Modulation of motor area activity during observation of unnatural body movements

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ARTICLE INFO

ABSTRACT

The mirror neuron system (MNS) is activated when observing the actions of others. However, it remains unclear whether the MNS responds more strongly to natural bodily actions in the observer's motor repertoire than to unnatural actions. We investigated whether MNS activity is modulated by the unnaturalness of an observed action by inserting short pauses in the middle of the action (0, 2, and 6 pauses; no-pause, pause-1, and pause-2 conditions, respectively). The results indicated that the number of pauses significantly affected motor area activity. Subsequent analyses revealed significant differences between the pause-1 and pause-2 conditions ($P < 0.01$), as well as the no-pause and pause-2 conditions ($P < 0.05$). There was significant activation in the pause-1 condition ($P < 0.001$), while significant deactivation was observed in the pause-2 condition ($P < 0.05$). These results indicate that MNS activity is modulated by the kinematic characteristics of the observed action. We suggest the possibility that a slightly deviated action may enhance the MNS activity during action observation, while a highly unnatural action would lead to a strong attenuation (deactivation) of activity in the MNS.

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1. Introduction

Several motor-related brain areas are activated not only when an individual performs an action, but also when they observe the same action performed by others (Rizzolatti, Fogassi, & Gallese, 2001). This network of areas is referred to as the mirror neuron system (MNS). The characteristic resonance of motor areas suggests a role of motor areas in representing the internal sensorimotor states of other people, which is likely to underpin human social cognitive abilities (Gallese, 2003). Previous studies have confirmed that motor areas, including ventral and dorsal premotor cortex, the inferior parietal lobe, and the primary motor cortex, constitute the putative human MNS (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Hari et al., 1998; Iacoboni et al., 1999; Rizzolatti et al., 2001).

Although the existence of MNS in humans has been thoroughly demonstrated, the exact characteristics of MNS are still unresolved. A widely accepted characteristic of MNS is its 'mirror-matching' property: the MNS is more activated when observing an action that is in the observer's own motor repertoire compared with an action that is not (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Cross, Hamilton, & Grafton, 2006).This mirror-matching property of MNS, employing one's own motor representation, enables the observer to grasp a 'richer' understanding of another's internal state, such as intention and feeling (Rizzolatti & Sinigaglia, 2010).

However, other studies have reported that the MNS also responds to biologically impossible hand movements (Costantini et al., 2005; Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005). Recent studies also reported that the motor area of expert sportspeople responded more strongly to an erroneous action of another expert player than to a successful action (Aglioti, Cesari, Romani, & Urgesi, 2008; Shimada, 2009). These findings raise the question of whether the MNS is activated most strongly by observing an action that is exactly the same as in the observer's motor repertoire.

The predictive coding model of MNS (Kilner, Friston, & Frith, 2007) may account for those counterintuitive findings. The predictive coding model posits that MNS generates plausible sensory input (the sight of the executed action) from a presupposed intention or goal of the others. This is done by a generative (or forward) model of the existing motor control circuit. If there is a prediction error, that is, the difference between inferred and actual sensory input, MNS modifies the representation of the supposed intention of the others until prediction error is minimized. Therefore, the predictive coding account predicts that MNS activity is enhanced when observing an erroneous action or an action that is deviated from one's own motor repertoire, while the mirror-matching account does not.

While erroneous actions have been reported to lead to stronger activation in the MNS (Aglioti et al., 2008; Shimada, 2009), our previous study showed that an unnaturally deviant action lead to a 'deactivation' of MNS (Shimada, 2010). In that study, we measured MNS activity during the observation of human and robot actions and found that the MNS was significantly deactivated when

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observing a human agent perform a jerky robot-like action. This activity was significantly lower than when observing a human agent perform a smooth action. These findings suggest that kinematics of the observed action is a critical factor for modulation of MNS activity and that there should be a boundary condition where the prediction error enhances or suppresses MNS activation.

The present study investigated how kinematics of the observed action modulates MNS activity during action observation. To this end, we manipulated the unnaturalness or 'jerkiness' of the observed action by inserting short pauses in the middle of it. To ensure that trajectory of the movement was identical between the conditions, each stimulus was generated with computer-generated (CG) software (note that actions with different trajectories may be classified as different actions, resulting in differential activation in MNS). The difference among conditions was the number of pauses inserted in the stimuli (0, 2, or 6 pauses). We confirmed that increasing the number of pauses affected subjective reports of unnaturalness ('jerkiness'; see Methods and Results sections for details). The motor cortical activity during action observation was measured using near-infrared spectroscopy (NIRS), as in our previous study (Shimada, 2010). By examining the modulation of motor area activity, we were able to determine how MNS activity is influenced by the unnaturalness of the observed action.

2. Material and methods

2.1. Participants

Fourteen healthy subjects participated in the experiment (one female and 13 males, aged 22–24 years). Among them, four subjects (Subject A–D) also underwent 3D digitizer measurement of NIRS optode locations (see below). All subjects were right-handed and had normal or corrected-to-normal vision. Written informed consent was obtained from all subjects. The experiments were approved by the ethics committee of the School of Science and Technology, Meiji University, and conducted according to the principles and guidelines of the Declaration of Helsinki.

2.2. Procedure

The subjects observed pantomime actions of a CG character grasping and holding up an object placed on a table with the right hand (Fig. 1); the character was generated using 3ds MAX software (Autodesk Corporation, California, USA). It should be noted that several studies have reported that a pantomimed action is sufficient for the human MNS to be activated (i.e., Molenberghs,

Brander, Mattingley, & Cunnington, 2010) and is useful for assessing imitation deficits in neuropsychological patients with left fronto-parietal lesions (Haaland, Harrington, & Knight, 2000; Poizner et al., 1998). In the animated stimuli, a pause (suspending the action for 0.07 s) was inserted to increase the unnaturalness (jerkiness) of the action. The number of pauses was varied across conditions (0, 2, and 6; no-pause, pause-1, pause-2 conditions, respectively). In the no-pause condition, the arm of the CG agent moved to the putative object on a table and grasped it. After grasping, the arm returned to the initial position (beside the torso) with the reverse trajectory. In the pause-1 condition, a pause was inserted at 1.33 s from the onset of the stimulus, when the agent's hand had moved to just above the edge of the table and was about to start the grasping movement (Fig. 1, middle). Another pause was inserted at the same point as the first one, but as the hand was returning to the starting position (4.67 s). In the pause-2 condition, compared with the pause-1 condition, four more pauses were inserted (0.67, 2.00, 4.00, and 5.33 s from the onset) when the agent's hand was moving halfway toward the edge of the table (Fig. 1, top) and where the hand started to close to hold a putative cup (Fig. 1, bottom), and in the same two places when the hand was returning to the starting position. Only the body parts of the agent from the neck down were visible throughout the movie stimuli. The duration of each stimulus was 6 s.

The experiment was conducted in a quiet room. The movie clips were displayed on a 20-in. liquid–crystal color monitor. Subjects were seated comfortably on a chair in front of the monitor and instructed to watch the monitor throughout the experiment. The viewing distance was approximately 1 m. Each movie clip lasted for 6 s (action observation period), and the interstimulus interval was 12 s, during which a still image of the agent was presented (control period). The experimental session consisted of 18 trials: six trials each for the three conditions. The movie clips were presented in a pseudorandom order.

2.3. NIRS recordings

NIRS measurements were performed throughout the experiment. A multichannel NIRS unit operating at 780, 805, and 830 nm wavelengths (OMM-3000, Shimadzu, Kyoto, Japan) was used to measure temporal changes in concentrations of oxyhemoglobin (oxy-Hb), deoxyhemoglobin, and total hemoglobin. Sixteen optodes constituted 24 channels and were placed on the motor area of the left hemisphere, including C3 of the international 10/20 system (9 × 9 cm square area, Fig. 2). These channels are likely to have been placed on the motor areas (Okamoto et al., 2004). It
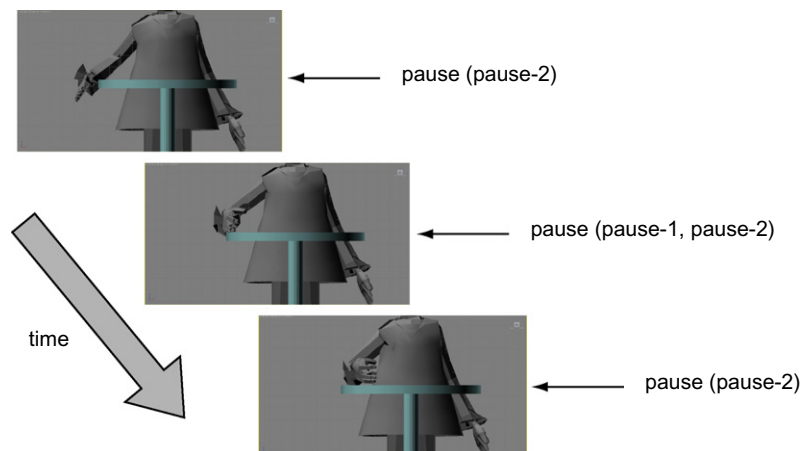

Fig. 1. Stimuli used in the experiment. Short pauses were inserted in the middle of the action to increase the perceived unnaturalness of the action.