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Research Report

Neural processing of observed oro-facial movements reflects multiple action encoding strategies in the human brain

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ABSTRACT

In this experiment, the oscillatory responses of the MEG were characterized during the observation of four viewing conditions: (a) observation of mouth movements, (b) observation of a non-biological motion stimulus (a mechanical aperture opening and shutting), (c) observation of object-directed mouth movements and (d) observation of speech-like mouth movements. Data were analyzed using synthetic aperture magnetometry (SAM) in three frequency bands, beta (15–35 Hz), gamma (35–70 Hz) and alpha/mu (8–15 Hz). Results showed that observations of biological motion resulted in beta desynchronization over lateral sensorimotor areas, while observations of non-biological motion resulted in a more medial desynchronization, an effect that may be related to the processing of a structured event sequence. Observation of linguistic movements resulted in less alpha/beta desynchronization in posterior brain regions in comparison to biological motion stimuli, suggesting that linguistically-relevant stimuli are processed with different neuronal systems than those recruited by normal action observation. We suggest that non-linguistic actions recruit dorsal systems while linguistic actions engage ventral processing systems. Object-directed movements showed the largest sensorimotor activations, suggesting that, as is the case for observations of hand movements, motoric processing is particularly sensitive to the viewing of goal-directed actions. Taken together, the results indicate that the brain utilizes multiple action encoding strategies, tailored to the function of the observed movement.

1. Introduction

Perception and motor control have conventionally been viewed as quite separate processes, subserving distinctive functions and even utilizing independent sets of neural mechanisms (e.g. Goodale and Milner, 1992; Jeannerod, 1994). An alternative view emphasizes the tight integration between perception and action apparent in the performance of real world tasks and suggests a much more direct functional–anatomical relationship between the two processes (Rizzolatti et al., 2001). The notion of a relatively direct mapping of perception onto action has come from reports that visuomotor neurons in areas of the monkey cortex called "mirror neurons" selectively fire in response to purposeful movements performed by other individuals and when the monkey performs those same actions (di Pellegrino et al., 1992; Gallese et al.,

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1996). It has been proposed that this mirror-neuron system may be the neurophysiological basis by which we comprehend the goal-directed action of others, by mapping observed actions onto our own motor programs for the same actions (Rizzolatti and Craighero, 2004; Rizzolatti et al., 2001). A direct relationship between perception and motor control also has implications for high-level cognitive processes such as language: the so-called motor theory of speech perception posits that speech is perceived in terms of how it is produced rather than in terms of its acoustic properties (Liberman et al., 1967).

Evidence for motor involvement in biological motion perception has come from a number of recent studies measuring brain activity during observations of oro-facial movements. Studies using various imaging techniques have reported activation of a large number of motor and motor-related cortical areas, including premotor cortex, Broca's area, superior temporal sulcus, parietal cortex, primary motor cortex, primary sensory cortex, MT and fusiform gyrus (Buccino et al., 2001; Buccino et al., 2004; Miki et al., 2004; Muthukumaraswamy et al., 2004a; Nishitani and Hari, 2002). However, different classes of human oro-facial movements can serve a variety of informative functions, ranging from motions directed towards objects or food to the motions involved in linguistic communication. It remains unclear how different types of functional oro-facial movements are encoded by the brain, that is, are the same mechanisms utilized to achieve understanding of linguistic and non-linguistic mouth movements, or are they processed via functionally and anatomically distinctive routes?

We addressed this question by measuring brain responses with MEG during visual observations of different classes of oro-facial movements and non-biological movements. In the *Biological Motion* condition, undirected sucking and biting movements were shown. In the *Object-Directed Action* condition, the same movements were shown directed towards a straw. In the *Linguistic Motion* condition, participants viewed the silent articulation of words. Finally, in the *Non-Biological Motion* condition, subjects viewed a mechanical aperture opening and closing with similar temporal parameters to that of the *Biological Motion* condition.

2. Results

Fig. 1a shows the significant source power decreases/event-related desynchronization (ERD) for each of the four conditions for the beta (15–35 Hz) and alpha/mu (8–15 Hz) frequency bands. No significant power increases/event-related synchronizations (ERS) were seen in the alpha/mu or beta frequency bands. For the beta rhythm, the Biological Motion, Object-Directed Action and Linguistic Motion conditions show ERD in lateral sensorimotor areas whereas the distribution of these central power decreases was in more medial sensorimotor areas for the Non-Biological Motion condition. Smaller areas of lateral sensorimotor power decrease were seen in the Linguistic Motion condition. The three conditions containing biological motion stimuli all showed bilateral posterior occipito-parietal ERD, predominantly in the right hemisphere whereas these source power changes were not present in the Non-Biological Motion condition. For the alpha/mu band, no changes in source power were seen for the Linguistic Motion condition. The predominant changes in the alpha/mu band were in right occipital areas for the Biological Motion and Object-Directed Action conditions. The Object-Directed Action condition also showed changes in mu rhythms over sensorimotor areas. Grand averaged virtual sensor time-frequency plots from peak locations in left and right sensorimotor cortex and left and right occipital cortex are presented in Fig. 1b for the Biological Motion condition. Concurrent alpha and beta power ERD can be seen in these plots. These plots show that the time course of ERD followed the onset and offset events of the stimulus with a slight time delay. Other conditions showed similar patterns but only weak ERD was seen in the Linguistic Motion condition (Tables 1 and 2).

The results for each of the contrasts conducted are illustrated in Fig. 2 and Table 3 summarizes the local maxima. For the Non-Biological motion contrasts, the most notable feature was enhanced ERD in posterior areas in the alpha and beta band and the medial sensorimotor ERS. A more lateral sensorimotor ERD in the right hemisphere and a smaller sub-threshold ERD occurred in the left sensorimotor area. For the Object-Directed Action contrast, there was relatively more ERD in this condition in the alpha/mu and beta bands over primary sensorimotor areas compared to the Biological Motion condition. There was also an area of increased ERD overlapping the left middle and inferior frontal gyri. For the Linguistic Motion comparison, there was a broad area of increased ERD in the Biological Motion condition in occipito-parietal regions extending into sensorimotor regions.

Of the 24 offset response SAM images, only two images showed significant peaks. This was for the mu band in the Biological Motion condition where power peak decreases occurred in the right superior parietal lobule ($x = 30$, $y = -51$, $z = 66$, pseudo $T = 6.52$) and right sensorimotor cortex ($x = 36$, $y = -12$, $z = 66$, pseudo $T = 6.03$) and for the gamma band in the Object-Directed Action condition where gamma power increases occurred in the cingulate gyrus ($x = -9$, $y = -57$, $z = 27$, pseudo $T = -5.59$). No contrasts were conducted on these images.

For the gamma band analysis, significant source power changes were only seen in the Non-Biological Motion condition, manifested as gamma ERD over sensorimotor cortex ($x = -33$, $y = -18$, $z = 30$, pseudo $T = -4.93$) and gamma ERS in bilateral occipital areas ($x = -18$, $y = -81$, $z = 9$, pseudo $T = 9.01$, $x = -33$, $y = -18$, $z = 30$, pseudo $T = 5.71$). No effects were seen when a contrast was conducted on this condition vs. Biological Motion. Event-related field analyses were conducted on all conditions and no evoked responses were seen to the stimuli.

3. Discussion

In all conditions in this experiment, decreases in SAM source power were seen in the beta band and in three conditions (Biological Motion, Object-Directed Action, Non-Biological Motion) decreases in SAM source power were seen in the alpha/mu band. Decreased power in these frequency bands related to some stimulus event is called ERD and in these particular frequency bands ERD is generally regarded as being an indicator of active processing (Pfurtscheller and Lopes da Silva, 1999) whereas ERS has been associated with inactive or "idling" cortex