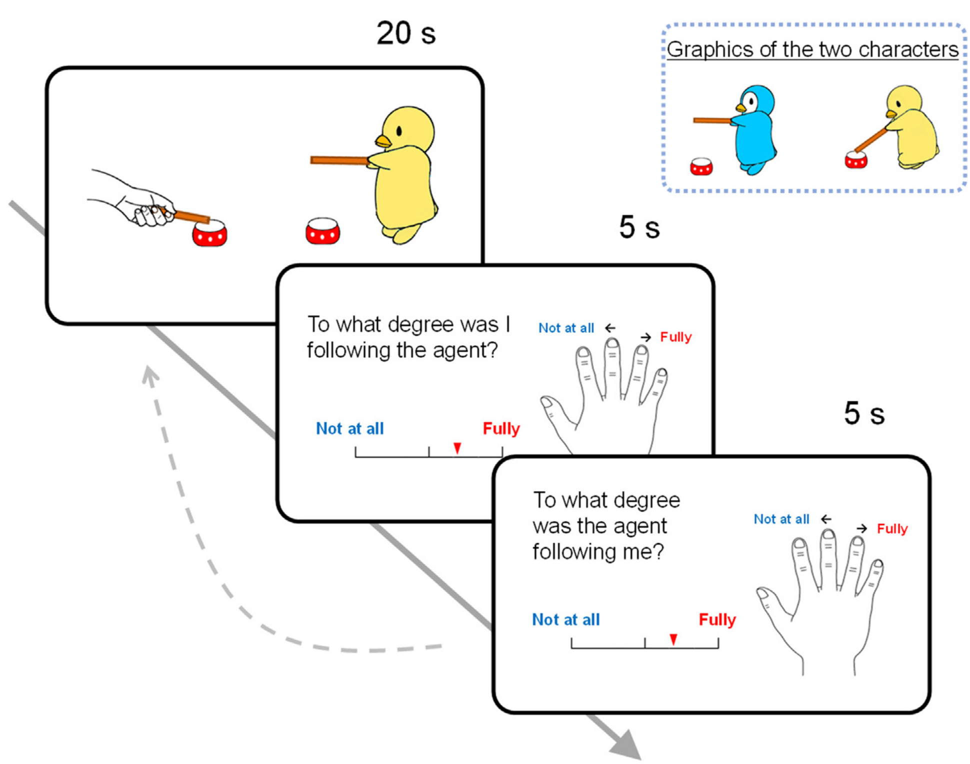

Fig. 1. Experimental task procedure. In each trial, the participants were asked to perform an alternating drum-hitting task with one of two virtual agents (blue or yellow penguin). After each trial, they were asked to evaluate the degree to which they felt that they followed the agent and the degree to which they felt that they were followed by the agent, using a visual analogue scale (VAS).

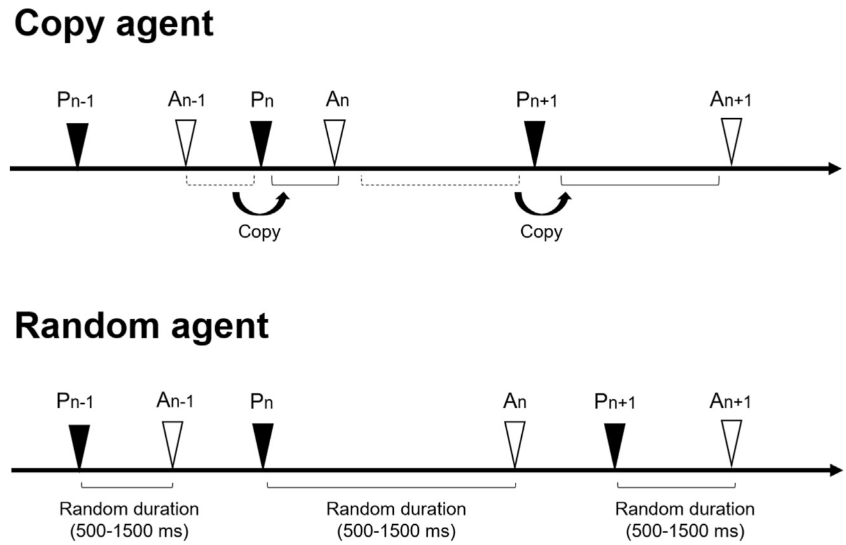

Fig. 2. Rules of drum-hitting followed by the agents (Copy agent and Random agent).
The Copy agent hit the drum (A_n) after a participant's hitting (P_n) by copying the time interval between the agent's hitting (A_{n-1}) and the next hitting of the participant (P_n). The Random agent hit the drum after a participant's hitting within a time interval randomly predetermined between 500 and 1500 ms.

ticipant. On the left half of the screen, an animation of a human left hand, with a stick and a drum underneath, was displayed. The participants could control the timing of hitting the drum with this hand, by pressing the leftmost button of the response box with their right index finger. The participants were instructed to rhythmically hit the drum alternately to the virtual agent. The participants could see an animation of the hitting, by the displayed left hand and by the virtual agent, and they could also hear the sound of the drum that was generated in synchronization to their hitting.

During the 10-s rating period after each trial, the participants were asked to rate both conditions regarding the degree to which they felt that their hitting was followed by the virtual agent and regarding the degree to which they felt that they followed the agents. The first question displayed was "to what degree was the agent following me?" in Japanese. Likewise, the second question, displayed in Japanese, was "to what degree was I following the agent?". Each question appeared for 5 s. To each question, the participants had to reply by rating their impressions using a visual analogue scale (VAS; Fig. 1); the left end point of the scale corresponded to "not at all," whereas the right end point corresponded to "fully." The participants could move a pointer along the scale, either to the left by continuously pressing the middle-left button with their right middle finger, or to the right by continuously pressing the middle-right button with their right ring finger. The pointer appeared in a random starting position on the scale, in order to minimize experimental bias. "Not at all" was equated with 0 and "fully" was equated with 100. Based on this scale, we calculated a value (from 0 to 100) for each answer.

Two types of virtual characters were developed: the Copy agent and the Random agent, as mentioned above (Fig. 2). The Copy agent was designed to hit the drum after a participant's hitting, following a particular rule. In each trial, we performed online processing of the time intervals between the agent's hitting (A_n hitting) and the participant's hitting (P_n hitting) and between A_{n-1} hitting and P_n hitting (Fig. 2). The Copy agent always hit the drum (A_n hitting) after the participant's hitting (P_n hitting), by copying the time interval between A_{n-1} hitting and P_n hitting. The Copy agent always followed this rule and thus changed its hitting timing depending on the participant's hitting timing.

In contrast, the Random agent was designed to hit the drum at a random timing after the participant's hitting, without considering the time interval of the previous pair of hitting events (i.e., between A_{n-1} hitting and P_n hitting). The time interval was randomly predetermined, between 500 and 1500 ms. Before the beginning of a trial, we generated random integers between 500 and 1500, and used these values for the time intervals during the trial. In each experimental run, the participants performed a total of 12 trials alternately with each virtual agent, starting with the Random agent (Random agent, Copy agent, Random agent, and so on).

For nine of the participants, the character of a blue penguin was used as the Copy agent, and a yellow penguin was used as the Random agent (Fig. 1). For the remaining eight participants, the designation of the characters was reversed. The participants were not informed about the differences in hitting rules. After all fMRI runs were completed, the participants were asked about the penguin they preferred (blue or yellow), in a binary forced-choice manner.

2.3. fMRI data acquisition

Functional images were acquired using T2*-weighted, gradient echo, echo-planar imaging (EPI) sequences, with a 3T MR imager (Siemens Trio system). We collected a total of 185 volumes in each run. Each volume consisted of 30 slices, acquired in ascending order at a thickness of 5.0 mm, that covered the entire brain. The time interval between each two successive acquisitions of the same slice was 2000 ms, with an echo time of 30 ms and a flip angle of 80°. The field of view was 192 mm × 192 mm and the matrix size 64 × 64, at a voxel dimension of 3 mm × 3 mm.

2.4. Behavioral data analysis

2.4.1. Objective measure

Firstly, we evaluated how accurately each agent copied the participant's hitting rhythm (Fig. 2). This objective measure was calculated by the following formula:

$$C = -(\log_2 T_1) * T_1 - (\log_2 T_2) * T_2$$

in which T_1 corresponds to the time interval between a virtual agent's hitting (A_{n-1}) and the successive participant's hitting (P_n), and T_2 corresponds to the time interval between the participant's hitting (P_n) and the successive agent's hitting (A_n). In the Copy agent condition, since the agent always copied T_1 for the next T_2, C should be 1. This means that the virtual agent precisely followed the participant's hitting rhythm. We also calculated C in the Random agent condition in order to evaluate how precisely the Random agent followed the participant's hitting rhythm. This was done because T_2 was randomly generated, independently of T_1, and it might incidentally have become equal to T_1 in some events, as in the Copy agent condition. We calculated C for each participant's hitting in one trial, and the average C value (objective measure) was computed for each trial, for each participant, and was used as a parametric regressor in the design matrix for the individual analysis of fMRI data (see below). We also calculated the average C value across participants for each condition (Copy agent or Random agent). One-sample *t*-test (against 1) was performed to confirm that C was significantly smaller than 1 in the Random agent condition.

2.4.2. Subjective measure

We further analyzed the rating scores, both for the extent to which the participants felt that they were followed by the virtual agent and for the extent to which the participants felt that they followed the virtual agent, in each trial of the Copy agent or Random agent conditions. In order to reduce the dimensionality of the two rating scores, we performed principle component analysis (PCA) by pooling the data obtained from all participants (Pearson, 1901). We found two main components, and employed the first component score (subjective measure), for each trial, in the individual analysis of fMRI data (see below).

2.5. fMRI data analysis

Functional imaging analysis was performed using the Statistical Parametric Mapping software (SPM12, The Wellcome Trust Centre for Neuroimaging, London, UK), implemented in Matlab R2015b. After correcting for differences in slice timing within each image volume, head motion was corrected using the realignment program. Following realignment, the volumes were normalized to the Montreal Neurological Institute (MNI) space (Evans et al., 1994) using a transformation matrix, which was obtained from the normalization process of the first EPI image of each participant, to the EPI template. Finally, the spatially normalized functional images were filtered using a Gaussian kernel with a full-width-at-half-maximum of 8 mm along the x-, y-, and z-axes.

2.6. Contrast analysis

A general linear model (GLM; Friston et al., 1995; Worsley and Friston, 1995) was used for the analysis of the fMRI data. In the single-subject analysis, the design matrix consisted of two regressors: (i) Copy agent trials and (ii) Random agent trials. To correct for residual motion-related variance after the realignment, the six realignment parameters were also included in the design matrix, as regressors of no interest. The weighted sum of the parameter estimates, in the single-subject analysis, constituted contrast images that were used for the second-level analysis. We first constructed appropriate contrast images to examine brain areas showing different effects for the two conditions; that is, areas that showed higher activity in the Copy agent condition than in the Random agent condition (Copy agent vs. Random agent) and vice versa (Random agent vs. Copy agent).

The number of hittings (both by a participant and an agent) was matched between the two conditions (average number of hittings per trial, across participants: Copy agent: 19.71 ± 1.90, Random agent: 19.18 ± 0.68; average number of agent's hittings per trial: Copy agent: 19.43 ± 1.86, Random agent: 19.60 ± 0.30). Simple sensorimotor, visual, and auditory effects could thus be eliminated by these contrasts, allowing evaluation of the condition effect associated with performing the task with each different agent. In addition, the effect of the color of the virtual agent (the penguin's color; see above) was set off in the following second-level group analyses. Finally, our baseline period was not a perfect resting period, as the participants had to rate their subjective impression about the virtual agent during the 10-s period after each trial. However, this was equally done in both conditions. We therefore assumed brain activity during baseline periods to be similar in the two conditions.

At the second-level group analyses, the contrast images from the single-subject analyses were entered into random-effects models to make statistical inferences at the population level (Holmes and Friston, 1998). One-sample t-tests were performed using the contrast images. We produced a statistical parametric map of the effects of the different virtual agents (Copy agent vs. Random agent and Random agent vs. Copy agent). We first generated a voxel-cluster image, with a cluster-defining height threshold of $p < 0.001$ uncorrected, and evaluated the significance of its spatial extent using a threshold of $p < 0.05$ corrected for multiple comparisons (family-wise error, FWE) for the entire brain.

2.7. Parametric modulation analysis

We constructed a second GLM for parametric modulation analysis (independently of the first GLM), in order to test whether or not the activity of the reward-related brain regions is modulated by the objective measure (the C value) and by the subjective measure (the PCA value). The design matrix for this GLM contained one regressor of the Copy agent and the Random agent trials, and its two corresponding linear parametric modulation regressors, that is, the objective and subjective measures. Since these two measures mildly correlated with each other (average correlation coefficient across participants = 0.332), these values were used without being orthogonalized to each other. As in the first GLM, the six realignment parameters were also included in the design matrix, as regressors of no interest.

For the parametric modulation analyses, we performed the second-level group analyses. We first generated a voxel-cluster image, with a cluster-defining height threshold of $p < 0.001$ uncorrected. As we had hypothesized, we found activity (93 voxels) in the left caudate nucleus, which is one of the reward-related brain regions. As we had an anatomical hypothesis (see Introduction), we performed a region-of-interest (ROI) analysis (Worsley et al., 1996). We set a ROI in a sphere with a 16-mm radius around the peak of the left caudate nucleus (-8, 14, 2). This peak was selected because the area is activated in association with social reward processing (Izuma et al., 2008), and the radius was chosen based on the final smoothness of our functional imaging data. We evaluated the significance of the left caudate activity in terms of its spatial extent in the ROI (FWE-corrected threshold of $p < 0.05$ after small-volume correction).

3. Results

3.1. Behavioral results

3.1.1. Objective measure

The evaluation of the accuracy with which each agent copied the participant's hitting rhythm confirmed that the average C value, across participants, was 1.00 in the Copy agent trials, indicating that this agent precisely copied the participant's timing. The average C value in the Random agent trials across participants was significantly lower than 1 (0.898 ± 0.012; one-sample *t*-test against 1; $t(16) = 18.4$, $p < 0.001$). Thus, as expected for our original design, the Copy agent and the Random agent reacted to the participants' hitting pace differently.

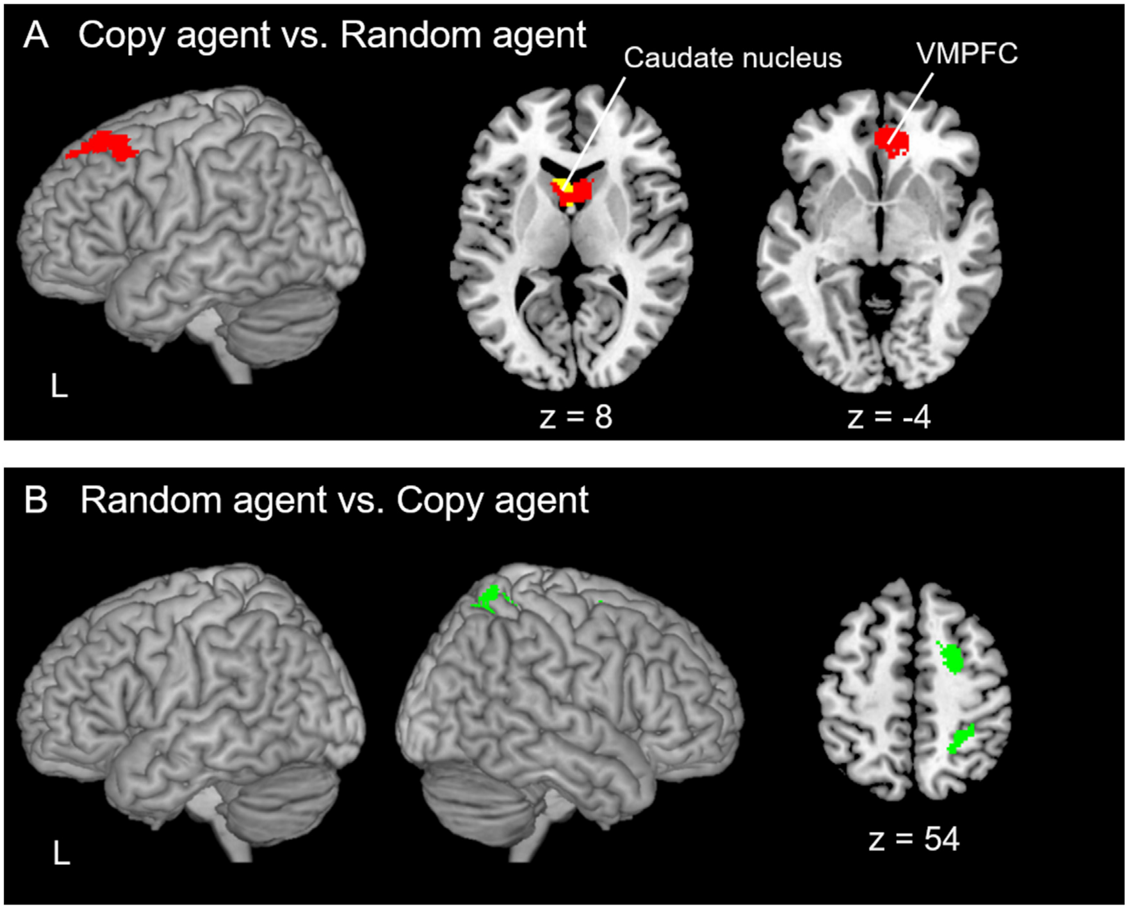

Fig. 3. Brain activity during the alternating drum-hitting task. (A) Brain regions (red) that showed significantly higher activity in the Copy agent condition than in the Random agent condition. (B) Brain regions (green) that showed significantly higher activity in the Random agent condition than in the Copy agent condition. In the panel A, the brain activities are rendered onto the left hemisphere and the transverse slices (z = +8 and -4) in the Montreal Neurological Institute (MNI) standard brain. The brain activity (yellow) that positively correlated with the subjective feeling of being followed by the virtual agent is also displayed (caudate activity, in the transverse slice [z = +8]). In the panel B, the brain activities are also rendered onto the MNI standard brain. We also display right superior frontal and postcentral activities in the transverse slice (z = +54). VMPFC, ventromedial prefrontal cortex.

3.1.2. Subjective measure

The analysis of the two subjective rating scores (sense of being followed or sense of being a follower) showed that the participants gave different scores to the two virtual agents. The score of their sense of being followed ("the agent followed me") was significantly higher for the Copy agent than for the Random agent [$t(16) = -22.0$, $p < 0.001$]. In contrast, the score of their sense of being a follower ("I followed the agent") was significantly higher for the Random agent than for the Copy agent [$t(16) = 6.76$, $p < 0.001$].

The PCA analysis for the subjective ratings revealed two representative orthogonal axes (first and second components). The contribution rates of the first and second components were 80.3% and 19.6%, respectively. The first component score showed a positive value for the Copy agent (average across participants = 31.4) and a negative value for the Random agent (average across participants = -31.4). Thus, we defined this score as the subjective measure of how much the participants felt that "the agent followed them" (the sense of being followed), and we used this value as a parametric covariate in the subsequent fMRI analysis.

3.1.3. Preference of agent

After the fMRI experiment was completed, the participants were asked which agent they preferred, in a binary forced-choice manner. Almost all (16 out of 17) participants reported they preferred the Copy agent over the Random agent. Since the participants had the impression that they were imitated by the agent in the Copy agent condition and that they followed the agent in the Random agent condition (see above), their preference of the Copy agent indicates that they preferred the virtual agent that seemed to follow them.

3.2. Imaging results

When we examined the participants' brain regions that were more activated in the Copy agent condition than in the Random agent condition (Copy agent vs. Random agent), we found significant activation in the left caudate nucleus, in the right ventromedial prefrontal cortex (VMPFC), as well as in the left superior and middle frontal gyri (Fig. 3 and Table 1). Thus, these brain regions were more activated when the participants performed the task with the agent perceived as their follower. The caudate activation appeared quite robust, as this activation became significant when we considered the entire brain.

For the opposite contrast (Random agent vs. Copy agent), we found significant activation in the superior frontal gyrus, postcentral gyrus (cytoarchitectonic area 2), and superior parietal gyrus in the right hemisphere (area 5 L; Fig. 3). These brain regions are usually considered higher-order sensory-motor association areas, rather than reward-related areas. Indeed, these regions have been shown to increase their activity when participants performed an irregular-paced finger tapping task (Lutz et al., 2000). For this contrast, we could not find any active-voxel clusters in the caudate

Table 1
Brain regions more strongly activated in the Copy agent condition than the Random agent condition.

Clusters	Size	MNI coordinate x	y	z	T-value	Areas
Copy agent* vs. *Random agent						
L caudate cluster	321	−8	14	8	4.37	Left caudate nucleus
VMPFC cluster	425	4	42	−2	5.57	ACC
		14	42	−4	4.99	Middle orbital gyrus
L middle/superior frontal cluster	515	−16	30	58	7.10	Superior frontal gyrus
		−42	20	48	5.71	Middle frontal gyrus
Random agent* vs. *Copy agent						
R parietal cluster	446	28	−42	50	6.12	Postcentral gyrus (area 2)
		22	−56	68	5.67	Superior parietal gyrus (area 5 L)
R superior frontal cluster	291	24	−2	52	4.93	Superior frontal gyrus

Uncorrected height threshold, $p < 0.001$; extent threshold, $p < 0.05$, FWE-corrected in the entire brain. Size = number of active voxels. Abbreviations: ACC, anterior cingulate cortex; VMPFC, ventromedial prefrontal cortex.

regions. This suggests that the Random agent condition did not provide positive reward to the participants.

When we tested whether the activity of reward-related brain regions was modulated by the subjective measure (the PCA value), we found that the activity of the left caudate nucleus positively correlated with the subjective measure (peak MNI coordinates of activity [x, y, z] = [−4, 16, 14], T = 4.93, 93 voxels). Importantly, this region overlapped with the region identified in the above contrast analysis (Copy agent vs. Random agent; Fig. 3). Such a positive correlation was not observed when we used the objective measure (the C value, i.e., the level of accuracy with which each virtual agent copied the participant's hitting pace). These results suggest that it was not the objective accuracy of the agent coping the participant's hitting pace, but the subjective feeling of being followed by the agent that modulated the activity in the caudate nucleus, which is associated with social reward processing (Izuma et al., 2008; Wake and Izuma, 2017).

4. Discussion

In the current study, we clearly demonstrate that people can subjectively feel that an agent follows their hitting pace when the agent, objectively, keeps copying the time interval between the agent's hitting and the participant's hitting in the previous pair of hitting events. Such regularity in the agent's reaction ensures that if a participant hits the drum at a relatively slower (or faster) pace (relative to the preceding hitting by the agent), the agent would also hit the drum at a relatively slower (or faster) pace. This experimental condition in our study gave the participants the impression that the virtual agent adapted its hitting pace to their pace, which might have contributed to the generation of the feeling that this agent followed the participants. Furthermore, an interesting finding of the present study is that most participants showed preference for the virtual agent that seemed to be following them. Thus, the participants preferred being followed by an agent to following.

When people are jointly dancing and singing, their movements tend to become temporally aligned to those of others. Such an interpersonal rhythmic synchronization may evoke pleasant feelings, and strengthen social binding between individuals (Anshel and Kipper, 1988; Wiltermuth and Heath, 2009; Kirschner and Tomasello, 2010; Cirelli et al., 2014; Hove and Risen, 2009). For example, it has been shown that joint singing in a group strengthens trustworthiness and induces cooperative behaviors between the members of the group (Anshel and Kipper, 1988). Likewise, the degree of synchrony between a participant and an experimenter in a finger-tapping task affects the subsequent rating of the level of affinity felt by the participant for the experimenter (Hove and Risen, 2009). These are examples in which interpersonal rhythms are synchronized. Our results further imply that the sense of being followed by others during interpersonal rhythmic interaction is preferable (that is, more pleasant than following others), even when it is without substantial interpersonal rhythmic synchronization.

In our fMRI analysis, we show that the interaction between the participants and the Copy agent activates the caudate nucleus and the VMPFC, significantly more than the interaction with the Random agent (Fig. 3). Especially the activity of the caudate nucleus was modulated by the participants' subjective feeling of being followed by the agent in the rhythmic interaction. These brain regions are important constituents of the reward system (Sescousse et al., 2013; Wake and Izuma, 2017; Haber and Knutson, 2010). Hence, in addition to the cases of the being imitated by others and of joint attention shared by others (Schilbach et al., 2010; Decety et al., 2002), the sense of being followed by others in an interpersonal rhythmic interaction might also be perceived as a reward. Furthermore, our results suggest that this could occur even when a human interacts with a non-human virtual agent.

It is known that, in an interpersonal rhythmic synchronization task, synchronization with other people activates brain regions associated with reward processing (i.e., the caudate nucleus; Kokal et al., 2011). However, our results suggest that merely the sense of being followed by others, during an interpersonal rhythmic interaction, is enough to activate the human reward system, without requiring substantial interpersonal rhythmic synchronization. The sense of being followed by an agent can be interpreted as if the individual is taking a role of a leader who mainly gives the rhythm (Fairhurst et al., 2014). Therefore, the present results might also indicate that taking the leader role in an interpersonal rhythmic interaction is pleasant for humans, in terms of brain activity.

5. Conclusions

We show here that it is not the objective accuracy of an agent coping a participant's hitting pace but the subjective feeling of being followed by an agent that modulates activity in the caudate nucleus, which is associated with social reward processing. Hence, the sense of being followed, that is, feeling like a leader, during a course of interpersonal rhythmic interaction may activate reward-related brain regions such as the caudate nucleus, as observed on fMRI, which suggests that this is a pleasant experience for humans.

Conflicts of interest

None.

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