Role of the Lateral Prefrontal Cortex in Visual Feedback Processing Following Self-generated Finger Movement

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This study examined cortical activity associated with the processing of visual feedback following self-generated finger movement. We used near-infrared spectroscopy (NIRS) to measure cortical activity in the lateral prefrontal cortex. Participants were required to click on the left or the right button of a computer mouse. This action was immediately followed by visual feedback showing a photograph of either their hand and the mouse carrying out a left or right click, or their hand alone (no mouse) showing a left- or right-clicking index finger. The experimental conditions included type of visual feedback (hand with mouse or hand only) and congruence between the actual action and the visual feedback (congruent or incongruent). A significant interaction was found in the left inferior frontal cortex, with an increase in relative oxy-hemoglobin concentration for the incongruent condition compared to the congruent condition, but only for the hand condition. This result suggests that the activity in the left inferior frontal area is modulated by the discrepancy between the visual result predicted by self-produced finger movements and the actual results.

Key words: NIRS, Prediction, Incongruency effect, Self-generated finger movement, Left inferior frontal gyrus

Introduction

Humans are able to predict the sensory consequences of self-generated actions. The elimination of the tickling sensation is an example of this sensory prediction; it is assumed that self-produced tactile stimulation does not provide a tickling sensation, because it can be predicted by the motor command. However, the sensory consequences predicted from self-generated motor commands are not always congruent with actual sensory feedback. It has been reported that sensory feedback that is incongruent with a predicted sensation of externally produced stimuli, elicits stronger sensations (sensory attenuation in prediction-congruent sensory feedback). This is concomitant with increased brain activation in sensory areas and the cerebellum, compared with prediction-congruent feedback (Blakemore, Frith, & Wolpert, 1998; Blakemore, Wolpert, & Frith, 1998; 2000).

The current study examined the processing of prediction-incongruent visual feedback (FB) presented after self-generated finger movement. The congruency between actual movement

and visual FB was manipulated using mouse-click actions. For example, a prediction-incongruent visual FB consisted of the presentation of a picture in which the right button of a mouse was being pressed after the participant had actually pressed a left mouse button (Fig. 1). We also controlled the appearance or absence of the mouse presented in the FB, to control for mouse manipulation (i.e., the congruency of the mouse press and the visual FB) in FB processing.
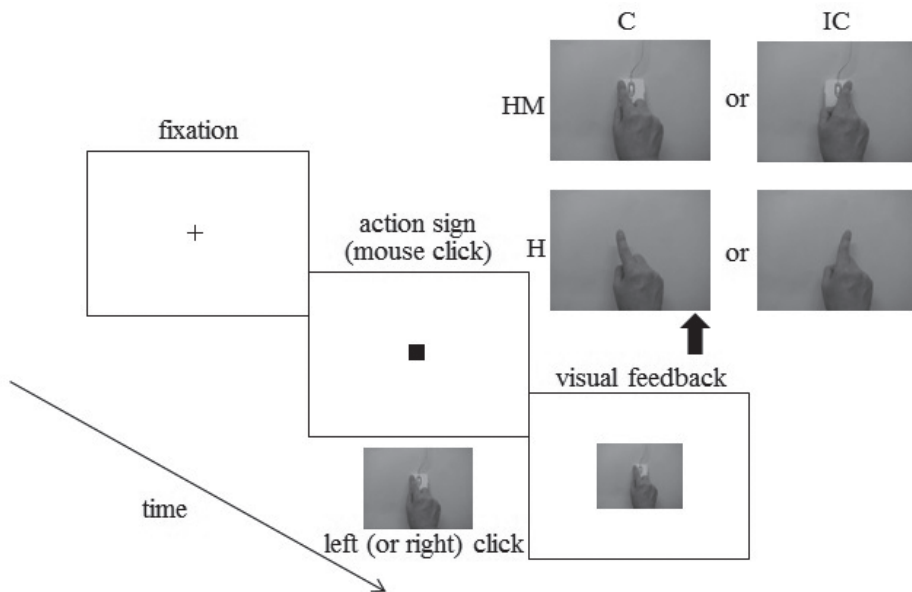
Figure 1.   Schematic representation of the experimental design. HM, hand and mouse condition; H, hand condition; C, congruent condition; IC, incongruent condition.

We focused on activity in the lateral prefrontal cortex (LPFC) detected using near-infrared spectroscopy (NIRS). It is believed that the inferior frontal gyrus (IFG), located in the LPFC, is a component of the mirror neuron system (MNS), and plays an important role in action recognition, including intentions, goals, and outcomes (Iacoboni & Dapretto, 2006; Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2001). Recent studies have also shown that the LPFC is related to the recognition of context-incongruent actions (Shibata, Inui, & Ogawa, 2011; 2013). The current study aimed to investigate the role of the LPFC in the processing of incongruent visual FB presented, following self-generated movement.

Methods

Sixteen healthy individuals participated in this experiment. Of these, one participant was excluded because the optimal condition for measurement could not be achieved due to probe

placement failure. The data from the remaining 15 right-handed participants (7 male and 8 female; age range 20-24 years) were analyzed. All participants provided written informed consent to take part. The ethics committee of the Graduate School of Arts and Letters, Tohoku University approved the study.

Before the experiment, photographs were taken of the participants' own right index finger performing a left and a right click with the mouse (hand and mouse [HM]), and a left- or right-clicking finger without the mouse (hand [H]). These pictures were used as the visual FB stimuli.

During the experiment, participants sat in front of a 19-inch cathode-ray tube monitor (Trinitron Multiscan G420, Sony, Japan) with their heads placed on a chin rest. Each trial began with the presentation of a fixation cross for 20 s (see Fig. 1 for the schematic). This was replaced on the screen by a square, which cued the participant to click the mouse button at any point within 5 s. We instructed the participants to alternate between left and right mouse-button click in each subsequent trial. Immediately after the button click, a FB stimulus was presented for 1 s and the participant was instructed to view it attentively. The experiment was run using the PPT2TTL software (WAWON DIGITECH, Japan).

Experimental factors were the congruency between the click action and the FB stimulus (congruent [C] and incongruent [IC]) and the content of visual FB (HM and H). The experiment consisted of four runs, with 16 trials per run. There were an equivalent number of congruent and incongruent trials, presented pseudorandomly. The FB factor was changed between the second and third run, and the order was counterbalanced between participants. Before the first and third run, participants completed a small number of practice trials. After completion of the four runs, participants were asked to complete a questionnaire on a 7-point rating scale. They rated their subjective impression for action-incongruent compared to action-congruent FB (0 = no incongruent impression, 6 = very incongruent impression).

We used a multi-channel NIRS system (FOIRE-3000, Shimadzu, Japan) to measure cerebral activity in the LPFC area. The system comprises infrared light emitter and detector probes, used to calculate the concentration changes in the relative oxy-hemoglobin (-Hb), deoxy-Hb, and total-Hb in each measurement channel. We used a whole-head probe cap (Fig. 2). The probes were placed over the LPFC area of each hemisphere, each consisting of a 3×4 array, with six emitters and six detectors, constituting 17 channels per hemisphere. We arranged these probes with reference to the international 10-20 system, such that the most posterior channels (channel 4, 11, 24, and 31) ran along on a line through T7-Cz-T8, and the lowest channels (channel 15, 16, 17, 32, 33, and 34) ran along a line through T7-Fp1-Fp2-T8.

The sampling rate at each channel was 10 Hz. We focused on concentration of oxy-Hb as an index of neural activation, because this is more sensitive to changes in regional cerebral blood flow than the deoxy-Hb and total Hb concentrations (Hoshi, 2003). The raw oxy-Hb data were high-pass-filtered at 0.02 Hz to remove signal drift (Taga, Asakawa, Maki, Konishi, & Koizumi, 2003). The data were then smoothed once using a Savitzky-Golay filter with a 25-point window. Data were averaged for each participant and each condition and converted
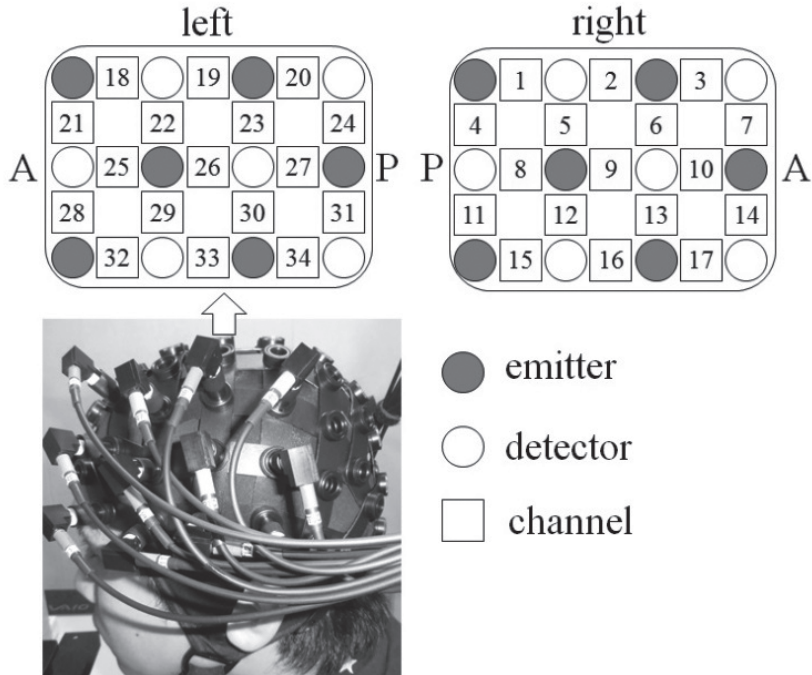
Figure 2.   Positions of the probes used in near infrared spectroscopy measurements. A, anterior; P, posterior.

into *z*-scores (Otsuka, Nakato, Kanazawa, Yamaguchi, Watanabe, & Kakigi, 2007; Schroeter, Zysset, Kruggel, & von Cramon, 2003), so that the mean values and the standard deviations of the baseline period (5 s before FB stimulus onset) were 0 and 1, respectively. Considering the slow dynamics of hemoglobin changes, the oxy-Hb values between 3-9 s after FB stimulus onset (analysis period) were averaged across participants, and the average data in this period were used to index processing associated with visual FB.

To estimate the cortical regions corresponding to each channel, we measured three-dimensional (3D) coordinate data of each probe from two participants (1 male and 1 female) using a 3D digitizer (FASTRAK, Polhemus, Vermont, USA). The 3D coordinate data were averaged across participants. Channel coordinates were calculated as the midpoint between the nearest two probes, and channel positions were registered to the Montreal Neurological Institute (MNI) space using NIRS-SPM software (Jang, Tak, Jung, & Jang, 2009; Singh, Okamoto, Dan, Jurcak, & Dan, 2005; Ye, Tak, Jang, Jung, & Jang, 2009).

Results

Mean reaction times measured from the onset of the action sign to the mouse button press were 1.4 s (standard deviation, $SD = 0.6$) in both the HM and H conditions. The mean

subjective impression rating for incongruent FB was 3.3 (SD = 1.2) in the HM condition and 2.8 (SD = 1.6) in the H condition, indicating that participants had, at least to some extent, a subjective impression of "incongruence" while giving incongruent FB. There was no significant difference between the two incongruent conditions [$t(14)$ = 1.26, n.s.].

We then analyzed oxy-Hb concentration changes in the analysis period. A two-way ANOVA was performed for each channel. Significant differences were found in channels 3 and 33. Figure 3 shows the time course changes (Fig. 3a) and the averages for the analysis period (Fig. 3b) in these channels. Channel 3 showed a main effect of FB [$F(1,14)$ = 6.37, p < .05], characterized by an increase in oxy-Hb concentration for the HM compared to the H condition. Channel 33 showed an interaction between FB and congruence [$F(1,14)$ = 4.77, p < .05]. The simple main effect of H condition showed that the oxy-Hb concentration was more increased in the IC condition than in the C condition [$F(1,28)$ = 7.19, p < .05]. The same analysis of IC condition showed increased oxy-Hb concentration in the H condition than in the HM condition [$F(1,28)$ = 4.83, p < .05]. Cortical regions corresponding to channels 3 and 33 were estimated as regions centered on the right DLPFC (dorso-LPFC: Brodmann area [BA] 9; MNI coordinates, [x, y, z = 35, 40, 46]) and the left IFG (BA44; MNI coordinates, [x, y, z = -60, 16, 14]), respectively.
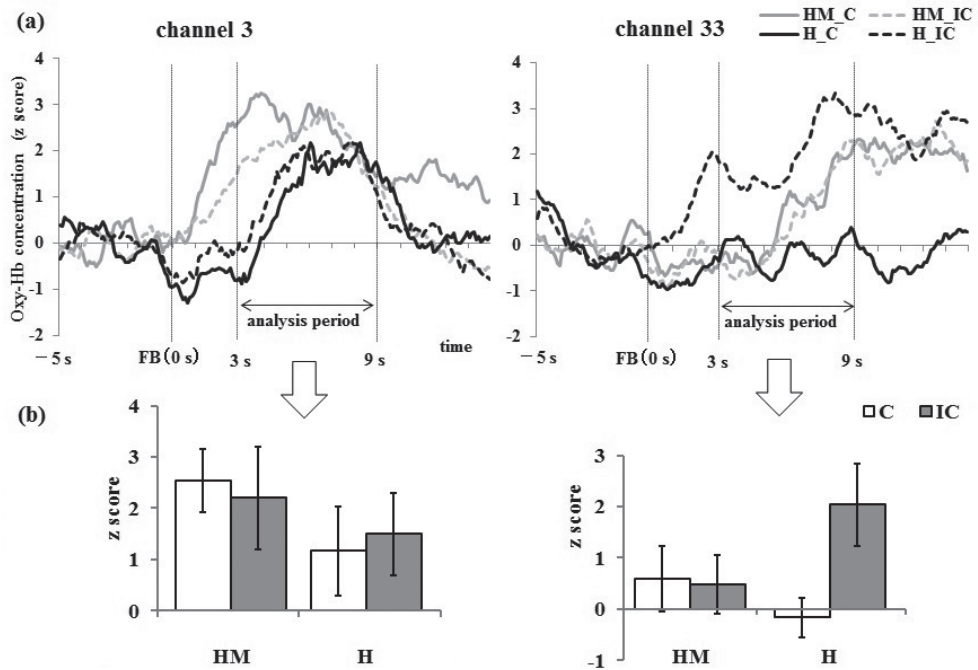
Figure 3. Concentration changes in oxy-hemoglobin for channels showing significant condition differences. (a) Time course changes for channels 3 and 33. (b) Averages of the analysis period in the four conditions, with error bars representing the standard error. FB, Feedback; HM, hand and mouse condition; H, hand condition; C, congruent condition; IC, incongruent condition.

Discussion

The oxy-Hb concentration in the left IFG increased mainly in the H and IC condition (H_IC), suggesting that this region is involved in processing the discrepancy between actual movement and visual FB. The left IFG activity, however, showed an interaction effect; the incongruency effect was found only in the H condition. This result suggests that activity associated with the incongruency effect is modulated by the type of visual FB, not simply the detection of the discrepancy.

The IFG region is reported to be a key component in the MNS. Previous studies have reported that mirror neurons in monkeys respond to transitive actions (object-directed actions), but not intransitive actions or pantomime actions (nonobject-directed actions) (Rizzolatti & Craighero, 2004; Umilta, Kohler, Gallese, Fogassi, Fadiga, Keysers, & Rizzolatti, 2001). In contrast, some functional magnetic resonance imaging studies in humans have reported that activity in the MNS areas correlates with the manipulation of intransitive actions (Bello, Modrono, Marcano, & Gonzalez-Mora, 2013; Iacoboni, Woods, Brass, Bekkering, Mazziotta, & Rizzolatti, 1999; Koski, Iacoboni, Dubeau, Woods, & Mazziotta, 2003; Tanaka & Inui, 2002), in addition with transitive actions. In the current study, the difference between the FB conditions was the presence or absence of the mouse: a transitive action (mouse-directed action) in the HM condition and an intransitive action (finger movement without the mouse) in the H condition. Previous studies have shown that imitation (i.e., observation and execution) of intransitive action increases activity in regions including the left IFG (Iacoboni, *et al.*, 1999; Tanaka & Inui, 2002). Tanaka & Inui (2002) reported that visual FB was important for finger imitation because one can see one's own finger when imitating another's hand postures. It therefore follows that the activity observed in the left IFG in this experiment might be related to the process of matching between intransitive finger movements and the visual FB of finger movements.

It is assumed that the MNS is involved with inner models (e.g., Miall, 2003): Forward models convert an action plan into a visual representation predicted by the action, and inverse models convert a visual representation into a potential action plan. For the inverse model, the discrepancy between an actual finger movement and the observed visual FB would generate a more complex motor representation, because the motor representation is related to an actual movement (e.g., index finger points to the left) plus a contrasting FB (e.g., index finger points to the right). The increased activity in the left IFG would thus be due to processing the complex motor representations for both the actual and predicted finger configurations.

The discrepancy between visual and proprioceptive sensations could offer an alternative interpretation for the increased activation observed in the left IFG. Fink, Marshall, Halligan, Frith, Driver, Frackowiak, and Dolan (1999) found that the right ventral LPFC was more activated by the discrepancy between visual and proprioceptive FB without intentional movement, compared with the right DLPFC, which was associated with maintaining intentional actions during the evoked discrepancy. In the current study, actual proprioception

and visual FB differed in the IC conditions. Left IFG activity might therefore be modulated by the discrepancy between visual and proprioceptive information, irrespective of action execution.

We did not find an incongruency effect in the brain for the HM condition. This may be due to the FB in the HM condition being involved in object-based action recognition, i.e., the right button of the mouse was pressed in the FB but the left button of the mouse was pressed in reality. Although we used NIRS to elucidate the role of the LPFC, other brain imaging methods may be useful for identifying the neural mechanisms associated with the incongruency effect in the HM condition. For example, in a meta-analysis, it was highlighted that the posterior medial PFC is associated with cognitive processes such as response conflict and the detection of unfavorable outcomes (e.g., Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004).

Activity in the right DLPFC increased more in the HM condition than in the H condition. The DLPFC is assumed to play a role in executive function such as working memory (Curtis & D'Esposito, 2003). We therefore interpret this effect in the right DLPFC as an increase in working memory load, due to associating the observed hand with the mouse in the HM but not the H condition.

Conclusion

We examined the role of the LPFC in the processing of visual FB after self-generated finger movement. The left IFG showed an interaction effect, suggesting that modulation of activity was associated with an incongruency effect dependent on the type of visual FB, not simply the detection of the incongruency.

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