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Research report

Recognition of point-light biological motion: Mu rhythms and mirror neuron activity

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Abstract

Changes in power in the mu frequency band (8–13 Hz) of the electroencephalogram (EEG) is thought to indirectly reflect the activity of mirror neurons in premotor cortex. Activation of these neurons by self-performed, observed or imagined motor actions is assumed to produce asynchronous firing and a reduction in mu rhythm oscillation (referred to as mu suppression) in sensorimotor cortex. A recent fMRI study by Saygin et al. [Saygin AP, Wilson SM, Hagler Jr DJ, Bates E, Sereno MI. Point-light biological motion perception activates human premotor cortex. J Neurosci 2004;24:6181–8] revealed that the premotor brain regions containing mirror-neurons are also activated in response to point-light human motion. The perceived movement of these light cues are integrated into one percept of a complete human action (e.g. jumping jacks), rather than seen as individual moving lights. The present study examined whether recruitment of the mirror neuron system, as reflected in mu rhythm suppression, mediates recognition of point-light biological motion. Changes in mu power were recorded while subjects viewed point-light biological motion videos, matched scrambled versions of these animations, and visual white-noise (baseline). The results revealed that point-light biological animations produced mu suppression relative to baseline, while scrambled versions of these animations did not. This supports the hypothesis that the mirror neuron system is involved in inferring human actions by recovering object information from sparse input.

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1. Introduction

The capacity to understand and imitate actions plays a crucial role in the ability of individuals to be integrated effectively within their social milieu, enabling humans to learn to perform skilled actions, use tools, and transmit culture [2,3]. These abilities also help establish normal social interactions by facilitating the ability to predict the behaviors of others [4]. This is presumably achieved through a variety of mechanisms, but one that may be particularly relevant is the mapping of the visual representation of observed actions onto the observer's own motor representations of the same action [3,5,6]. Evidence for this "direct-matching" mechanism comes from studies of the mirror

neuron system (MNS)¹ in monkeys and humans [7]. These studies suggest that mirror neurons mediate action understanding or the implicit grasp of others' actions and feelings by directly recreating or matching observed actions onto the observer's own motor cortex.

Mirror neurons were originally discovered in area F5 of the rhesus monkey's premotor cortex [3,5,8], and later found in the inferior parietal cortex [9]. These unique visuomotor neurons discharge in response to self-initiated movements as well as to the observation of similar actions by other agents (i.e., a conspecific or human experimenter) [3]. Mirror neurons in monkeys are not activated in response to the visual image of the target or object alone, even when the object is

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¹ MNS (mirror neuron system); IFG (inferior frontal gyrus); TMS (transcranial magnetic stimulation); MEP (motor evoked potential); MEG (magnetoencephalography); EEG (electroencephalography).

salient, but only to object-directed actions involving grasping, manipulating, placing, tearing, or holding the object. Hence, an interaction between the actor and the object involving the hand or mouth appears necessary [4]. Audiovisual mirror neurons that fire when animals perform or observe a specific action independent of sound or when they hear the related sound (e.g. breaking peanuts) have also been discovered in the ventral premotor cortex [10]. All these studies are congruent with the idea that mirror neurons play a critical role in action understanding; and that partially seen or heard sensory features of actions are essential to mirror neuron activation insofar as they trigger the motor representation of the same action within the perceiving agent [4].

The existence of such a system in the human brain is supported by neurophysiological and brain-imaging studies [11–16]. These studies show the existence of cells in the rostral part of the inferior parietal lobule, the caudal sector (pars opercularis) of the inferior frontal gyrus (IFG) [3], and the ventral premotor cortex including Broca's area [7,11,14]. The latter findings are particularly relevant given the proposed homology of Broca's area with area F5 in macaque monkeys [17].

The human MNS differs from the macaque system in that the former is activated in response to a wider range of actions including the observation of intransitive or non-goal directed movements as well as to motor imagery [18,19]. Using transcranial magnetic stimulation (TMS) Fadiga et al. [18] demonstrated that motor evoked potentials (MEPs) increased significantly when subjects observed movements. Furthermore, the pattern of firing while observing movement was similar to the pattern elicited during the execution of movement. This added support to the direct-matching hypothesis, and implied that humans possess a mirror neuron system that produces similar neuronal firing patterns for identical gestures, either observed or executed.

The human MNS has been extensively investigated through analyses of functional magnetic resonance (fMRI) [3,16] as well as magnetoencephalography (MEG) [20] and electroencephalography (EEG), in particular mu frequency band oscillations recorded with scalp electrodes over sensorimotor cortex [21–23]. The mu rhythm is an 8–13 Hz oscillation generated in sensorimotor cortex [24] that reaches maximal amplitude when individuals are at rest. When subjects move, imagine movement, or observe movements, neurons in this area fire asynchronously, thus reducing mu amplitudes [23–26].

This mu rhythm suppression has been linked to frontal mirror neuron activity (for a review see [27]). Recently, Muthukumaraswamy et al. [28] found that mu rhythms are suppressed by object-directed actions, and to a lesser extent, during the observation of flat-hand extensions [21]. These results support the idea that mu rhythms reflect downstream premotor cortex modulation of primary sensorimotor areas [21,28]. During self-initiated movements, various populations of motor neurons within the premotor, motor, and sensorimotor regions are activated. Therefore, mu suppression to self-movement most likely results from the activation of both motor and visuomotor (mirror) neurons, making these neuronal populations indistinguishable. Yet, in the absence of overt movement, mirror neurons are selectively activated in these regions during the imagination and observation of

movement [29]. It is therefore hypothesized that mu suppression to observed biological actions can be exclusively attributed to the discharge of mirror neurons and may, consequently, provide a selective index of MNS functioning [21].

The use of mu suppression as an index of mirror neuron activity is also validated by anatomical and physiological evidence of strong cortico-cortico connections between human and non-human primate ventral premotor cortex (including the region thought to contain mirror neurons) and primary sensorimotor cortex where the mu rhythm is generated and recorded [30–32].

The role of the mirror neuron system in action comprehension suggests that it must be engaged by motion perception since motion perception is essential for predicting the actions of others. Johansson [33] deviced point-light biological stimuli as a way to study motion without interference from shape. Point-light biological motions are image sequences created by marking the limb articulations of animate bodies (dressed in black against a completely black set) with lights. When these actors are in motion, they simulate different behaviors that can be perceived as biological motion. Even the gender, emotional state and the identity of specific individuals can be inferred from these displays [34,35]. Saygin et al. [1] recently reported pointlight activation of the premotor cortex. They measured fMRI activity of subjects who viewed point-light biological motion, matched scrambled biological motion, and stationary point-light images. Results indicate that point-light biological motion activates the frontal cortex, while scrambled biological motion does not. These findings suggest that the motor system of the observer may be recruited to "fill in" these simplified displays, in a manner similar to the way mirror neurons are activated in order to assist in action understanding.

The present study investigated the relationship between mu rhythms and mirror neurons and specifically whether mu rhythm activity is affected by cues in the form of point-light biological motion. A positive finding would support the hypotheses that mu rhythms are an index of mirror neuron activity. Furthermore, since point-light biological motion depicts actions, it is an open question whether their perception involves recruitment of the MNS, allowing humans to recover object information from sparse input. We hypothesized that oscillations in the 8–13 Hz frequency band would be suppressed during the observation of point-light biological motion images; whereas there should be little or no suppression to scrambled motion. Such results would indicate that the MNS is recruited to recover object information from sparse input and, therefore, assist in action understanding.

2. Results

2.1. Behavioral performance

Subjects responded correctly 94% of the time to a continuous performance task (an attention color-monitoring task) during both the biological and scrambled motion viewing conditions. Therefore, differences in attentional states during the viewing of these different movements cannot account for differences in mu suppression.

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