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RESEARCH****Research Report**

Mirror activity in the human brain while observing hand movements: A comparison between EEG desynchronization in the μ -range and previous fMRI results

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ARTICLE INFO

Article history:

Accepted 23 May 2009

Available online 3 June 2009

Keywords:

Mu rhythm

Alpha

EEG

ABSTRACT

Mu (μ) rhythms are EEG oscillations between 8–13 Hz distinguished from alpha by having more anterior distribution and being desynchronized by motor rather than visual activity. Evidence accumulating during the last decade suggests that the desynchronization of μ rhythms (μ suppression) might be also a manifestation of a human Mirror Neuron System (MNS). To further explore this hypothesis we used a paradigm that, in a previous fMRI study, successfully activated this putative MNS in humans. Our direct goal was to provide further support for a link between modulation of μ rhythms and the MNS, by finding parallels between the reported patterns of fMRI activations and patterns of μ suppression. The EEG power in the μ range has been recorded while participants passively observed either a left or a right hand, reaching to and grasping objects, and compared it with that recorded while participants observed the movement of a ball, and while observing static grasping scenes or still objects. Mirroring fMRI results (Shmuelof, L., Zohary, E., 2005. Dissociation between ventral and dorsal fMRI activation during object and action recognition. *Neuron* 47, 457–470), μ suppression was larger in the hemisphere contra-lateral to the moving hand and larger when the hands grasped different objects in different ways than when the movement was repetitive. No suppression was found while participants observed still objects but μ suppression was also found while seeing static grasping postures. These data are discussed in light of similar parallels between modulations of alpha waves and fMRI while recording EEG in the magnet. The present data support a link between μ suppression and a human MNS.

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1. Introduction

Since the seminal discovery of the Mirror Neuron System (MNS) in the monkey by Rizzolatti and his colleagues (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996) several aspects of perception and action are considered part of an integrated system assigned to understanding actions and

intentions of others (Buccino et al., 2001; Gallese and Goldman, 1998; Rizzolatti et al., 2001). More recent developments of this conceptualization generalized the principles initially discovered in the monkey to humans, expanding the role of this system to form the basis for imitation (Iacoboni et al., 1999; Iacoboni, 2005; for a recent review see Iacoboni (2009)), language development (Rizzolatti and Arbib, 1998; for a recent

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extensive discussion and commentaries see [Arbib \(2005\)](#)) and even accounting for higher-level social skills such as Theory of Mind and empathy (for reviews see [Decety and Meyer \(2008\)](#), [Gallese \(2001\)](#) and [Preston and de Waal \(2002\)](#)).

Tentative support for the existence of a human analog to the MNS has been provided primarily by neuroimaging studies in which paradigms like those used in the monkey, elicited similar activations in response to performing an act or perceiving its performance by others. For example, [Buccino et al. \(2001\)](#) used fMRI to localize brain areas that were active during the observation of object-related and non-object-related actions, made with different effectors (mouth, hand and foot). Observation of both object-related and non-object-related actions determined a somatotopically organized activation of premotor cortex, similar to that of the classical motor cortex homunculus. Furthermore, during the observation of object-related actions, additional somatotopically organized activations were found in the posterior parietal lobe. Many other studies reported similar activations in this perceptual-motor network including the ventral part of the premotor gyrus (BA 6), the inferior frontal gyrus (BA 44), as well as regions in the parietal lobe (e.g. the intra-parietal sulci) and the superior temporal gyrus extending the role of the mirror system in the monkey to a more complex mirror mechanism in humans (e.g. [Decety et al., 2002](#); [Grafton et al., 1996](#); [Grezes et al., 2003](#); [Iacoboni et al., 2005](#); [Iacoboni and Wilson, 2006](#); [Lamm et al., 2007](#); [Molnar-Szakacs et al., 2005](#); for a recent review see [Fabbri-Destro and Rizzolatti, 2008](#)).

In the last few years another neural manifestation has been tentatively associated with the MNS in humans. It refers to the suppression of the EEG amplitude in the frequency range between 8–13 Hz. Initially found over somato-sensory regions while the subject performs a motor act, these EEG oscillations were labeled μ rhythms ([Gastaut, 1952](#); for a review see [Pineda \(2005\)](#)).

Like the “alpha block” ([Berger, 1929](#); see also, for example, [Goodman et al. \(1980\)](#)), the suppression of μ rhythms is considered to reflect an event-related desynchronization (ERD) of the EEG caused by an increase in neural activity ([Kuhlman, 1978](#)). It should be noted, however, that μ rhythms are dissociated from the alpha waves on several important dimensions. First, magneto-encephalographic (MEG) studies localized the cortical sources of the alpha waves around the parieto-occipital sulcus and the μ rhythms along the somato-sensory cortex ([Hari et al., 1997](#)). Consequently, the μ EEG rhythms show a more anterior focus with some inter-hemispheric asymmetry compared to the more posterior and bilateral distribution for the classical alpha oscillations ([Kuhlman, 1978](#); [Pfurtscheller, 1989](#)). Second, in contrast to alpha, μ rhythms are not modulated primarily by visual stimulation, but rather are desynchronized and their power attenuated by the onset of motor activity ([Gastaut, 1952](#)).

Although several studies provided evidence tentatively linking the μ rhythms modulation with MNS phenomena (e.g. [Cochin et al., 1998](#); [Cochin et al., 1999](#); [Muthukumaraswamy et al., 2004](#); [Oberman et al., 2005](#); [Ulloa and Pineda, 2007](#); [Yang et al., 2009](#)) the characteristics of μ modulation and the relations between this electrophysiological manifestation and the MNS are insufficiently elaborated to date. A particularly intriguing question is whether the experimental manipulations known to activate the MNS would similarly modulate the fMRI and μ ERD, both presumed to be signatures of this system in humans. In addition to linking both effects to a similar (motor) neural mechanism, confirming that both fMRI and EEG studies display comparable modulations to similar experimental procedures should strengthen the notion that we are indeed looking at a human analog of the monkey's MNS. To this end, our current goal was to examine the pattern of μ suppression using the same stimuli and a similar design to that previously used in an fMRI study, which reported MNS-like phenomena in humans ([Shmuelof and Zohary, 2005](#)).

In [Shmuelof and Zohary's \(2005\)](#) fMRI study, participants passively observed different hand movements. Either the left or the right hand was observed reaching to and grasping either different objects or the same object, either in the same repetitive way or in different grasping variations. Comparing the amount of adaptation while observing repetitive and non-repetitive movements, these authors found higher adaptation for the former than the latter condition in parietal areas, which are putatively part of the MNS in humans, such as anterior intra-parietal sulcus (aIPS; cf. [Culham et al., 2003](#); [Rizzolatti et al., 1996](#)). Importantly, they showed a greater BOLD signal in the hemisphere contralateral to the moving hand (i.e., contralateral preference).

In the present study we used the same stimuli as used by [Shmuelof and Zohary \(2005\)](#), investigating the differences in μ suppression following the observation of different grasping of objects. We explored μ suppression and its lateralization while participants viewed either a right or a left hand grasping the same or different objects, replicating the repetitive and non-repetitive conditions from the fMRI study. If the fMRI pattern is seen in EEG, we expected to find more μ suppression in the non-repetitive relative to the repetitive conditions and an interaction between the observed hand and the lateralization of μ suppression, which should be larger in the hemisphere contralateral to the observed hand.

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2. Results

Relative to the non-biological movement baseline condition, μ suppression was evident primarily in regions above the somato-sensory cortex ([Fig. 1](#)).

On the basis of this distribution and previous reports (e.g. [Cochin et al., 1998](#); [Muthukumaraswamy et al., 2004](#); [Oberman et al., 2005](#)), we focused on the modulation of the μ rhythm at the central-lateral sites C3 and C4, which are putatively sensitive particularly to sensory-motor hand areas. In addition, since the μ suppression was conspicuous primarily at central sites, we also analyzed it more medially, at C1 and C2. A suppression index (see Experimental procedures) was analyzed first using an omnibus ANOVA with repeated measures. The factors were Hand (left, right), Hemisphere (left, right), Site (medial, lateral), Grasping (repetitive, different) and Object (same, different).

A main effect of Hemisphere, showed that suppression was larger at right (log ratio = −0.16) than at left hemisphere sites [log ratio = −0.13; $F(1,23) = 4.3$, $MSe = 0.27$, $p < 0.05$]. Also, a main effect of Grasping, showed that suppression was larger for different (log ratio = −0.17) than for repetitive grasping [log

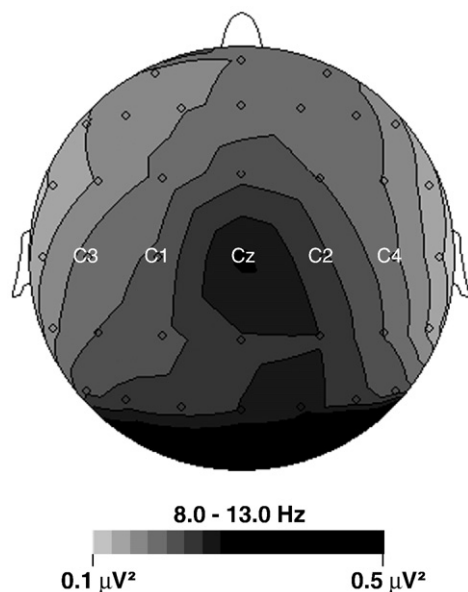


Fig. 1 – The distribution of mu suppression, as calculated by subtracting the mean EEG power in the 8–13 Hz range recorded during the “Different grasping of different objects” condition from the “balls” baseline condition. Note the spatial distinction between the desynchronization at the occipital lobes, probably reflecting the modulation of alpha and the more anterior distribution of the μ suppression.

ratio = -0.12; $F(1,23)=4.6$, $MSe=0.08$ $p<0.05$). There were no other significant main effects (all $F_s<1.0$).

There was no Hemisphere \times Hand interaction [$F(1,23)=1.0$], but this interaction was modulated by a significant second-order Hemisphere \times Hand \times Site interaction [$F(1,23)=15.1$, $MSe=0.003$, $p<0.001$], which suggested that the Hemisphere \times Hand interaction was different at more medial and more lateral sites (Fig. 2). The analysis of this second-order interaction was based on separate ANOVAs for the lateral

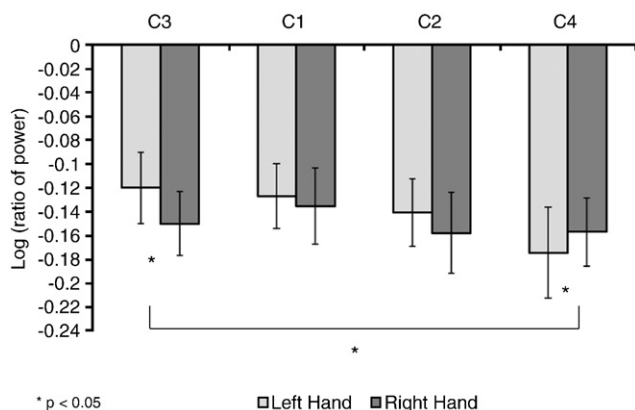


Fig. 2 – Mu suppression at the central electrodes expressed as log of the ratio of the power as a function of the observed hand. Note that the suppression is higher at lateral sites over the hemisphere that is contralateral to the observed moving hand. This interaction is evident at the more lateral (C3 and C4), but not at the more medial sites (C1 and C2).

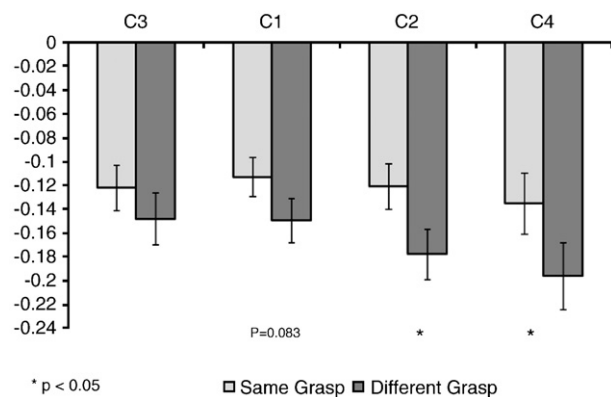


Fig. 3 – Mu suppression expressed as the log of the ratio of the power in the different and same grasp conditions. Note that at all sites the suppression is larger in the non-repetitive than in the repetitive conditions, but this effect is significant only at right hemisphere sites.

and medial sites. These analyses revealed indeed, that the Hemisphere \times Hand interaction was significant at the more lateral sites [C3 versus C4; $F(1,23)=4.4$, $MSe=0.012$, $p<0.05$], but not at the more medial sites [C1 versus C2; $F(1,23)<1.0$]. The significant interaction at the more lateral sites revealed larger μ suppression at C3 (left hemisphere) than at C4 (right hemisphere) while observing the movement of the right hand and, vice versa, larger μ suppression at C4 than at C3 while observing the movement of the left hand. The Hemisphere \times Hand interaction at the lateral sites was also qualified in this analysis by a second-order interaction with Object [$F(1,23)=5.1$, $MSe=0.04$, $p<0.05$]. Separate ANOVAs for the repetitive and same Object conditions revealed that the Hemisphere \times Hand interaction was significant when the grasped objects differed [$F(1,23)=8.6$, $MSe=0.008$, $p<0.05$] but not when they were the same [$F(1,23)<1.0$].

The main effect of Grasping was qualified by a significant Grasping \times Hemisphere interaction [$F(1,23)=16.3$, $MSe=0.002$, $p<0.001$] suggesting that the Grasping effect was larger at right than at left hemisphere sites. This interaction, however, was also qualified by a second-order interaction of Grasping \times Hemisphere \times Site [$F(1,23)=4.8$, $MSe=0.001$, $p<0.05$]. Separate ANOVAs showed that the Hemisphere \times Grasping interaction was significant for the more medial sites [$F(1,23)=10.0$, $MSe=0.001$, $p<0.005$] as well as for the more lateral sites [$F(1,23)=16.0$, $MSe=0.002$, $p<0.001$]. For both, the Grasping effect was more conspicuous over the right hemisphere than over the left (Fig. 3).

Two additional conditions were examined. The first was a condition in which different tools were shown in isolation (Tools), and the second were static pictures (Static) depicting different grasping types of different objects (see Experimental procedures).¹ As expected, no suppression was found for the Tools condition relative to baseline (at no site was the log ratio of the difference significantly different from zero [$t(23)<1.0$ for

¹ These conditions were not included in Shmuelof and Zohary's (2005) study, and could not be nested in the previous design. Therefore these analyses were performed separately rather than being included in the omnibus ANOVA.

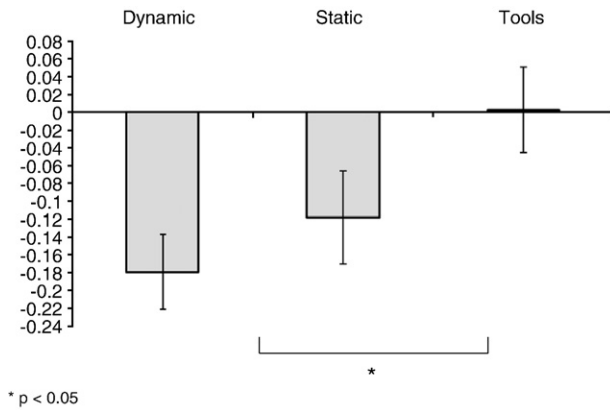


Fig. 4 – Mu suppression condition expressed as the log of the ratio of the power, collapsed across sites, in the dynamic (“Different grasp–Different objects”) and static conditions and the Tools conditions.

all tests)). In contrast, the EEG power in the μ range in response to Static pictures was significantly suppressed relative to baseline [$t(23) = -3.5, p < 0.005$]. There were no additional main effects or interactions for Hand, Hemisphere or Site. Interestingly, although numerically the suppression looked greater in the dynamic condition than in the static condition (Fig. 4), this difference was not statistically significant [$F = 1.749, MSe = 0.204, p = 0.199$].

3. Discussion

The goal of this study was to further explore the μ rhythm as an index of mirror neuron activity in humans. To achieve this goal we compared the pattern of μ suppression induced by grasping with patterns of fMRI indices of human cortical activity, as found in a previous study that demonstrated perceptual–motor mirror manifestations (Shmuelof and Zohary, 2005). By and large, the current results validated the correspondence between the EEG and fMRI manifestations of

the MNS in humans: The μ suppression recorded over Rolandic cortical regions was smaller in response to seeing repetitive movements than in response to seeing movements in which the grasping gestures changed along with changes in the grasped object. Furthermore, the μ suppression recorded over the hemisphere contralateral to the observed moving hand was larger than that recorded over the hemisphere ipsilateral to the moving hand. Both effects replicate, in fact, the pattern reported by Shmuelof and Zohary in their fMRI experiment. Interestingly, the hemispheric laterality effect in the present study was more pronounced at the more lateral sites, putatively placed closer to the hand region in the sensory–motor homunculus. As far as we know, this result is new in the μ literature, where most studies reported bilateral suppression following observed motion, with no significant difference between hemispheres (e.g. Muthukumaraswamy et al., 2004).

A possible account for the lateralization of μ suppression in the present study is that despite instructions, participants inadvertently activated muscles in the hand that matched the observed grasp. Although we continuously monitored their behavior using a video-camera, and did not observe any overt hand movements, since we did not record EMG we cannot be sure that covert muscle contractions did not occur. However, other studies reported that even when actual movements have been requested, μ suppression was larger in the hemisphere contralateral to the planned moving hand prior to the initiation of the movement (Stancak and Pfurtscheller, 1996). Similar contralateral preponderance was reported in MEG studies of “Rolandic rhythms” modulated by somato-sensory stimulation, as well as self-paced finger movements (Salenius et al., 1997). Although considering the contralateral cortical control of the hands such asymmetry should be expected, it is interesting to find the same pattern in the current study in which participants observed hand movements but did not move the hands overtly. Yet, the possibility that this asymmetry reflects actual rather than simulated muscle contraction is a caveat that needs to be addressed in the future.

Also intriguing is that Stancak and Pfurtscheller (1996) found that right-handed participants showed larger lateralization of μ -rhythms ERD prior to right-finger as compared to left-finger

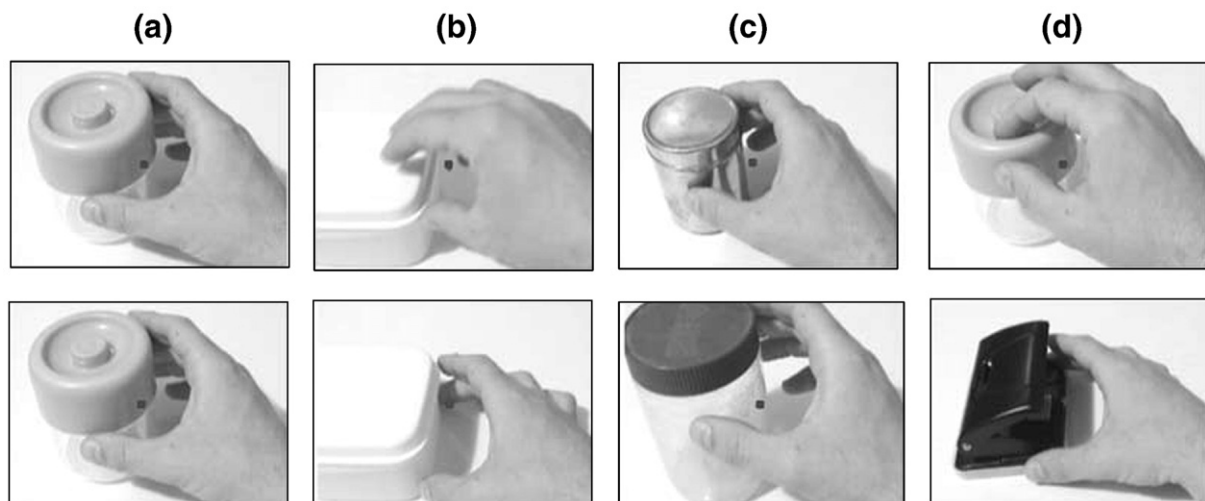


Fig. 5 – Examples of the stimuli used (still-pictures of grasping examples are provided). (a) Same grasp, same object; (b) Different grasp, same object; (c) Same grasp, different object; (d) Different grasp, different object.

flexion. They interpreted this finding suggesting that it might reflect a higher motor specialization in the dominant hemisphere. Since all our participants were right-handed, the present findings do not address the issue of handedness directly. Nevertheless, it is worth noting that the current laterality effects were also larger in response to seeing right hand movements than in response to seeing left hand movements.

Laterality aside, although EEG and fMRI were not recorded simultaneously in this study, the correspondence between the pattern of μ suppression (i.e., EEG desynchronization) and the pattern of BOLD signal changes in experiments tapping the human MNS is noteworthy. The same conditions that enhanced the BOLD signal reduced the EEG power in the μ range. For example, the largest suppression was found in the “Different grasps–Different objects” condition, the same condition in which the BOLD signal change in the aIPS was the highest (Shmuelof and Zohary, 2006). Perhaps not surprising, a similar inverse relationship was found between the amplitude of alpha rhythms recorded at posterior temporal sites and regional cerebral blood flow (rCBF) in the occipital lobes (Sadato et al., 1998) as well as BOLD signals in the parietal and visual cortices (Feige et al., 2005; Goldman et al., 2002; Laufs et al., 2003a). Although, as mentioned in the Introduction, the antecedents of the μ and alpha suppression are distinguished, both these EEG rhythms are desynchronized when the relevant neural networks (motor and visual, respectively) are activated (e.g. Pfurtscheller et al., 1996). Hence, as previously suggested, synchronous EEG oscillations within the range of 8–13 Hz may be a general manifestation of reduced cortical activity (“idling rhythms”; Pfurtscheller and Aranibar, 1977), possibly modulated by the thalamus (Feige et al., 2005; Steriade and Llinas, 1988) and desynchronized by the initiation of cortical activity in a multitude of functional neural networks. In other words, whereas different neural mechanisms might account for the desynchronization of cortical rhythms in the 8–13 Hz range, all EEG rhythms within this range, per se, might reflect a general mechanism of cortical idling. A more extensive elaboration of this hypothesis is outside the scope of the present report. However, it clearly calls for additional studies in which experimental procedures would allow a better comparison between the modulation of alpha and μ EEG rhythms, as well as studies in which μ suppression and changes in the BOLD signal are recorded simultaneously.

Finally, it is also interesting to note that static pictures of grasping were enough to induce μ suppression, although with no further differences between hemispheres or the hands viewed. This pattern might be a manifestation of canonical neurons (Grezes et al., 2003). However, it could also hint to the possibility that μ suppression can be induced to some extent by only suggesting biological motion even without actually observing it. Studies showing μ suppression during motor imagery tasks (e.g. Pfurtscheller et al., 2006) seem to support such a possibility. Alternatively, it may be that the fast viewing of a sequence of grasping pictures elicited an illusion of motion, and thus suppression occurred.

In conclusion, this paper provides further evidence for the proposed relationship between a putative human MNS and the ERD observed in the μ EEG rhythms. The results demonstrated comparable modulations of cortical activity as evidenced by fMRI and EEG while participants performed tasks that tap the mirror activity of a perceptual–motor system. Additional

investigations should include simultaneous recording of EEG and fMRI while manipulating different characteristics of the MNS and its putative development in humans.

4. Experimental procedures

4.1. Participants

The participants were 24 undergraduates (9 male) from the Hebrew University ranging in age from 20 to 28 (mean age 24.38). They participated in the experiment for payment or course credit. All participants were right-handed, reported normal or corrected to normal visual acuity and had no history of psychiatric or neurological disorders. They signed an informed consent, which was approved by the Hebrew University ethical committee.²

4.2. Task, materials and design

The task was a modified version of that used by Shmuelof and Zohary (2005). The stimuli were 18 black and white video clips, 80 s long presenting a hand movement, as follows: Right hand clips were composed of 900–1500 footages of a right hand reaching to a small object (e.g. jars, cups, scissors) from the right side, grasping the object in different ways and releasing (examples are depicted in still images and presented in Fig. 5). The left hand clips were generated by a “flip horizontal” operation on the footages (see Shmuelof and Zohary, 2005).

A $2 \times 2 \times 2$ factorial design contrasted a repetitive grasp with different grasps of the same object, or of different objects, performed with the left or the right hand. Hence, following Shmuelof and Zohary, for each hand there were 4 experimental conditions: (1) Same grasp–Same object; (2) Different grasps–Same object; (3) Same grasp–Different objects; (4) Different grasps–Different objects. There were two Same-object conditions — one depicting a cup and one a jar, which, after ensuring there was no difference between them, were later collapsed. The baseline condition consisted of balls moving from side to side, once from the left and once from the right. This baseline block was presented twice, randomly intertwined among the experimental conditions. An additional baseline was used, identical to Shmuelof and Zohary’s “scramble” condition. In this condition an object manipulation clip was decomposed to frames (24 frames a second), and every frame was spatially scrambled (36×24 fragments in each frame), ensuring that the picture could no longer be recognized. This condition also appeared 4 times within the experiment. Since the pattern of suppression relative to this baseline was very similar to that observed relative to the moving balls, we preferred using the latter since it supported the hypothesis that the suppression was induced by a biological movement (rather than by a movement of any kind). Two additional conditions,

² Four additional participants were tested but showed no μ suppression. These participants have been replaced. The replacement was made because our main interest was in the modulation of μ suppression by different conditions rather than in the absolute level of suppression. To this end, we considered the data derived from these participants uninformative.

not appearing in Shmuelof and Zohary's study, were also contrasted with the above baseline: (1) Static pictures of different grasping of different objects (Fig. 5), taken from the video clips, once presenting a right hand and once a left. This condition was presented in order to investigate whether μ suppression can be manipulated by the image of grasping itself without actual movement; (2) Pictures of different tools, presented in order to make sure that the tools themselves do not affect the μ rhythm. Since right or left conditions were irrelevant, this condition was presented twice. Both conditions were 80 s long, during which the static pictures changed at a rate of a second a picture. Altogether there were 24 blocks of 80 s each (a total of 32 min). Between every four blocks there was a break in which the participants could rest, and the experiment renewed at their request. All the experimental control and baseline blocks were randomized.

The video clips were presented on a monitor 60 cm away from the subject's eyes with the stimuli subtending approximately 14° of visual angle. A fixation point appeared throughout the experiment. To ensure that, on the one hand, participants maintained attention on the screen throughout the experiment and, on the other hand the responses would not require overt motor activity such as pressing buttons, the participants were asked to engage in a monitoring task (see Pineda and Oberman, 2006). Between four and seven times during the 80-second video clip, the stimuli stopped moving for approximately 1 s. Participants sat comfortably in an armchair, were instructed to avoid movements while counting the number of times a stop occurred, and to report their count upon completion of each trial block. They were not allowed to use their fingers for counting and received feedback on their accuracy.

4.3. Data acquisition and analysis

4.3.1. EEG recording

The EEG analog signals were recorded continuously by 64 Ag-AgCl pin-type active electrodes mounted on an elastic cap (ECI) according to the extended 10–20 system, and from two additional electrodes placed at the right and left mastoids, all reference-free. Eye movements, as well as blinks, were monitored using bipolar horizontal and vertical EOG derivations via two pairs of electrodes, one pair attached to the external canthi, and the other to the infraorbital and supraorbital regions of the right eye. Both EEG and EOG were sampled at 1024 Hz using a Biosemi Active II system (www.biosemi.com).

4.3.2. Data processing

Data were analyzed using Brain Vision Analyzer software (Brain Products; www.brainproducts.com) and house-made Matlab routines. Raw EEG data was 0.5 Hz high-pass filtered (24 dB) and re-referenced off line to the average of the two mastoids. Eye movements were corrected using an ICA procedure (Jung et al., 2000). Remaining artifacts exceeding $\pm 100 \mu\text{V}$ in amplitude at the central sites were rejected. Because EEG oscillations in the 8–13 Hz frequency are influenced by states of expectancy and awareness (e.g. Laufs et al., 2003b), and the μ frequency band overlaps with the posterior alpha band, it is possible that our frontal recordings might be affected by this posterior activity, which is more related to

visual processing. Therefore, as suggested by Pineda and Oberman (2006), the first and last 10 s of each block were excluded from the analysis to reduce the possibility of attentional transients due to the initiation and termination of the stimulus. A 1-min EEG data following the initial 10 s was obtained, which was further segmented into segments of 2 s, beginning at the start of the segment. For each such segment, the integrated power in the 8–13 Hz range was computed using a Fast Fourier Transform (FFT) performed at 0.5 Hz intervals (based on 2048 points per segment, using a Hanning window).

The dependent variable for statistical analyses was the ratio of the power during the experimental conditions relative to the power during the baseline conditions (right hand movements were divided by the balls moving from the right and left hand movements by the balls moving from the left). A ratio (as opposed to a simple subtraction) was used to control for variability in absolute μ power as a result of individual differences such as scalp thickness and electrode impedance (Pineda and Oberman, 2006). Since ratio data are inherently non-normal as a result of lower bounding, a log transform was also 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. Based on previous studies as well as on the observed distribution of the group-average μ suppression (Fig. 1) we computed and analyzed the suppression at the lateral sites C3 and C4 and the more medial sites C1 and C2.

Acknowledgments

This study was supported by an Israeli Science Foundation (ISF) grant to Shlomo Bentin. We thank Lior Shmuelof and Ehud Zohary for kindly sharing their stimuli with us.

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