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Illusion of sense of self-agency: discrepancy between the predicted and actual sensory consequences of actions modulates the sense of self-agency, but not the sense of self-ownership

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Abstract

It is proposed that knowledge of motor commands is used to distinguish self-generated sensation from externally generated sensation. In this paper, we show that the sense of self-agency, that is the sense that I am the one who is generating an action, largely depends on the degree of discrepancy resulting from comparison between the predicted and actual sensory feedback. In Experiment 1, the sense of self-agency was reduced when the presentation of the tone was unpredictable in terms of timing and its frequency, although in fact the tone was self-produced. In Experiment 2, the opposite case was found to occur. That is, participants experienced illusionary sense of self-agency when the externally generated sensations happened to match the prediction made by forward model. In Experiment 3, the sense of self-agency was reduced when there was a discrepancy between the predicted and actual sensory consequences, regardless of presence or absence of a discrepancy between the intended and actual consequences of actions. In all the experiments, a discrepancy between the predicted and actual feedback had no effects on sense of self-ownership, that is the sense that I am the one who is undergoing an experience. These results may suggest that both senses of self are mutually independent.

Keywords: Forward model; Motor awareness; Sense of agency; Sense of ownership; Self-recognition

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1. Introduction

When we act, we normally feel ourselves causing our own actions. It appears too self-evident to require further investigation. If I say “I think it is a beautiful day today”, I could be wrong about the weather. But it seems that I could not be wrong about the “I”. I could not misidentify myself when I state that it is I who am thinking (Wittgenstein, 1958). Such use of the first-person pronoun is thought to be immune to error through misidentification (Shoemaker, 1984). However, certain schizophrenic experiences including auditory hallucination, thought insertion and delusions of control could be counterexamples to the immunity principle. Auditory hallucinations typically consist of hearing spoken voices, which were misattributed to external force by patients although in fact they themselves spoke. The essence of delusions of control is that patient experiences his or her will as replaced by that of some other agency or force. In other terms the patient feels that he or she is not at the origin of his or her own acts. A schizophrenic patient who suffers from thought insertion might claim that he or she is not the one who is thinking a particular thought, when in fact he or she is the one who is thinking the thought. These symptoms are in common characterized by an inability to distinguish self- and externally produced actions.

Based on a established model of motor learning and control (Wolpert, 1997), Frith proposed that abnormalities in forward model might underlie these symptoms (Frith, 1992; Frith, Blakemore, & Wolpert, 2000). To optimize motor control and learning, the central nervous system has been thought to require containing internal models, which represent aspects of one’s own body and its interaction with the external world. There are two types of internal model: inverse model and forward model (Wolpert, Ghahramani, & Jordan, 1995). The inverse model provides the motor commands necessary to achieve a certain goal based on the desired state. By contrast, the forward model makes predictions about the behavior of the motor system and its sensory consequences. Predictions can be used in several ways. First, prediction of the actual outcome of motor command can be compared with the desired outcome. This comparison enables rapid error correction before sensory feedback is available (Greenwald, 1970). Second, when a movement is made, an efference copy of the motor command is used to make a prediction of the sensory consequences of the movement. This sensory prediction can then be compared with the actual sensory feedback from the movement. This prediction can be used to anticipate and cancel the sensory effects of movement, as in the case during eye movements (Helmholtz, 1867). More importantly, this prediction can be also used to attenuate the sensory effect of self-generated movement and thereby enables differentiating self-produced sensation from externally generated sensations. Self-produced sensations can be correctly predicted from motor commands. As a result, there will be little or no sensory discrepancy resulting from the comparison between the predicted and actual sensory feedback. This accurate prediction can be used to attenuate the sensory effects of self-produced movement. In contrast, externally generated sensations are not associated with any efference copy and cannot be predicted by the forward model. As a result this comparison will produce a higher level of sensory discrepancy. As the discrepancy between the predicted and actual sensations increases, so does the likelihood that the sensation is externally produced.

According to Frith, using such a mechanism, it is possible to distinguish self-generated actions from actions produced by other agents.

Consistent with Frith's hypothesis, Weiskrantz, Elliott and Darlington (1971) reported that participants rated the self-administered tactile stimulus as less tickly than the same tactile stimulus generated externally. Blakemore, Wolpert and Frith (1998) using functional magnetic resonance imaging showed a reduction in activity of the secondary somatosensory cortex and the anterior cingulate gyrus when the tactile stimulus was self-produced relative to when it was externally produced. However, schizophrenic patients with auditory hallucinations or delusions of control did not show a decrease in their perceptual ratings for tactile stimuli produced by themselves as compared with those produced by the experimenter (Blakemore, Smith, Steel, Johnstone, & Frith, 2000). The same goes for other modalities. Curio, Neuloh, Numminen, Jousmaki and Hari (2000) using magnetoencephalography showed that responsiveness of the auditory cortex to vowel sounds was reduced when participants spoke them compared with when they were listening to the sound played back. Again, it was reported that schizophrenic patients did not exhibit normal reduction of the response in the auditory cortex to self-generated vowel sounds compared to the same sounds played back (Ford et al., 2001).

Recently, Gallagher (2000) has proposed that self-consciousness can be divided into two important aspects: the "minimal self" and the "narrative self". The former is defined as a consciousness of oneself as an immediate subject of experience, unextended in time. The latter involves personality identity and continuity across time. The "minimal self" includes the sense of self-agency, that is the sense that "I am the one who is causing or generating an action", and the sense of self-ownership, or the sense that "I am the one who is undergoing an experience". The purpose of the present studies was to directly investigate whether the prediction of the sensory consequence of actions made by forward model would modulate the sense of self-agency. If the sense of self-agency depends on a comparison between the predicted and actual sensory consequences, participants should misattribute self-produced tones to an external force when the actual feedback is discrepant with the prediction (Experiment 1). On the contrary, participants should experience the illusionary sense of self-agency when there is little or no discrepancy between the predicted and actual sensory feedback, even if in fact an experimenter produces them (Experiment 2). Moreover, the sense of self-agency should rely on a comparison between the prediction made by forward model and the actual sensory consequence, rather than on a comparison between the intended and actual sensory feedback (Experiment 3).

2. Experiment 1

Previous studies demonstrated that both tickliness rating and action recognition, i.e. judgment of whether the movement that participants saw was their own, were affected by angular deviation and temporal delay between action and its consequences (Blakemore, Frith, & Wolpert, 1999; Franck et al., 2001). In Experiment 1, we directly investigated whether the degree of congruency between the predicted and actual sensory feedback modulated the sense of self-agency. The degree of congruency was manipulated in terms of stimulus types and temporal delay. Moreover, we also examined whether the sense of self-ownership varied with the degree of congruency between the predicted and actual sensory feedback.

2.1. Method

2.1.1. Participants

Sixteen healthy right-handed volunteers participated in this study. Participants were eight males and eight females raging in age from 21 to 35 years, with a mean age of 23.8 years ($SD = 2.61$ years). None had a history of neurological or psychiatric disease. All participants gave written informed consent, but were naïve as to the purpose of the experiment.

2.1.2. Design

The design in Experiment 1 had two within-participants factors: types of stimulus (congruent or incongruent tone with prediction), and temporal delay (0, 200, 400, or 600 ms delay from the timing predicted).

2.1.3. Procedure

Upon entering the laboratory, participants were led to a cubicle and seated in front of a computer screen with a pair of headphone. Prior to the experiment, participants performed 300 learning trials to learn the relationship between action and its consequence. Participants were told to press the left button with the left index finger and the right button with the right index finger in turn. After each button press, a certain tone was immediately presented for 200 ms through in-ear headphones: a 600 or a 1000 Hz tone. The assignment of tones to buttons was consistent for each participant and counterbalanced across participants. Participants were explicitly told that each button pressing would evoke a certain tone. Tones were identical in duration and sound pressure throughout the experiment.

In Experiment 1, participants made self-paced button press and heard one of which tones had followed button presses in the learning session. Under congruent tone condition, each button press evoked the same tone that had followed each button press in the learning session. By contrast, under incongruent tone condition, the different tone from prediction followed each button press. Under delay conditions, the congruency was manipulated in terms of stimulus timing. Participants received 8 trials per condition. After each trial, participants were asked to answer two items from “totally disagree” (score = 0) to “totally agree” (score = 100). The sense of self-agency was assessed by the first item that “I was the one who produced the tone”, and the sense of self-ownership was assessed by the second item that “I was the one who was listening to the tone”. Prior to the rating, participants were told that there were two cases: in one case they might hear tones as a result of their button press, but in another case the experimenter might produce the tones. Under a control condition, participants passively listened to two tones. The trials were presented in random order. The mean rating score of 8 trials in the same condition was used as dependant variables.

To control the increase in Type I error, the degree of freedom was adjusted using the Greenhouse and Geisser (1959) coefficient when appropriate. Post-hoc tests of simple effects were performed using the Bon Ferroni correction with a significance level of $P < .05$.

2.2. Results and discussion

The rating scores on the sense of self-agency were analyzed using a repeated measures analysis of variance (ANOVA) with two factors (Tone congruency × Delay). This analysis revealed a main effect of tone congruency, $F(1, 15) = 9.50$, $p < 0.01$, and a main effect of delay, $F(2.39, 35.77) = 20.97$, $p < 0.0001$. But there wasn't an interaction between tone congruency and delay, $F(2.32, 34.84) = 0.64$, *n.s.*. The main effect of tone congruency was caused by higher scores when actual and predicted tones were congruent ($M = 71.88$, $SEM = 3.55$) than incongruent ($M = 56.25$, $SEM = 5.96$). On the delay effect the sense of self-agency was significantly reduced as the delay from the timing predicted increased (*Ms* (*SEM*s) = 87.50(2.96), 66.88(4.76), 55.31(5.92), vs. 46.56(6.99), respectively). Under the control condition, the sense of self-agency was rated as 0 by all participants, which suggests that acting makes an important contribution to the sense of self-agency. Without movement, there was no prediction made by forward model on the basis of motor command, which caused a lack of attenuation of sensations. Thus, it was very easy for participants to judge the tones as externally produced. In Experiment 1, although the tones were actually produced as a consequence of their actions in all conditions except the control condition, the sense of self-agency was reduced in the condition in which self-produced tones were unpredictable in terms of timing and frequency. In contrast, on the sense of self-ownership, all participants scored 100 in all the conditions. Taken together, these results suggest that the predictability of the sensory consequences of actions modulates the sense of self-agency, but does not always affect the sense of self-ownership. Results are summarized in Fig. 1.

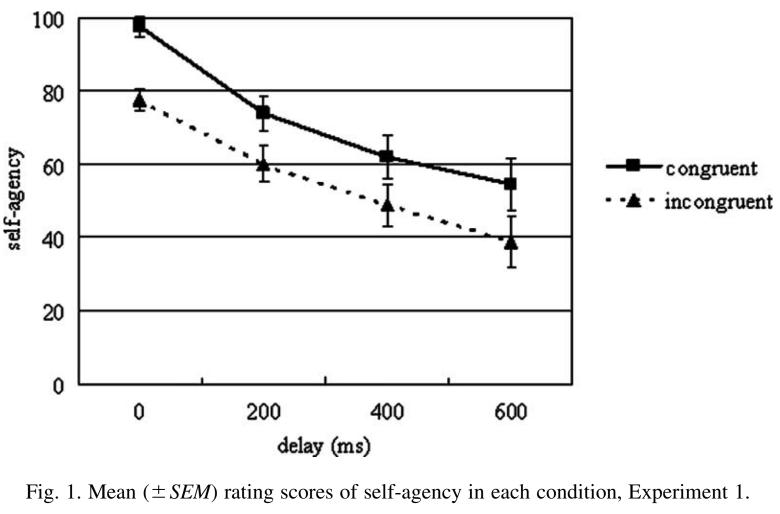

Fig. 1. Mean (± *SEM*) rating scores of self-agency in each condition, Experiment 1.

3. Experiment 2

In Experiment 1, we showed that as the discrepancy between the predicted and actual sensory feedback increased, participants were more likely to misattribute self-generated tones to an external source. The purpose of Experiment 2 was to investigate whether participants experienced the sense of self-agency when externally generated sensations happened to match the prediction made by forward model. If such a phenomena of illusion of sense of self-agency occurs, we can suggest that the sense of self-agency strongly depends on congruency between the predicted and actual feedback.

3.1. Method

3.1.1. Participants

Ten healthy right-handed volunteers participated in this study. Participants were five males and five females ranging from 22 to 29 years, with a mean age of 22.7 ($SD = 2.18$ years). None had a history of neurological or psychiatric disease. All participants gave written informed consent for participation in the experiment.

3.1.2. Design

The design in Experiment 2 had three within-participants factors: actual agency (self or other), types of stimulus (congruent or incongruent tone with prediction), and temporal delay (0, 200, 400, or 600 ms delay from the timing predicted).

3.1.3. Procedure

In Experiment 2, we attempted to make a situation in which the timing of presentation of externally generated tone happened to match the prediction based on motor command. For that purpose, we used a choice reaction time task (see below). Upon entering the laboratory, participants were led to a cubicle and seated in front of a computer screen with a pair of headphone. Prior to the experiment, participants performed 300 learning trials to learn relationship among stimulus, action and its consequence. Each trial began with a fixation point presented for 500 ms, which was then replaced by the target stimulus. Participants were told to press the left button with the left index finger whenever a red square appeared on the screen and the right button with the right index finger whenever a blue square appeared on the screen as quickly and accurately as possible. The target stimuli remained on the screen until participants responded. After each button press, a certain tone was immediately presented for 200 ms through in-ear headphones: a 600 or a 1000 Hz tone. The assignment of stimulus and tones to buttons was consistent for each participant and counterbalanced across participants. Participants were explicitly told that each button pressing would evoke a certain tone. Tones were identical in duration and sound pressure throughout the experiment. The learning session consisted of 150 red square trials and 150 blue square trials. The trials were presented in random order.

In Experiment 2, participants were instructed to press the left button with the index finger of the left hand after the red square appeared and the right button with the index finger of the right hand after the blue square appeared as quickly and accurately as possible in the same way as the learning session. After each response, participants heard one of which tones had followed button presses in the learning session. Under the other agency conditions, the tones were presented a certain ms after the presentation of target stimuli. Based on a mean reaction time in the learning session, the inter-stimulus interval between the onset of target stimulus and the onset of tone was individually adjusted to correspond to prediction. By using this procedure, the timing of tone presentation occasionally corresponded to the prediction made by forward model, although each tone was presented irrespective of participant's response. After each response a reaction time was checked. And then, only trials in which a reaction time was ranging from 0 to $+15$ ms of the mean reaction time in the learning session were accepted for analysis. The other conditions were the same as in Experiment 1. Trials continued until sample numbers reached 8 trials per a condition. Additionally, participants received 8 control trials, in which they passively listened to two tones. Immediately after each trial, participants were asked to answer the same items as used in Experiment 1. The trials were presented in random order. The mean rating score of 8 trials in the same condition was used as dependant variables. Data were analyzed in the same method as Experiment 1.

3.2. Results and discussion

The rating scores on the sense of self-agency were analyzed using a repeated measures analysis of variance (ANOVA) with three factors (Actual agency × Tone congruency × Delay). This analysis revealed a main effect of tone congruency, $F(1,9) = 7.65, p < 0.05$, and a main effect of delay, $F(1.44, 12.96) = 18.33$, $p < 0.0001$. But there was no significant main effect of actual agency, $F(3,45) = 0.13$, *n.s.*. None of the other terms in this analysis reached significance. The main effect of tone congruency was caused by higher scores when actual and predicted tones were congruent ($M = 55.06$, $SEM = 6.06$) than incongruent ($M = 40.25$, $SEM = 6.59$). On the delay effect the sense of self-agency was significantly reduced as the delay from the timing predicted increased (*Ms* (*SEMs*) = 81.25(5.09), 47.63(6.56), 37.50(8.53), vs. 24.25(9.33), respectively). Under the control condition, the sense of self-agency was rated as 0 by all participants. On the sense of self-ownership of experience, all participants scored 100 in all the conditions. Results are summarized in Fig. 2.

Consistent with Experiment 1, participants misattributed self-generated tones to an external source when actual sensory feedbacks did not match predictions. In contrast, participants misjudged externally generated tones as their own generated when there happened to be little or no sensory discrepancy resulting from the comparison between the predicted and actual feedback. Taken together, these results suggest that the sense of self-agency largely depends on discrepancy between the predicted and actual feedback.

4. Experiment 3

In Experiments 1 and 2, participants executed intended actions, and there was no discrepancy between intended and actual responses. Therefore, it remained unresolved whether the sense of self-agency was built on the comparison between the sensory prediction made by forward model and actual sensory feedback or on the comparison

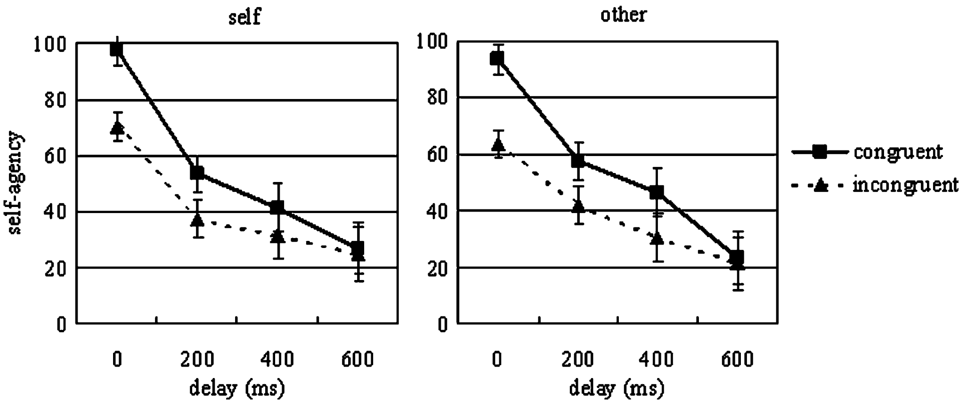

Fig. 2. Mean (± *SEM*) rating scores of self-agency in each condition, Experiment 2.

between intended and actual consequence. In Experiment 3, we examined which of them contributed to the sense of self-agency by separating intended response from actual response. Participants performed a letter version of the Eriksen flanker task (Eriksen & Eriksen, 1974), which is a choice reaction time task in which the target letter is flanked by distractor letters. These flankers can be associated with either the same response (i.e. congruent) as the target or the opposite response (i.e. incongruent). It is well known that when participants are instructed to respond quickly to such incongruent stimulus arrays, they tend to make many errors (Coles, Gratton, Bashore, Eriksen, & Donchin, 1985). Whereas such errors are unintended responses, actual responses are congruent with intentions in correct responses. If the sense of self-agency is reduced whenever participants commit errors, it turns out to be that the recognition of oneself as the agent of an action depends on the comparison between intended and actual sensory consequence. However, if there is no significant decline in the sense of self-agency, it is suggested that they are built on the comparison between the sensory prediction made by an internal forward model of the motor system and the actual sensory feedback.

4.1. Method

4.1.1. Participants

Sixteen healthy right-handed volunteers participated in this study. Participants were seven males and nine females ranging from 21 to 35 years, with a mean age of 23.8 ($SD = 3.05$ years). None had a history of neurological or psychiatric disease. All participants gave written informed consent for participation in the experiment.

4.1.2. Design

The design in Experiment 3 had three within-participants factors: congruency between intended and actual responses (correct response or error response), types of stimulus (congruent or incongruent tone with prediction), and temporal delay (0, or 400 ms delay from the timing predicted).

4.1.3. Procedure and materials

Upon entering the laboratory, participants were led to a cubicle and seated in front of a computer screen with a pair of headphone. Prior to the experiment, participants performed 300 learning trials. On each trial, 500 ms after fixation onset, the target stimulus (i.e. "H" or "N") was presented for 100 ms on the center of the screen. Participants were told to press the left button with the left index finger as quickly and accurately as possible whenever a "H" appeared on the center of the screen and the right button with the right index finger whenever a "N" appeared on the screen. After each button press, a certain tone was immediately presented for 200 ms through in-ear headphones: a 600 or a 1000 Hz tone. The assignment of stimulus and tones to buttons was consistent for each participant and counterbalanced across participants. Participants were explicitly told that each button pressing would evoke a certain tone. Tones were identical in duration and sound pressure throughout the experiment. The learning session contained 150 trials with each of the two possible stimuli. The trials were presented in random order.

In Experiment 3, each trial started with the onset centrally presented fixation sign. Five hundred milliseconds after fixation onset, a five-letter array (i.e. HHHHH, NNNNN, HHNHH, or NNHNN) was presented for 100 ms. Participants were instructed to respond to one of the two target letter (central H or N) with one finger and to the other letter with the other finger as quickly as possible and not to correct their responses even if they made errors. The assignment of responding finger to target letter was the same as the learning session and counterbalanced across participants. Immediately after each trial, participants were asked whether the preceding response was correct or error. There are at least two types of actual errors: unintended response and unnoticed error. In unnoticed error, participants might intend to give that response which was actually false but they believed to be correct. Analysis was conducted only on unintended responses that participants correctly judged as errors. Trials continued until each participant committed at least 4 unintended responses and made at least 4 correct responses, which were correctly judged as correct, per a condition except the response factor. Additionally, participants received 4 control trials in which they passively listened to two tones. After each trial, participants were asked to answer the same items as used in Experiment 1. The trials were presented in random order. The mean rating score of 4 trials in the same condition was used as dependant variables. Data were analyzed in the same manner as Experiment 1.

4.2. Results and discussion

The rating scores on the sense of self-agency were analyzed using a repeated measures analysis of variance (ANOVA) with three factors (Congruency between intended and actual responses × Tone congruency × Delay). This analysis revealed a main effect of tone congruency, $F(1, 15) = 69.36$, $p < 0.0001$, and a main effect of delay, $F(1, 15) = 35.80$, $p < 0.0001$. But there was no significant main effect of congruency between intended and actual responses, $F(1, 15) = 2.36$, *n.s.*. The main effect of tone congruency was caused by higher scores when actual and predicted tones were congruent ($M = 66.73$, $SEM = 5.84$) than incongruent ($M = 18.65$, $SEM = 3.67$). The main effect of delay was caused by higher scores under the 0 ms delay condition ($M = 59.02$, $SEM = 4.65$) than under the 400 ms delay condition ($M = 26.37$, $SEM = 4.91$). ANOVA also revealed the following significant interactions: Congruency between intended and actual responses × Tone congruency ($F(1, 15) = 10.19$, $p < 0.01$), and Congruency between intended and actual responses × Delay ($F(1, 15) = 5.96$, $p < 0.05$). None of the other interactions reached significance. Post-hoc analysis revealed that under the tone congruent condition the sense of self-agency was significantly higher when intended and actual responses were congruent ($M = 73.42$, $SEM = 4.33$) than incongruent ($M = 60.05$, $SEM = 8.16$), whereas under the tone incongruent condition there was no significant effect of congruency between intended and actual responses (congruent condition: $M = 17.81$, $SEM = 3.72$; incongruent condition: $M = 19.50$, $SEM = 4.00$). Post-hoc analysis also revealed that under the 0 ms delay condition the sense of self-agency was significantly higher when intended and actual responses were congruent ($M = 65.28$, $SEM = 3.11$) than incongruent ($M = 52.76$, $SEM = 6.88$), whereas under the 400 ms delay condition there was no significant effect of congruency between intended and actual responses (congruent condition: $M = 25.95$, $SEM = 4.97$; incongruent condition: $M = 26.79$, $SEM = 5.66$). Under the control condition, the sense of self-agency was rated as 0 by the all the participants. On the sense of self-ownership, all the participants scored 100 in all the conditions. Results are summarized in Fig. 3.

In Experiment 3, the sense of self-agency was reduced when there was a discrepancy between the predicted and actual sensory consequence irrespective of correct or error response. Without a discrepancy between the predicted and actual sensory consequence, the sense of self-agency was reduced when there was a discrepancy between the intended and actual sensory consequence. However, even under the error condition, participants experienced more or less the sense of self-agency if the actual sensory consequence was congruent with the prediction based on motor command, although most of them spontaneously admitted that they could not control their own responses and its consequences. These results suggest that the sense of self-agency depends on a comparison between intention and actual consequences of movements but does not totally depend on it. Rather, it seems that the sense of self-agency might mainly depend on a comparison between the predicted and actual consequences of actions. Consistent with this suggestion, schizophrenia patients with delusions of control had no difficulty

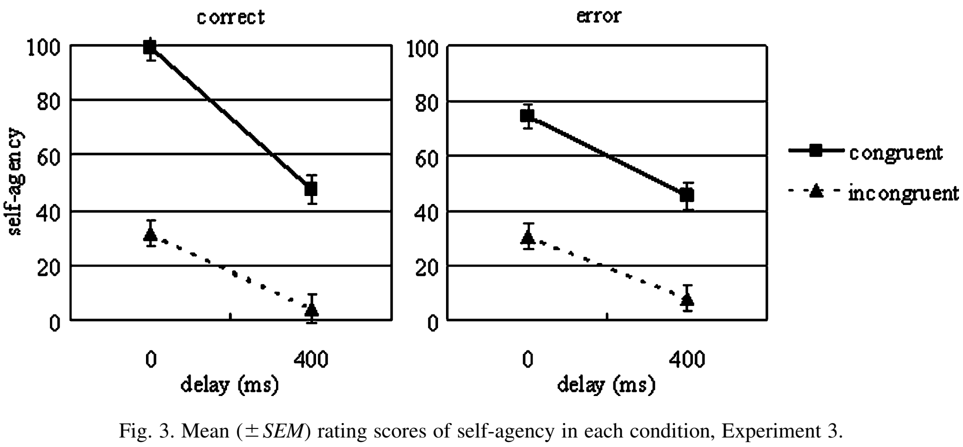

Fig. 3. Mean (± *SEM*) rating scores of self-agency in each condition, Experiment 3.

correcting error on the basis of sensory feedback about limb positions, although they failed to make rapid error corrections based on a comparison between intended and predicted limb positions (Frith & Done, 1989). This result suggests that schizophrenic patients with such a symptom have no problem with motor control based on a comparison of intended movement and sensory feedback. Nonetheless, they remain convinced that they are under the control of aliens forces. Thus, this result supports the notion that the sense of self-agency does not totally rely on a comparison of the intended and actual sensory feedback. In fact, in most cases the very same actions that the patient feels controlled by aliens forces are not discrepant with his or her intentions.

5. General discussion

The ability to recognize oneself as the agent of a behavior is one way by which self builds as an entity independent from the external world. Without the ability to attribute a behavior to its proper agent, social communication could not be properly established. In the present paper, we investigated whether the degree of discrepancy between the predicted and actual feedback affected such a basic aspect of self-consciousness. In Experiment 1, participants made self-paced button press and heard one of which tones had followed button presses in the learning session. The sense of self-agency, that was the sense that “it is I who am producing the tone”, was reduced when the presentation of the tone was unpredictable in terms of timing and its frequency, although in fact the tone was produced by participant. In Experiment 2, the opposite case was found to occur. That is, participants experienced the sense of self-agency when the externally generated sensations happened to match the prediction made by forward model. In Experiment 3, the sense of self-agency was reduced when there was a discrepancy between the predicted and actual sensory consequences, regardless of presence or absence of a discrepancy between the intended and actual consequences of actions. In all the experiments, when there was no movement as in the control condition, all participants correctly judged the tones as externally produced.

In a seminal paper, Daprati et al. (1997) compared groups of normal controls and of schizophrenic patients with or without hallucinations or delusions of control, when required to make judgements about the origin of action. In their study, participants saw on a television screen a hand that is either their own or the experimenter’s performing movements that were either congruent or incongruent with the participant’s own hand movement. The task for the participants was to determine whether the moving hand seen on the screen was theirs or not. Using this paradigm, Daprati et al. (1997) showed that when normal participants and schizophrenic patients saw the experimenter’s hand performing a different movement they correctly denied seeing their own hand regardless of presence or absence of symptoms. By contrast, when they saw the experimenter’s hand performing the same movement, even normal participants misjudged the hand as theirs in about 30% cases. The error rate amounted to 80% in the patients with delusions of control or 77% in the patients with hallucinations, whereas in the patients without hallucinations, it was around 50%. In this condition, participants had to use as cues slight differences in timing and kinematic pattern between the predicted and actual feedback in order to give the correct response. Provided schizophrenic patients with hallucinations or delusions of control have deficit in making a prediction of the sensory consequences of motor command, they will be unable to detect a discrepancy between their predicted movements and actually presented feedback, leading to increase of error rate. Recently, Daprati and Sirigu (2002) using the similar paradigm developed by Daprati et al. (1997) showed that the ability to correctly attribute a movement to its proper agent was reduced when participants were asked to recognize the non-preferred hand. These results indicate that the sense of self-agency is affected by asymmetries similar to those present in motor skills, thus suggesting that the system responsible for the sense of self-agency is profoundly nested within the mechanisms controlling motor production.

The results of the present study also add evidence to the common-coding theory. In the common-coding theory, it is assumed that actions are coded in terms of perceivable effects that they should generate (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Knoblich & Flach, 2003). According to this theory, it follows that one can distinguish between self- and other-generated actions based on the differential activation of the common codes. In many cases, people have different way of performing actions, for example, walking, throwing, drawing and so on. Because the observed events is more similar to the common codes when one perceives one's own past actions, these codes should be more activated when observing one's own past actions and their consequences than when observing others'. Knoblich and Prinz (2001) demonstrated that participants could recognize the kinematics of one's own handwriting based on velocity information, in which there were inter-individual differences. By contrast, if the other person performs the observed actions in a similar way as one would perform, one might misattribute externally generated effects to one's own generated, as shown in Experiment 2. Taken together, these results further support the notion that the action system makes a great contribution to self-recognition.

An important question for future research concerns the neural basis of the sense of self-agency. Sirigu, Daprati, Pradat-Diehl, Franck and Jeannerod (1999) using the paradigm developed by Daprati et al. (1997) showed that patients with left parietal lesions, who failed to simulate hand actions mentally (Sirigu et al., 1996), were more impaired in correctly identifying the viewed hand as experimenter's hand than controls, only when they saw the experimenter's hand performing the same movement as their owns. The left inferior parietal cortex is activated when participants simulate actions from their own perspectives, and when participants imitate someone else's action, whereas the right homologous region is more activated when participants mentally simulate actions from someone else's perspectives, and when they observe their own actions being imitated by another person (Decety, Chaminade, Grezes, & Meltzoff, 2002; Ruby & Decety, 2001). Furthermore, overactivity of the right inferior parietal cortex was observed in schizophrenic patients with delusions of control when they experienced their acts as being under alien control (Spence et al., 1997). These results suggest that the inferior parietal lobe is profoundly involved in producing a sense of self-agency. There is accumulating evidence that the cerebellum is also involved in the distinction between self-produced and externally produced actions. For example, Blakemore, Wolpert and Frith (1999) demonstrated that activity in the thalamus, the primary somatosensory cortex, and the secondary somatosensory cortex showed a significant regression on activity in the cerebellum when tactile stimuli were self-produced but not when they were externally produced. Forward model was proposed to be stored in the cerebellar cortex (Imamizu et al., 2000). Consistent with this proposal, activity in the lateral cerebellar cortex increased as the degree of the discrepancy between the predicted and actual sensory feedback increased (Blakemore, Frith, & Wolpert, 2001). Future research is required to directly investigate the joint contribution of the inferior parietal cortex and the cerebellum to the production of the sense of self-agency.

In the present studies a discrepancy between the predicted and actual feedback had no effects on the sense of self-ownership. At first glance, these results seem to be incongruent with the results using action recognition task. For instance, van den Bos and Jeannerod (2002) demonstrated that participants had difficulty in judging whether the hand that participants saw was theirs or not when they were not acting. This result suggests that participants may judge the owners of body based on the prediction of forward model, if they are acting. Without action, participants could not use the prediction of forward model as cues to judge the owner of body, which make action recognition more difficult. However, experience includes both active and passive ones. In passive experience, there is no prediction made by forward model. Even in such a case, normal participants clearly experienced the sense of ownership although they never experienced the sense of self-agency. Consistent with these results, patients showing anarchic hand sign never deny that their hands belong to themselves, although they feel their hands not under their control (Banks et al., 1989). It seems quite plausible that patients can experience the sense of self-ownership of body based on proprioception that unambiguously pertains to them. These evidences suggest that although in the normal experience of willed action the self-agency and the sense of self-ownership coincide and appear indistinguishable, both may be partly independent and have different processes by which each of them is constructed. On the sense of self-ownership of the body, Botvinick and Cohen (1998) positioned a life-sized rubber hand in front of participant, while their real hand was hidden by a screen from the participant's view. Then, tactile stimulation was applied simultaneously to the real hand and the rubber hand at which participant was required to be looking. After several minutes, participants experienced an illusion in which they felt the touch at the locus of the rubber hand, not of their real hand. In addition, participants even experienced the rubber hand as belonging to themselves. These results suggest that in passive experience the intermodal matching between vision, touch and proprioception contributes to the sense of self-ownership, although vision plays a predominant role over other senses in self-recognition. Future research must be conducted to prove the validity of such a suggestion.

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