Available online at www.sciencedirect.com
ScienceDirect
Behavioural Brain Research 183 (2007) 188–194
BEHAVIOURAL BRAIN RESEARCH
www.elsevier.com/locate/bbr

Research report

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

Erlinda R. Ulloa[a,d], Jaime A. Pineda[b,c,*]

[a] Department of Biology, UC San Diego, La Jolla, CA 92093-0346, USA
[b] Department of Cognitive Science, UC San Diego, La Jolla, CA 92093-0515, USA
[c] Department of Neurosciences, UC San Diego, La Jolla, CA 92093-0662, USA
[d] Department of Psychology, UC San Diego, La Jolla, CA 92093-0109, USA

Received 5 March 2007; received in revised form 24 May 2007; accepted 14 June 2007
Available online 19 June 2007

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.

Keywords: EEG; Mirror neurons; Mu rhythm

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

* Corresponding author at: UC San Diego, 9500 Gilman DriveLa Jolla, CA 92093-0515, USA. Tel.: +1 858 534 9754; fax: +1 858 534 1128.
E-mail address: pineda@cogsci.ucsd.edu (J.A. Pineda).

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

0166-4328/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.bbr.2007.06.007

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 point-light 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.

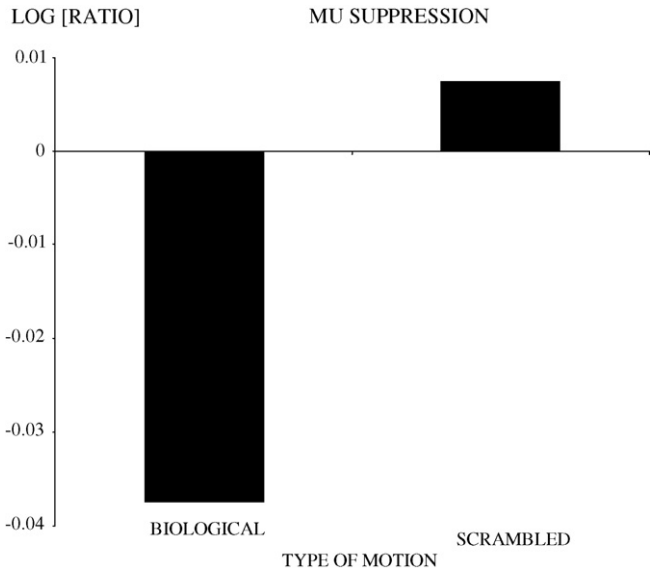

Fig. 1. Mu suppression was calculated as the ratio of the power during the experimental conditions (in the biological and scrambled motions) relative to the power during the baseline (white noise) condition across central scalp electrodes (C3, Cz, C4). Since ratio data are inherently non-normal as a result of lower bounding, a log transform was used for analysis. A log ratio of less than zero indicates suppression whereas a value of zero indicates no suppression and values greater than zero indicate enhancement.

2.2. Electrophysiology

An initial ANOVA on overall mu power showed a statistically significant main effect of motion, $F(2,38) = 4.42$, $p = 0.028$, see Fig. 1. A Tukey Honestly Significant Difference post-hoc analysis revealed that mu power for biological motion was significantly different from baseline ($p < 0.05$), while the scrambled to baseline and biological to scrambled were not ($p > 1$). No main effect of movement type was observed and hence no significant difference between the two point-light biological movements ("jumping jacks" and "kick") ($p > 0.1$). Therefore, data from these two movement conditions were collapsed for the analysis of mu suppression. Finally, there was no main effect of electrode site ($F < 1$) and only a marginally significant motion × electrode interaction, $F(2,38) = 2.27$, $p = 0.086$. That is, while there was no significant difference in mu suppression between the right (C4) and left hemispheres (C3) ($p > 0.1$) nor between the left (C3) and center (Cz) electrode ($p > 0.1$), there was a trend for the right (C4) being larger than the center (Cz) ($p = 0.037$).

For mu suppression values there was a significant *suppression* during the viewing of biological motion ($p < 0.05$), and a marginally significant *enhancement* for viewing scrambled motion ($p = 0.072$).

Step-down analyses for "jumping jacks" and "kick" movement types were analyzed separately to determine differences in suppression between electrode sites. For the jumping jacks there were no significant differences between any of the electrode sites ($p > 0.20$). In contrast, for the kick movement there was a difference between the right (C4) and center (Cz) electrodes ($t(19) = 2.09$, $p < 0.01$), although no differences between the left (C3) and right (C4) hemispheres ($t(19) = 1.73$, $p > 0.1$), nor between the left (C3) and center (Cz) electrodes ($t(19) = 2.09$, $p > 0.1$).

3. Discussion

The results of the present study suggest that point-light biological motion engages the mirror neuron system as reflected in mu rhythm suppression to biological motion but not to scrambled motion. This is consistent with fMRI studies showing activation of mirror neuron regions using point-light displays [1]. The present results extend those findings and suggest that activity in premotor cortex modulates activity in sensorimotor cortex as part of the circuit to infer human actions by recovering object information from sparse input. Mu suppression appears to be independent of movement type ("jumping jacks" versus "kick") and symmetrical across the left (C3) and right (C4) hemispheres. Attention differences cannot account for these findings since subjects responded correctly approximately 94% of the time (in both the biological and scrambled motion conditions) to an attention color-monitoring task. The small difference between the right (C4) and center (Cz) electrodes that was observed may be attributed to the inherent differences between the jumping jacks. The jumping jacks exhibit bilateral, symmetrical movements, whereas the kick produces asymmetrical movements biased towards the left. The kick follows a diagonal trajectory where the image (located on the left-hand side of the page) takes a "step-kick" to the right. The handedness of the kick animation may account for the differential, yet subtle, suppression in the right hemisphere relative to the center electrode. The suppression is "subtle" because it is significantly different from the suppression across the center electrode, but not the left electrode. The data support this idea. There were no significant differences between electrode sites in the jumping jacks, while perception of the kick animation produced a small difference between the center and right electrodes.

Activity at electrode Cz is thought to correspond to activity in the supplementary motor area (SMA), which lies anterior to the primary motor cortex [25]. The SMA generates an intrinsic mu-like rhythm [36] that may lead to wave attenuation across the midline. Given its role in processing movement complexity [37], the temporal structuring of movements [38], and in the preparing and planning of movements [39] and motor sequences retrieved from memory [40], the SMA may be involved in accurately processing and perceiving biological motion by recovering object information from sparse input.

Studies have shown that the SMA is activated during action execution, observation of actions and motor imagery, where motor acts are internally rehearsed in working memory without any overt motor output [41]. Likewise, the rostral portion of the SMA is selectively active when a mental representation of an action is engaged, in the absence of the overt motor action [42,43]. Researchers have hypothesized a role for SMA in terms of MNS activity in so far as mediating the processing between the superior temporal sulcus (STS) and the posterior parietal and frontal opercular cortices [44]. The idea that the SMA is part of the MNS is supported by anatomical evidence demonstrating that the posterior parietal cortex (areas PC, PE, and PEA), the

SMA (area F3 in monkeys), and STS regions are highly connected in the monkey brain [45]. This information coincides with data demonstrating that these same brain areas are activated in response to point-light biological motion, e.g., STS [41,46–48], parietal cortex [41,49], and frontal cortex [1].

Electrodes C3 and C4 correspond to activity in primary sensorimotor areas [50]. Mu rhythms in this area are thought to reflect downstream premotor cortex modulation of primary sensorimotor areas [21,28]. The dense interconnections and functional links between the premotor and motor cortex are further supported by anatomical [51] and electrophysiological experiments in primates [32,52]. In humans, support for such cortico-cortical connections has been provided by functional imaging data [53] and rTMS studies [54].

Premotor and sensorimotor areas can be activated by the observation of motion [55]. In a neuromagnetic study, Hari et al. [20] demonstrated that precentral motor activity is significantly modified when a subject observes another individual manipulating objects, albeit to a lesser extent than during action execution. They attribute this motor cortex activation as a residual function of mirror neuron activity in premotor areas. This finding suggests that when individuals perceive biological actions, an internal replica of that action is created in the premotor cortex via an observation–execution matching system (i.e. mirror neurons as simulation devices), which subsequently leads to residual activation of primary motor areas.

The perception of object-related and non-object related actions in fMRI studies have revealed that the premotor cortex is activated in a somatotopic manner [11]. This somatotopy approximately parallels the homunculus of M1 in monkeys, although with a greater amount of redundancy and overlap. The current study used point-light stimuli that are object- and non-objected related and reflect social actions. The kick animation, for example, is object-related. However, an object (ball) is not explicitly displayed but rather implied. The jumping jacks animation, on the other hand, is non-object related. The limbs (including legs, arms, and torso) of both motion types are clearly defined—they are distinctly represented by multiple point-light dots corresponding to the limb articulations of the actor. The prominent limb movements exhibited in these animations may recruit the limb and torso motor areas to a greater extent than the perception of scrambled-motion, where the perception of limbs is distorted. These inherent differences between the animations may account for the differential suppression exhibited between the two conditions, and further supports the existence of an action observation-execution matching system.

A number of investigators have argued that configural processing occurs in the perception of apparent biological motion [56,57]. In various masking experiments where point-light animations (e.g. an upright walker) have been displayed against a background of random moving dot masks and scrambled limb masks, the perception of the human actor was not impaired [58,59]. Shiffrar and colleagues [60] reported that human movement was correctly identified when subjects viewed animations of walking-stick figures through multiple apertures, while subjects were unable to detect non-biological animations of automobiles and scissors. Movement was critical for the recognition of the walker because when static images were utilized, subjects were unable to correctly identify the walker, car or scissors. This implies that non-biological and biological motions are processed differently, such that an internal representation may favor a global interpretation for biological stimuli, even when these stimuli are impoverished. In brain imaging studies, scrambled point-light biological animations do not activate the same brain areas (or do so to a lesser extent) as normal point-light animations [1,47].

Higher level top-down processing may also affect the interpretation of point-light stimuli. Research indicates that the speed at which point-light biological motion is processed is action-type dependent [61]. That is, biological actions, such as walking or climbing stairs, are recognized faster (and with more accuracy) than are social actions, such as greeting and dancing [61]. However, given enough time the social actions are correctly identified. This information suggests that humans have a system that stores motor patterns and that replicates those patterns in motor areas of the brain, in order to exert a top-down influence on the recognition of familiar sequences.

The scrambled conditions produced marginally significant enhancement (relative to baseline). This may be resolved by considering the highly sequenced nature of the motion and the inherent differences in the baseline and scrambled conditions. Some have suggested that the human visual system only needs a small pattern of familiar motion to recognize the action. These experimenters have argued that stored motor patterns may play a role in efficiently predicting, tracking and mentally animating the motion of familiar objects, such as point-light walkers. Since scrambled biological motion is highly sequenced as well, it may also recruit the same motor areas (albeit to a lesser extent) in an attempt to recruit stored motor schemas. In scrambled motion, familiar limb sequences are harder to identify and, therefore, simulate. This could explain why the perception of scrambled motion produced a slight mu enhancement, i.e., an index of reduced or absent mirror neuron engagement.

The movements in the scrambled conditions were not subtle in comparison to the white-noise baseline. The pronounced movement of dots could have partially activated motor areas but they apparently did not specifically activate mirror neuron activity. Lastly, the baseline condition did not control for attention whereas an attention task was included in the biological and scrambled-motion conditions. However, the fact that opposite effects were seen to biological and scrambled motion suggests that attention per se is not responsible for these differences.

The present results support the hypothesis that perception of point-light biological motion activates mirror neurons while scrambled versions of these same animations do not. This result is important because it suggests that sparse, familiar motion cues may be integrated into a complete human action through a process mediated by mirror neuron activity. To the best of our knowledge, this is the first study to demonstrate mu rhythm activation in response to point-light motion. Further support for this interpretation comes from a vast number of studies looking at biological motion, mirror neurons, and motor area connectivity. These studies support the idea that an action

observation-execution matching system exists. Our study further supports this claim, and illustrates that frontal mirror neurons rely on motion cues. The point-light displays used did not contain color, texture or form cues. Given the sparse information of these movements, connectivity and shape were still inferred from the coherent motion of neighboring lights. This suggests that a population of mirror-neurons in motor areas may be sensitive to motion.

This evidence is consistent with the perception-action account of visual stream processing proposed by Milner and Goodale [62,63]. They suggested that the ventral visual stream is fundamental for perception. In contrast, the dorsal stream provides high order visual information for the control of action. This conceptualization is different from the classic characterization of the functional role of the dorsal visual stream, which views it as being involved in space perception Ungerleider and Mishkin [64]. A recent study by Shmuelof and Zohary [65] points toward a dissociation between ventral and dorsal stream activation during observation of object manipulation, supporting the perception–action account. They showed that patients with damage to the ventral stream, which projects to the inferotemporal cortex, are unable to perceive the size, shape, and orientation of objects. However, some patients continue to show normal preshaping and rotation of the hand when they reach out to grasp the objects whose forms they fail to see. Other patients that have damage to their dorsal stream, which projects to the posterior parietal cortex, have difficulty using vision to control object-directed grasping movements, even though they can describe the location, size, shape, and orientation of the goal object they fail to grasp correctly.

4. Experimental procedure

4.1. Subjects

Subjects were 20 undergraduate students (16 female, 4 male) recruited through the University of California, San Diego Psychology and Cognitive Science Experiment subject pool. All subjects were at least 18 years old (mean = 19.4 years, S.D. = 1.3; range 18–22 years, with normal or corrected to normal vision). Each subject was informed about the experimental procedures and signed a consent form. Informed consent and experimental procedures were in accordance with and approved by the Institutional Review Board of the University of California, San Diego. Authors are aware of the Code of Ethics of the World Medical Association (Declaration of Helsinki) printed in the *British Medical Journal* (18 July 1964).

4.2. Experimental design & procedure

Subjects viewed two point-light biological motion animation videos (jumping jacks and kick), two matched scrambled versions of these animations, and one visual white noise. The five different videos were presented in randomized order across subjects. EEG data were collected during each of these presentations. Each video was shown for 80 s with a 1 min rest period between videos. The five videos were presented a second time, in the same order as the first run, so that a total of 160 s of EEG data were recorded per video.

The point-light biological videos were adapted from those used by other investigators [1]. They were originally created by videotaping an actor performing specific movements and then encoding the joint positions in the digitized videos [66]. Both the biological and scrambled motion sequences were composed of twelve small dots corresponding to the joints of the point-light actor (see Fig. 2). These animations were converted into vectors that were transported into Matlab so that the videos could be easily modified to create the scrambled motion controls.

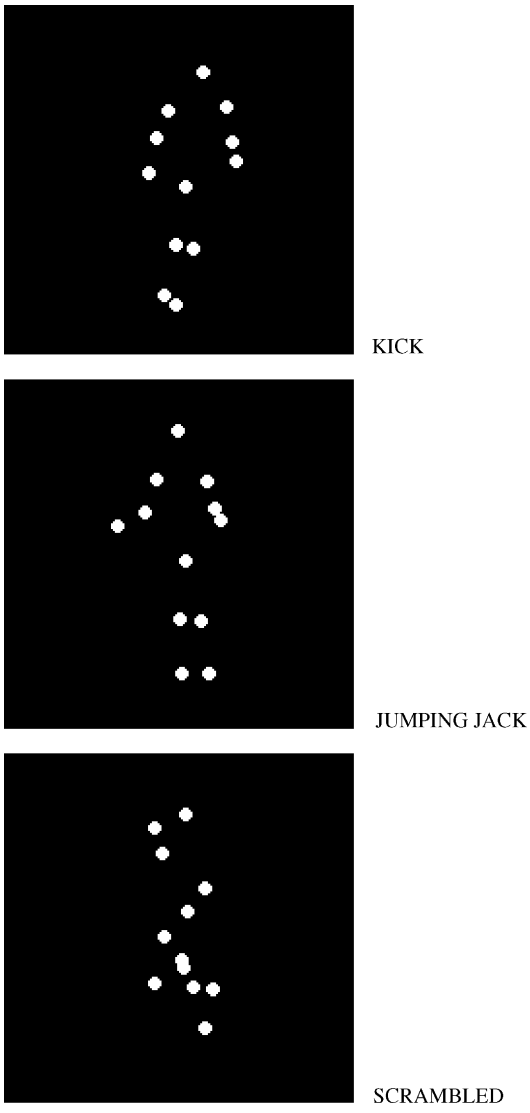

Fig. 2. Sample point-light displays for KICK, JUMPING JACKS, and SCRAMBLED actions from the motion videos.

The start positions of the point-light dots and their movement patterns across time were conserved in the biological motion animations. In the scrambled animations, the local motion cues were preserved but the temporal phases were scrambled about a central axis and the initial starting positions of the point-lights were randomized. This distorted the global motion so that a defined movement (e.g. jumping jacks) was not detectable. Similar matched scrambled animations have been used as control stimuli in previous studies of biological motion processing [47,67].

Both the biological and matched scrambled motion sequences were presented at a rate of 20 frames/s, with 5/100 s between frames using RealPlayer. All of the images were 3 in. × 3 in. in size and centered on the screen with a black background. Subjects viewed the stimuli from about 36 in. away. Therefore, the dots subtended approximately 4.5° of visual angle against a uniform black background. All of the animations were continuous and actions were looped. That is, there were no abrupt changes in the location of the dots in the transition from the final frame to the first frame of the action and subjects saw the same movement repeated every 2.5 s or approximately 32 times during the 80 s duration of the video. This allowed the natural flow of movement. The animations were adjusted so that the images appeared to be moving in place, which limited eye movements and maintained a central fixation.

To ensure that subjects attended to the stimuli across the various conditions, subjects participated in a continuous performance task. This involved an attention color-monitoring task in which the point-lights were presented in white but between four to six times during the 80-s video all the point-lights turned yellow for five frames, or one-fourth of a second. Subjects were asked to keep a mental note of this number, which they reported at the end of each block.

Following the International 10–20 method of electrode placement, 13 electrodes embedded in a cap were placed in the following scalp positions: F3, Fz, F4, C3, Cz, C4, P3, Pz, P4, T5, T6, O1, O2. Additional electrodes were placed above and below the eye to record the electrooculogram (EOG) and monitor eye blinks and other eye movements, and behind each ear (mastoids). The mastoid electrodes were used as reference electrodes by digitally linking them. Impedance was measured before and after testing in order to confirm a 5 kΩ reading at each site. After situating the cap and electrodes, subjects were seated in an acoustically and electromagnetically shielded testing chamber. Neuroscan Synamps (bandpass 0.1–30 Hz) were used to record the EEG data.

4.3. Data analysis

States of expectancy and awareness influence the EEG oscillations in the 8–13 Hz frequency recorded over the occipital cortex [68]. Therefore, the first and last 10 s of each block was eliminated from analyses in order to remove possible attentional transients associated with initiation and termination of the stimulus. The remaining 1-min segments were combined with data from the same conditions resulting in two, 2-min segments of data per condition.

Eye blinks and movement artifacts, identified by abrupt changes in the EOG waves, were removed manually prior to analyses. The number of such artifacts varied from individual to individual and from condition to condition but on average approximately 15–35 such artifacts were removed per 2 min of video. The power spectrum for this edited data was calculated by means of 1024-point Fast Fourier Transform (FFT). To control for artifacts resulting from data splicing, a cosine window was used. The data were normalized using a square-root transform. Mu suppression was calculated as the ratio of the power during the experimental conditions (in the biological and scrambled motions) relative to the power during the baseline (white noise) condition. A ratio was used to control for variability in absolute mu power as a result of individual differences such as scalp thickness and electrode placement and impedance, as opposed to mirror neuron activity. Since ratio data are inherently non-normal as a result of lower bounding, a log transform was used for analysis. A log ratio of less than zero indicates suppression whereas a value of zero indicates no suppression and values greater than zero indicate enhancement.

Mu power was initially analyzed using a three-way repeated measures analysis of variance (ANOVA) with factors of motion (biological/scrambled/baseline), movement type (jumping jack, kick), and electrode site (C3, Cz, C4). Greenhouse–Geisser corrections were applied to the degrees of freedom with only the corrected probability values reported. Because no differences occurred for movement type, data were collapsed across the two types of movements and mu suppression data analyzed using a two-way repeated measures ANOVA with factors of motion (biological, scrambled) and electrode site (C3, Cz, C4). Bonferroni corrections were applied to multiple comparisons.

Acknowledgements

We would like to thank Ayse Saygin and Andrew Stringfellow for their assistance with the creation of the stimuli.

References

[1] 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.
[2] Meltzoff AN, Decety J. What imitation tells us about social cognition: a rapprochement between developmental psychology and cognitive neuroscience. Philos Trans R Soc Lond B Biol Sci 2003;358:491–500.
[3] Rizzolatti G, Craighero L. The mirror-neuron system. Annu Rev Neurosci 2004;27:169–92.
[4] Gallese V, Keysers C, Rizzolatti G. A unifying view of the basis of social cognition. Trends Cogn Sci 2004;8:396–403.
[5] Gallese V, Fadiga L, Fogassi L, Rizzolatti G. Action recognition in the premotor cortex. Brain 1996;119(Pt 2):593–609.
[6] Rizzolatti G, Fogassi L, Gallese V. Neurophysiological mechanisms underlying the understanding and imitation of action. Nat Rev Neurosci 2001;2:661–70.
[7] Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G. Cortical mechanisms of human imitation. Science 1999;286:2526–8.
[8] di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G. Understanding motor events: a neurophysiological study. Exp Brain Res 1992;91:176–80.
[9] Hamzei F, Rijntjes M, Dettmers C, Glauche V, Weiller C, Buchel C. The human action recognition system and its relationship to Broca's area: an fMRI study. Neuroimage 2003;19:637–44.
[10] Kohler E, Keysers C, Umilta MA, Fogassi L, Gallese V, Rizzolatti G. Hearing sounds, understanding actions: action representation in mirror neurons. Science 2002;297:846–8.
[11] Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, Freund HJ. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. Eur J Neurosci 2001;13:400–4.
[12] Ruby P, Decety J. How would you feel versus how do you think she would feel? A neuroimaging study of perspective-taking with social emotions. J Cogn Neurosci 2004;16:988–99.
[13] Fadiga L, Craighero L. Electrophysiology of action representation. J Clin Neurophysiol 2004;21:157–69.
[14] Leslie KR, Johnson-Frey SH, Grafton ST. Functional imaging of face and hand imitation: towards a motor theory of empathy. Neuroimage 2004;21:601–7.
[15] Grezes J, Frith CD, Passingham RE. Inferring false beliefs from the actions of oneself and others: an fMRI study. Neuroimage 2004;21:744–50.
[16] Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G. Grasping the intentions of others with one's own mirror neuron system. PLoS Biol 2005;3:e79.
[17] Rizzolatti G, Arbib MA. Language within our grasp. Trends Neurosci 1998;21:188–94.
[18] Fadiga L, Craighero L, Olivier E. Human motor cortex excitability during the perception of others' action. Curr Opin Neurobiol 2005;15:213–8.
[19] Maeda F, Kleiner-Fisman G, Pascual-Leone A. Motor facilitation while observing hand actions: specificity of the effect and role of observer's orientation. J Neurophysiol 2002;87:1329–35.
[20] Hari R, Salmelin R, Makela JP, Salenius S, Helle M. Magnetoencephalographic cortical rhythms. Int J Psychophysiol 1997;26:51–62.
[21] Muthukumaraswamy SD, Johnson BW. Changes in rolandic mu rhythm during observation of a precision grip. Psychophysiology 2004;41:152–6.
[22] Oberman LM, Hubbard EM, McCleery JP, Altschuler EL, Ramachandran VS, Pineda JA. EEG evidence for mirror neuron dysfunction in autism spectrum disorders. Cogn Brain Res 2005;24(2):190–8.
[23] Pineda JA, Allison BZ, Vankov A. The effects of self-movement, observation, and imagination on mu rhythms and readiness potentials (RP's): toward a brain–computer interface (BCI). IEEE Trans Rehabil Eng 2000;8:219–22.
[24] Gastaut HJ, Bert J. EEG changes during cinematographic presentation. Electroencephalogr Clin Neurophysiol 1954;6:433–44.
[25] Babiloni C, Carducci F, Cincotti F, Rossini PM, Neuper C, Pfurtscheller G, Babiloni F. Human movement-related potentials vs desynchronization of EEG alpha rhythm: a high-resolution EEG study. Neuroimage 1999;10:658–65.
[26] Cochin S, Barthelemy C, Lejeune B, Roux S, Martineau J. Perception of motion and qEEG activity in human adults. Electroencephalogr Clin Neurophysiol 1998;107:287–95.
[27] Pineda JA. The functional significance of mu rhythms: translating "seeing" and "hearing" into "doing". Brain Res Brain Res Rev 2005;50:57–68.
[28] Muthukumaraswamy SD, Johnson BW, McNair NA. Mu rhythm modulation during observation of an object-directed grasp. Brain Res Cogn Brain Res 2004;19:195–201.
[29] Pfurtscheller G, Neuper C. Motor imagery activates primary sensorimotor area in humans. Neurosci Lett 1997;239:65–8.

[30] Dum RP, Strick PL. Frontal lobe inputs to the digit representations of the motor areas on the lateral surface of the hemisphere. J Neurosci 2005;25:1375–86.
[31] Shimazu H, Maier MA, Cerri G, Kirkwood PA, Lemon RN. Macaque ventral premotor cortex exerts powerful facilitation of motor cortex outputs to upper limb motoneurons. J Neurosci 2004;24:1200–11.
[32] Ghosh S, Gattera R. A comparison of the ipsilateral cortical projections to the dorsal and ventral subdivisions of the macaque premotor cortex. Somatosens Mot Res 1995;12:359–78.
[33] Johansson G. Visual motion perception. Sci Am 1975;232:76–88.
[34] Dittrich WH, Troscianko T, Lea SE, Morgan D. Perception of emotion from dynamic point-light displays represented in dance. Perception 1996;25:727–38.
[35] Pollick FE, Kay JW, Heim K, Stringer R. Gender recognition from point-light walkers. J Exp Psychol Hum Percept Perform 2005;31: 1247–65.
[36] Pfurtscheller G, Neuper C, Andrew C, Edlinger G. Foot and hand area mu rhythms. Int J Psychophysiol 1997;26:121–35.
[37] Shibasaki H, Fukuyama H, Hanakawa T. Neural control mechanisms for normal versus parkinsonian gait. Prog Brain Res 2004;143:199–205.
[38] Tanji J, Shima K. Supplementary motor cortex in organization of movement. Eur Neurol 1996;36(Suppl. 1):13–9.
[39] Cunnington R, Windischberger C, Deecke L, Moser E. The preparation and execution of self-initiated and externally-triggered movement: a study of event-related fMRI. Neuroimage 2002;15:373–85.
[40] Halsband U, Lange RK. Motor learning in man: a review of functional and clinical studies. J Physiol Paris 2006;99:414–24.
[41] Grezes J, Decety J. Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. Hum Brain Mapp 2001;12:1–19.
[42] Grafton ST, Fagg AH, Woods RP, Arbib MA. Functional anatomy of pointing and grasping in humans. Cereb Cortex 1996;6:226–37.
[43] Stephan KM, Fink GR, Passingham RE, Silbersweig D, Ceballos-Baumann AO, Frith CD, Frackowiak RS. Functional anatomy of the mental representation of upper extremity movements in healthy subjects. J Neurophysiol 1995;73:373–86.
[44] Koski L, Iacoboni M, Dubeau MC, Woods RP, Mazziotta JC. Modulation of cortical activity during different imitative behaviors. J Neurophysiol 2003;89:460–71.
[45] Seltzer B, Pandya DN. Parietal, temporal, and occipital projections to cortex of the superior temporal sulcus in the rhesus monkey: a retrograde tracer study. J Comp Neurol 1994;343:445–63.
[46] Beauchamp MS, Lee KE, Haxby JV, Martin A. FMRI responses to video and point-light displays of moving humans and manipulable objects. J Cogn Neurosci 2003;15:991–1001.
[47] Grossman E, Donnelly M, Price R, Pickens D, Morgan V, Neighbor G, Blake R. Brain areas involved in perception of biological motion. J Cogn Neurosci 2000;12:711–20.
[48] Puce A, Perrett D. Electrophysiology and brain imaging of biological motion. Philos Trans R Soc Lond B Biol Sci 2003;358:435–45.
[49] Bonda E, Petrides M, Ostry D, Evans A. Specific involvement of human parietal systems and the amygdala in the perception of biological motion. J Neurosci 1996;16:3737–44.
[50] Neuper C, Pfurtscheller G. Event-related dynamics of cortical rhythms: frequency-specific features and functional correlates. Int J Psychophysiol 2001;43:41–58.
[51] Morecraft RJ, Van Hoesen GW. Frontal granular cortex input to the cingulate (M3), supplementary (M2) and primary (M1) motor cortices in the rhesus monkey. J Comp Neurol 1993;337:669–89.
[52] Tokuno H, Nambu A. Organization of nonprimary motor cortical inputs on pyramidal and nonpyramidal tract neurons of primary motor cortex: an electrophysiological study in the macaque monkey. Cereb Cortex 2000;10:58–68.
[53] Fink GR, Frackowiak RS, Pietrzyk U, Passingham RE. Multiple nonprimary motor areas in the human cortex. J Neurophysiol 1997;77:2164–74.
[54] Rizzo V, Siebner HR, Modugno N, Pesenti A, Munchau A, Gerschlager W, Webb RM, Rothwell JC. Shaping the excitability of human motor cortex with premotor rTMS. J Physiol 2004;554:483–95.
[55] Jeannerod M, Frak V. Mental imaging of motor activity in humans. Curr Opin Neurobiol 1999;9:735–9.
[56] Thompson JC, Clarke M, Stewart T, Puce A. Configural processing of biological motion in human superior temporal sulcus. J Neurosci 2005;25:9059–66.
[57] Chatterjee SH, Freyd JJ, Shiffrar M. Configural processing in the perception of apparent biological motion. J Exp Psychol Hum Percept Perform 1996;22:916–29.
[58] Thornton IM, Vuong QC, Bulthoff HH. A chimeric point-light walker. Perception 2003;32:377–83.
[59] Hiris E, Humphrey D, Stout A. Temporal properties in masking biological motion. Percept Psychophys 2005;67:435–43.
[60] Jacobs A, Pinto J, Shiffrar M. Experience, context, and the visual perception of human movement. J Exp Psychol Hum Percept Perform 2004;30:822–35.
[61] Dittrich WH. Action categories and the perception of biological motion. Perception 1993;22:15–22.
[62] Milner AD, Goodale MA. Visual pathways to perception and action. Prog Brain Res 1993;95:317–37.
[63] Goodale MA, Milner AD. Separate visual pathways for perception and action. Trends Neurosci 1992;15:20–5.
[64] Ungerleider LG, Mishkin M. The striate projection zone in the superior temporal sulcus of *Macaca mulatta*: location and topographic organization. J Comp Neurol 1979;188:347–66.
[65] Shmuelof L, Zohary E. Dissociation between ventral and dorsal fMRI activation during object and action recognition. Neuron 2005;47:457–70.
[66] Ahlstrom V, Blake R, Ahlstrom U. Perception of biological motion. Perception 1997;26:1539–48.
[67] Servos P, Osu R, Santi A, Kawato M. The neural substrates of biological motion perception: an fMRI study. Cereb Cortex 2002;12:772–82.
[68] Klimesch W, Doppelmayr M, Russegger H, Pachinger T, Schwaiger J. Induced alpha band power changes in the human EEG and attention. Neurosci Lett 1998;244:73–6.