Brief report

Tool perception suppresses 10–12 Hz μ rhythm of EEG over the somatosensory area

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ABSTRACT

The perception of tools vs. other objects has been shown to activate the premotor (BA6) and somatosensory cortex (BA3), which neurally represent object affordance related to tool manipulability (Proverbio et al., 2011). The earliest tool/non-tool discrimination is represented by increased anterior negativity (210–270 ms) in response to tools. In this study, we analyzed μ desynchronization with wavelet analysis based on EEG recordings in response to 300 familiar objects vs. tools in 11 participants. The results showed an early 140–175 ms μ desynchronization over centro-parietal sites at approximately 10–12 Hz during tool perception. The surface scalp distribution of μ power is compatible with neural generators located in the somatosensory cortex, but no source analysis was performed. These results support the hypothesis that there is a temporal and functional relationship between the rapid and transient μ suppression over the centro/parietal area and the successive increase in time-locked post-synaptic potentials (ERPs) in regions processing tool motor affordance.

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1. Introduction

Previous reports have shown that premotor and/or motor cortices are activated during both action execution and observation (e.g., Fadiga et al., 2005; Grèzes and Decety, 2001; Rizzolatti et al., 1996; Turella et al., 2012). These cortical areas may be part of a human mirror neuron system (MNS) comparable to that discovered in macaques (Rizzolatti and Craighero, 2004). These neurons, "mirroring" the behavior of another, as if the observer was itself performing the action, have been recorded in humans in regions such as the premotor cortex and the inferior parietal cortex, in many tasks involving action perception and execution. Interestingly, also viewing graspable tools, but not other objects, activates motor-related regions such as the ventral premotor area, the posterior parietal cortex and the posterior middle temporal gyrus (Chao and Martin, 2000). It has been demonstrated that viewing a manipulable object automatically activates its motoric properties, including its affordance and the representation of the associated motor interaction. This has been shown for example by Grafton et al. (1997) with positron emission tomography (PET). In this pioneristic study it was shown an activation of the left premotor cortex during tool observation, possibly because it contained the motor representation of hand and arm movements. However, this first important study lacked the critical control of other non manipulable objects

(i.e., non-tools). It was later demonstrated with fMRI (Creem-Regehr and Lee, 2005) that viewing graspable tools, but not shapes, activates motor-related regions of the cortex (namely, the posterior middle temporal gyrus, ventral premotor area and posterior parietal cortex), therefore the MNS. The researchers concluded that the functional identity of graspable objects influences the extent to which they are associated with motor representations. Finally, some authors (Cardellicchio et al., 2011) have related the motor cortex activation during visual perception of tools with the actual possibility of reaching for the objects (i.e., to the spatial location of the objects and their motor affordances in relation to the observer).

The activity of the motor and the somatosensory cortex (during action execution, observation or imitation) gives rise to the desynchronization of the "resting state" represented by the rolandic μ rhythm of human EEG. Mu (μ) rhythm is a spontaneous oscillatory rhythm of human electroencephalogram (EEG)/magnetoencephalogram (MEG) that has 8–13 Hz frequency, appearing maximally over the central rolandic or sensorimotor area during a relaxed state. It is generally accepted as the idling rhythm engendered from the synchronized neurons involved in the thalamo-cortical loop (Matsumoto et al., 2010). The mu rhythm is attenuated by tactile stimulation, movement execution, and motor imagery, which are also referred to as event-related desynchronization (ERD). Since it has been established a correlation between an activation of regions belonging to the mirror neuron system (MNS) and a mu desynchronization over central or centro/parietal scalp sites, μ suppression has been successfully used to measure mirror neuron activity in both human adults (Behmer and Jantzen, 2011; Pfurtscheller et al., 2006) and infants (Nyström et al., 2011). For

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Fig. 1. Example of stimuli from the two categories.

example, Muthukumaraswamy and Johnson (2004) recorded EEG while a group of participants observed and imitated the precision grip of a manipulandum, showing lower amplitudes of μ rhythm amplitudes during observation of the precision grip than during observation of a simple hand extension without object interaction. In another study (Muthukumaraswamy et al., 2004) in which the precision grip of a manipulandum was compared with an empty grip using the same hand position, it was found that that the magnitude of the μ rhythm was significantly lower for the object grip condition than for the empty grip condition.

For tool perception, the suppression of the μ rhythm during tool vs. non-tool visual perception was an unprecedented finding. For example, μ suppression (8–13 Hz) has been shown in a previous ERP study (Perry and Bentin, 2009) during passive perception of reaching and grasping an object with the left and right hand (over the contralateral hemisphere at central-lateral sites: C3, C4), but not while observing still objects. In that study, it is possible that, without a visible grasping hand, the objects per se did not coercively evoke the image of a manipulative action ("I can grasp a jar but I cannot manipulate it.").

It was previously demonstrated (Proverbio et al., 2011) that viewing manipulable objects significantly activated the left somatosensory and premotor cortices, these regions being the neural generators of the synchronized surface electrical activity recorded in the 210–270 ms time window. According to the current model of μ suppression (Hari et al., 2006; Schnitzler et al., 2000), one might therefore expect a larger desynchronization of μ rhythm (over the somatosensory cortex) while viewing non-tools as compared to manipulable objects.

The purpose of the present study was to further investigate this matter by analyzing EEG oscillation frequencies, as a function of stimulus type, recorded on the same subjects and in response to the same stimuli to determine whether a μ desynchronization actually occurred when viewing manipulable vs. non-manipulable objects.

2. Material and methods

2.1. Participants

Participants were 11 individuals belonging to the group ($N = 15$) described in Proverbio et al. (2011). Some participants were discarded because of EEG artifacts (such as slow drifts or excessive impedance in selected electrodes), which heavily compromised whole-scalp EEG Fourier analysis. The final group therefore consisted of 6 men and 5 women with normal vision and a mean age of 23.2 years (SD = 2.32).

All participants were right-handed as determined by the Edinburgh Handedness Inventory. Experiments were conducted with the understanding and written consent of each participant according to the Declaration of Helsinki (BMJ 1991;302:1194), with approval from the Ethical Committee of the University of

Milano-Bicocca and in compliance with APA ethical standards for the treatment of human volunteers (1992, American Psychological Association).

2.2. Stimuli and procedure

The stimulus set, described in the ERP study (Proverbio et al., 2011), consisted of 300 pictures of familiar objects (see Fig. 1), half of which were manipulable and half of which were non-manipulable. The stimuli were matched for size (6°43′01″), average luminance (tools = 59.2, non-tools = 53.43 cd/cm²) and perceptual familiarity (on a 3-point scale with 2, 1 and 0 being extremely, moderately and somewhat familiar, respectively; tools = 1.71, non-tools = 1.68, t-value = −0.98; p = 0.33). Each slide was presented for 1000 ms at the center of a screen with an ISI of 1500–1900 ms.

The task consisted of responding as accurately and quickly as possible to photos of live plants (probability 12%) that were randomly presented and intermixed with tools and non-tools. Subjects responded by pressing a response key with the index finger of the left or right hand. The two hands were used alternately during the recording session. The order of the hand and task conditions was counterbalanced across subjects.

Participants sat in an acoustically and electrically shielded cubicle. They faced a PC screen located 120 cm from their eyes. They were instructed to gaze the fixation point, and to avoid any eye or body movements during the recording session.

2.3. EEG recording and analysis

EEG was continuously recorded from 128 scalp sites using tin electrodes mounted in an elastic cap (Electro-Cap). Sampling rate was 512 Hz. Horizontal and vertical eye movements (EOG) were also recorded. Linked ears served as the reference lead. The EEG was recorded using EEProbe recording software (ANT Software, Enschede, The Netherlands) and was amplified using an ANT digital amplifier with a half-amplitude band pass of 0.016–100 Hz. The EEG and EOG were amplified with a half-amplitude band pass of 0.016–100 Hz. Electrode impedance was maintained below 5 kΩ. EEG epochs were synchronized with the onset of stimuli presentation. Computerized artifact rejection was performed to discard epochs in which eye movements, excessive muscle potentials or amplifier blocking occurred. The artifact rejection criterion was a peak-to-valley amplitude exceeding ±50 μV; the rejection rate was ~5%.

EEG epochs were synchronized with the onset of stimuli presentation. ERPs were averaged off-line from −100 to 1000 ms and time-locked to the onset of visual stimulation. The number of EEG epoch per condition was about 145. Mu power (in μV²/Hz) was computed for each participant and condition (tools vs. non-tools) for the entire post-stimulus time range (0–1 s) (as in Nyström et al., 2011), and the presence of a mu desynchronization during the same time window used for ERP averaging in a previous study (Proverbio et al., 2011) was tested in a selected set of central and centro-parietal electrodes (CPz, CCP1h, CCP2h, C1, and C2). Additionally, for each participant and condition, the mean power of the 8–9, 9–10, 10–11 and 11–12 Hz EEG frequency bands was quantified separately for the CPz, CCP1h, CCP2h, C1, and C2 electrode sites in the two time latencies of 140 and 175 ms, which have been identified as regions of interest by analyzing the time–frequency plots of mu amplitude in wavelet analysis as performed by previous authors (Csibra et al., 2000) with gamma rhythm. The location of non-standard electrode sites is visible in topographic maps of Fig. 2.

Electrode selection was also justified by previous literature (Behmer and Jantzen, 2011; Nyström et al., 2011; Perry and Bentin, 2009; Perry et al., 2011; Pfurtscheller et al., 2006; Pineda et al., 2011), which precisely indicated a scalp localization of mu desynchronization over central (Cz, C1, C2, C3, and C4) and centro-parietal sites (CP3 and CP4).
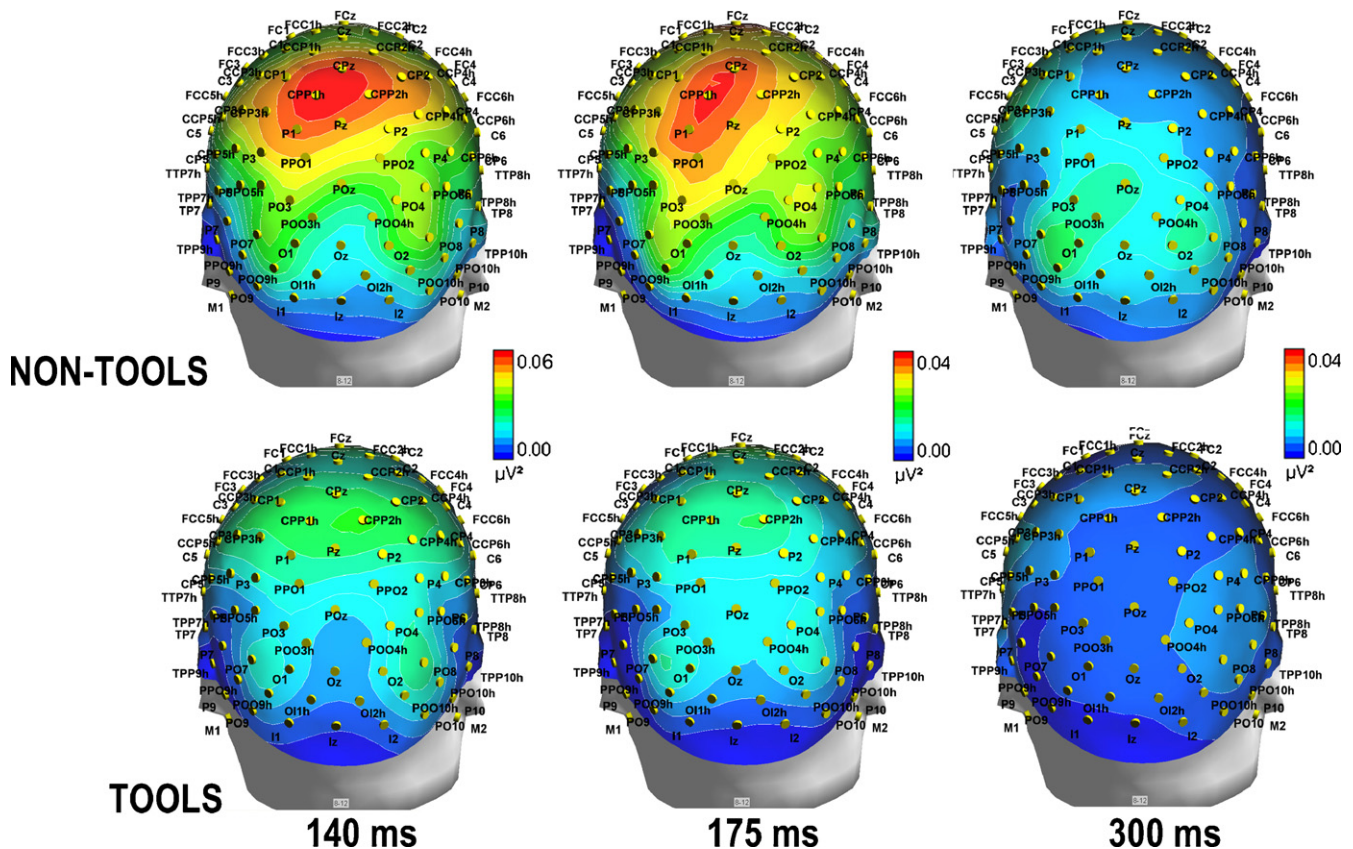
Fig. 2. Isocolour topographical maps of scalp distribution of μ rhythm (8–12 Hz) recorded at 3 different time ranges (namely: 140, 175, 300 ms post-stimulus) in response to tools and non tools.

Recorded values underwent two repeated measure ANOVAs (one for each time window), with factors of object manipulability (tools vs. non-tools), frequency band (8–9, 9–10, 10–11 and 11–12 Hz), and recording electrode (CPz, CCP1h, CCP2h, C1, C2). A post hoc Tukey test was used for mean comparisons. All statistically significant findings are reported below.

3. Results

The topographical maps of Fig. 2 show the surface scalp distribution of mu power measured in the 8–12 Hz range at 3 different latency times: namely, 140 ms, 175 ms, and 300 ms post-stimulus. It can be seen that Mu power was strongly focused over the centro-parietal area, while the alpha rhythm (which was almost absent) is localized more posteriorly over the occipital sites. It can also be noted a dissociation between alpha and mu rhythms as a function of time course. Indeed, while 8–12 Hz EEG rhythm was much stronger at 140 than 300 ms over central sites (gradually decreasing in Mu power) the alpha rhythm over the occipital area remained pretty constant. The scalp distribution of mu power was absolutely consistent with previous EEG literature. The comparison between stimulus types shows a strong effect of mu desynchronization in response to tools, as compared to non-tools, especially between 140 and 175 ms post-stimulus latency.

The statistical analysis performed on mean μ power recorded in the 0–1 s time window revealed a main effect of object manipulability ($F_{1,9} = 8.19$; $p < 0.019$), with a strong μ power in response to non-tools and a μ desynchronization in response to tools (see Fig. 3).

The ANOVA performed on μ power at 140 ms as a function of frequency band showed the significance of object manipulability per se ($F_{1,9} = 6.17$; $p < 0.03$) with higher μ power in response to non-tools ($0.06 \, \mu V^2$, SE = 0.06) than tools ($0.04 \, \mu V^2$, SE = 0.04). The further interaction of manipulability × electrode ($F_{4,36} = 4.26$;
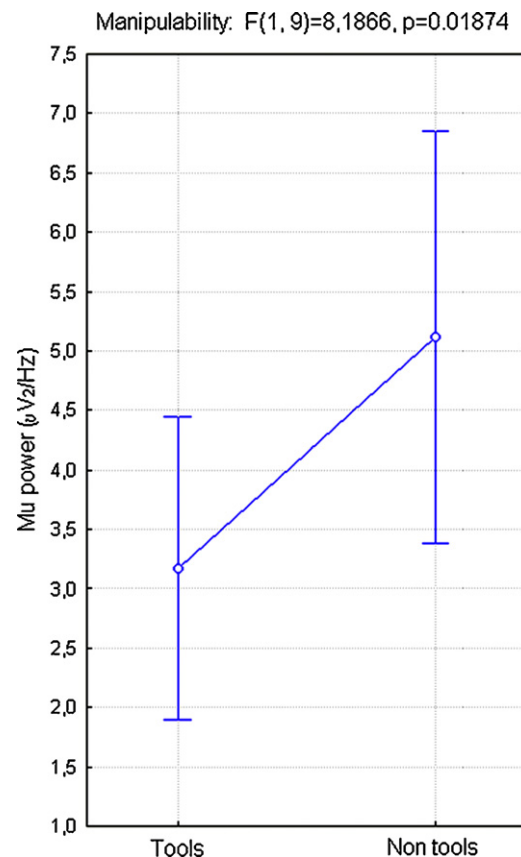

Fig. 3. Average power of μ rhythm (8–12 Hz) recorded in 10 Ss in the whole time window (1 s) after stimulus onset, as a function of stimulus class.
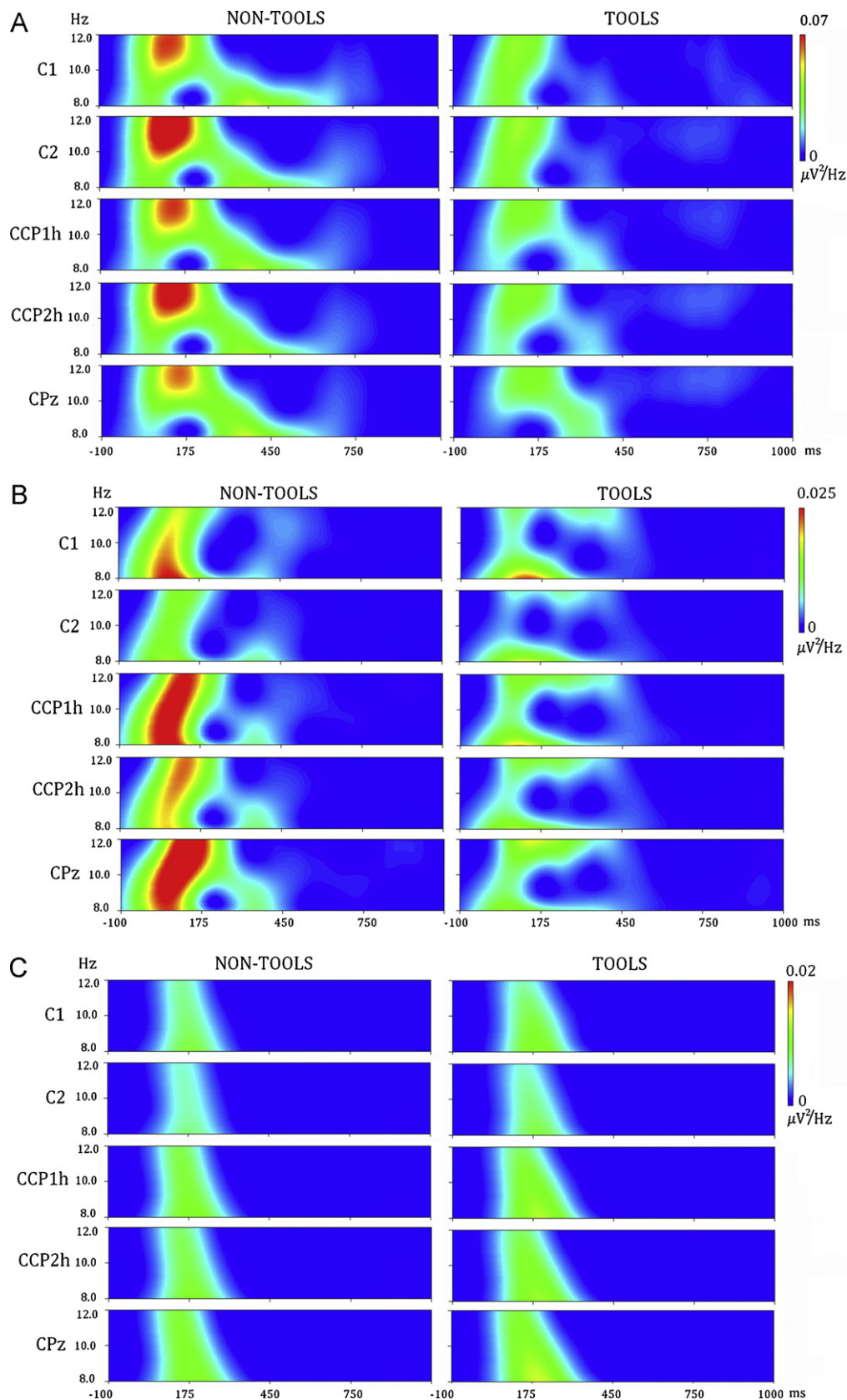
Fig. 4. (A) Wavelet analysis performed on a single subject (SS1) in the μ range (8–12 Hz) for the entire time window (from −100 to 1000 ms), for non-tools (left) and tools (right). All centro-parietal areas are involved in μ desynchronization between 140 and 175 ms in this specific subject. (B) Grand average (N = 10 Ss) wavelet analysis performed in the μ range (8–12 Hz) for the whole time window, as a function of stimulus manipulability. On average, a weaker μ desynchronization over central sites (especially over the right hemisphere) is evident. (C) Wavelet analysis performed on a single subject (SS11) in the μ range (8–12 Hz) during the −100 to 1000 ms time window for non-tools (left) and tools (right). A lack of μ desynchronization is evident in this subject, which, interestingly, is accompanied by a lack of effect in ERP waveforms at the latency of 210–270 ms (see Fig. 5).
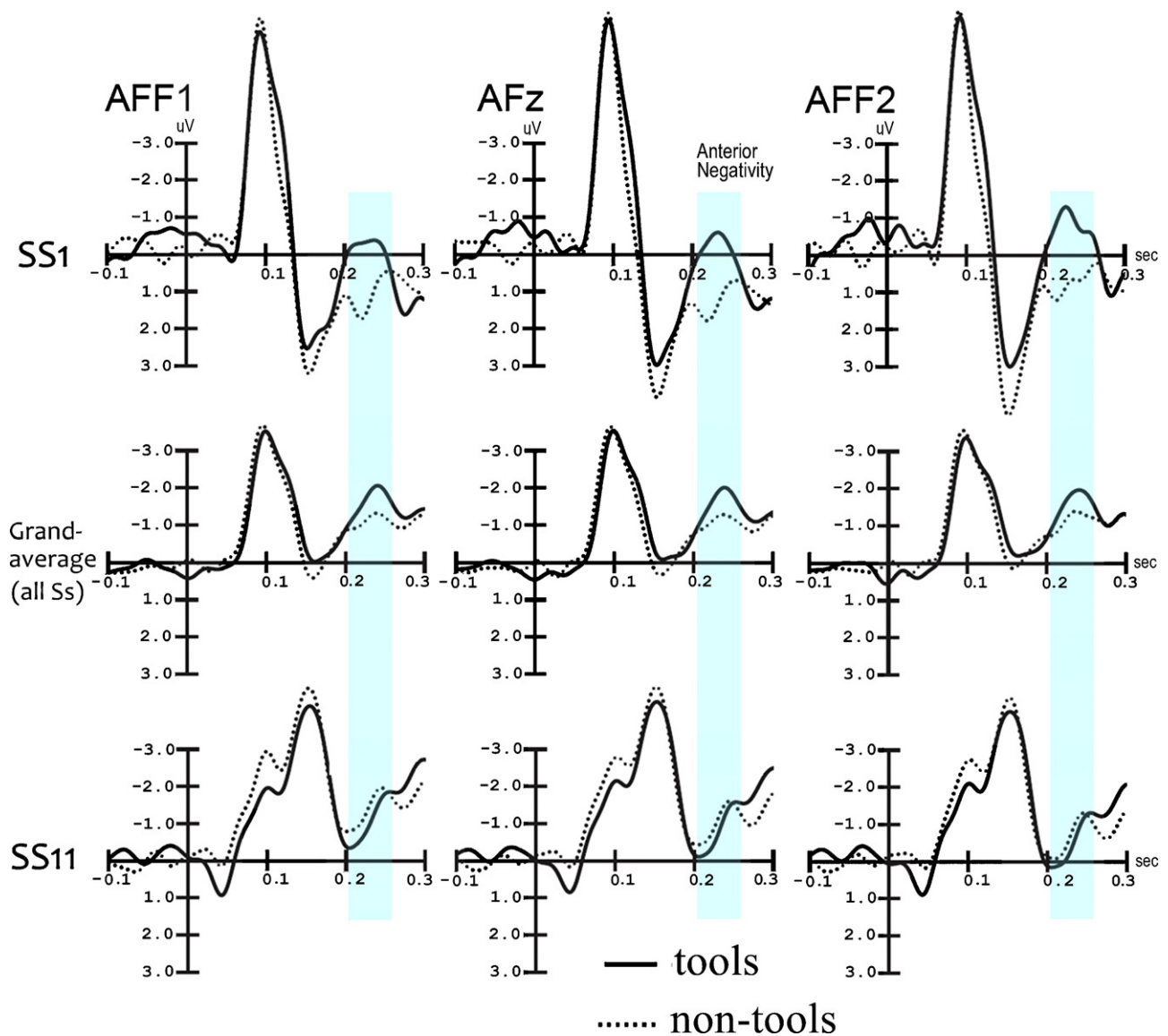
Fig. 5. Event-related potentials recorded in a single participant (Ss1, with wavelet analysis in Fig. 4A) in a group of 10 participants (grand-average ERPs, with wavelet analyses in Fig. 4B), and in another single participant (SS11) showing no effect at the level of anterior negativity (210–270 ms) or μ desynchronization according to wavelet analysis of Fig. 4C. In all participants (except for Ss11), tool perception is associated with the presence of an enhanced anterior negativity, as described in Proverbio et al. (2011).

$p < 0.006$) and relative post hoc comparisons indicated a lack of μ desynchronization at central sites (C1 and C2) and a strong suppression at centro-parietal sites. This effect can also be appreciated by looking at scalp distribution of Mu power in Fig. 2. The interaction of manipulability × frequency band ($F3,27 = 3.81$; $p < 0.02$) indicated that μ desynchronization was centered around 11 Hz (10–12 Hz), and did not involve lower frequencies such as 8 and 9 Hz.

The ANOVA performed on μ power at 175 ms as a function of frequency band showed the significance of object manipulability ($F1,9 = .5.56$; $p < 0.04$), with a μ desynchronization visible in all bands (but especially around 10–12 Hz). The further interaction of stimulus manipulability × electrode ($F4,36 = 4.3$; $p < 0.006$) indicated a lack of μ desynchronization over central sites (C1 and C2) and a strong suppression at centro-parietal sites (CPz, CPP1h, CPP2h), visible in Fig. 2 and also in Fig. 4A and B.

4. Discussion

The topography of μ desynchronization when viewing tools (visible in Fig. 2) was perfectly compatible with what reported by other studies in the literature with regard to object grasping (Perry and Bentin, 2009).

The μ desynchronization in response to tools was a very consistent effect that was visible in all individuals. It is interesting to note that one subject belonging to the group participating in a previous ERP experiment using the same stimuli (Proverbio et al., 2011), but not included in the experimental sample (Ss11), lacked both the μ desynchronization occurring at about 140–175 ms (see Fig. 4C) and the ERP effect in the form of an enhanced N2 anterior negativity (210–270 ms), thus suggesting a possible relation between the activation of the somatosensory cortex as revealed by a μ suppression and the enhanced synchronized activity occurring immediately after, between 210 and 270 ms, (see waveforms depicted in Fig. 5). Indeed, in the ERP study, an increase in the amplitude of the anterior N2 response to tools vs. non-tools was observed, especially over the left hemisphere. In that study, to locate the possible neural source of the object manipulability effect, two different swLORETA source reconstructions were separately performed for tools and non-tools during the 210–270 ms time window, showing that, although both classes of objects equally activated the
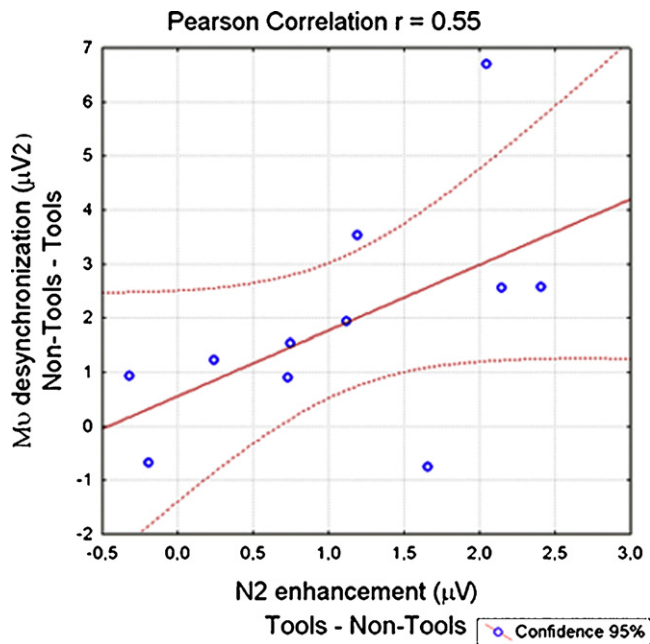
Fig. 6. Pearson's Rho correlation between the extent of μ desynchronization (computed by subtracting the μ power recorded in response to non-tools minus tools over the entire 1 s in the 8–12 Hz range) and the degree of N2 enhancement (computed by subtracting the mean amplitude of N2 (210–270-ms) recorded in response to tools–non-tools, according to the ERP study; Proverbio et al., 2011), for each individual subject (N = 11). The data show a positive correlation (r = 0.55, p < 0.05): the higher the μ desynchronization recorded over the somatosensory cortex between 140 and 175 ms, the greater the amplitude (in μV) of post-synaptic potentials in the extracellular space (ERPs), indexing the first access to motoric tool properties over a network of areas including the left postcentral gyrus (BA3).

occipito/temporal cortex (BA19/37), only tool perception was associated with the activation of the left postcentral gyrus (BA3) and the left and right premotor cortex (BA6). The finding of larger potentials over the somatosensory cortex (and especially on the left: $X–t = −38.5, Y–t = −21.0, z–t = 35.7$) in the 210–270 ms range may be related to the previous μ desynchronization occurring in response to tools. It is worth noting that, although this asymmetry did not reach statistical significance, μ suppression appeared stronger over the left than right centro-parietal cortex. The asymmetry may be due to the typical asymmetrical usage of tools. In fact, one might speculate that, because our subjects were all right-handed, the motor schemata activated by the observed tools (e.g., screwdriver) evoked a stronger involvement of brain areas devoted to the right hand representation, that is: left hemispheric areas. A similar effect was also found by Perry and Bentin (2009), who described a significant μ suppression over C3 than C4 site during the observation of movements performed by the right than left hand (and vice versa). Consistently, several studies provided evidence for preferential left-sided activation of the fronto/parietal circuits for action representation during object observation (Cardellicchio et al., 2011; Grafton et al., 1997). Recently, it was found that observing actions involving a right hand lifting heavy or light objects was associated with left centro-parietal μ desynchronization (Quandt et al., 2011).

The possible relationship between μ suppression at about 140–175 ms post-stimulus and the ERP response recorded after ~80 ms (210–270 ms) is supported by the strong correlation (Pearson's rho = 0.55, p < 0.05) existing between the individual scores relative to μ desynchronization, which was obtained by subtracting the average μ power recorded in the 1-s window following perception of non-tools minus tools, and the individual average amplitudes of the earliest ERP index of tool/non-tool discrimination, that is, anterior negativity (N2). The individual measures

and their correlation are displayed in Fig. 6. Obviously, further research is needed to better comprehend the relation between EEG frequency and ERP responses (EEG synchronized oscillations and stimulus-evoked extracellular post-synaptic potentials), but there seem to be a common neural circuit involved in the generation of both responses, namely, the somatosensory cortex. Indeed, the literature supports the notion of a special role of this region, particularly the AIP sulcus, in representing object motor affordance (Shikata et al., 2003), receiving inputs about objects 3D shape from the more caudal part of intraparietal sulcus.

One of the main intracranial generators of the anterior negativity, which was sensitive to object manipulability in the ERP study (Proverbio et al., 2011), was a region within the left precentral gyrus (−38.5, −21.0, 35.7). This area has been variously characterized in neuroimaging literature as being involved in visuomotor imagination and the generation of simple finger movements (−38, −38, 40; left anterioparietal; Deiber et al., 1998), viewing hand motion (−34, −8, 35; left precentral sulcus) (Wheaton et al., 2004), the observation of hand actions (−44, −20, 52; precentral gyrus) (de C Hamilton et al., 2006), mental imagery for complex hand actions (−38, −38, 44; left postcentral sulcus, extending into intraparietal sulcus) (Willems et al., 2009), right hand grasping (−39, −27, 41; superior and inferior parietal lobules) (Inoue et al., 2001), the imitation of non-symbolic finger configuration (−36, −16, 47; Tanaka et al., 2001), as well as the mental rotation of 3D objects (−32, −2, 41; left precentral gyrus) (Jordan et al., 2001) and the categorization of visually presented artifacts (−63, 7, 18, left precentral gyrus) (Gerlach et al., 2002). These studies indicated the specific role of this area in neurally representing how to manipulate tools, especially with the right hand, on the basis of their visual appearance.

5. Conclusions

In summary, the present study provided evidence that tool perception is associated with a μ desynchronization (particularly in the 10–12 Hz band) over centro-parietal sites, with a tendency toward a left lateralization (visible both in topographical maps of Fig. 2 and in the wavelet analysis displayed in Fig. 4B), particularly around 140–175 ms after stimulus presentation. A temporal and functional correlation has been suggested between μ suppression and the earliest tool/non-tool ERP discriminative response (anterior negativity), recorded in the same subjects and at the view of the same stimuli, after approximately 250 ms post-stimulus. In this regard, it is interesting to consider that according to some authors, the EEG oscillatory state may allow the regulation of the mean membrane potential level within a neuronal population and thereby control the input–output transfer of information (Lopes da Silva, 1991), which, for example, in this specific case, may come from the caudal part of the intraparietal sulcus (CIP) (providing information about object 3D shape) and be directed to a variety of regions, including the premotor cortex (Castiello, 2005).

The EEG oscillation found to be desynchronized in our study (μ, 10–12 Hz) shared several similarities with the rolandic cortical μ rhythm that is suppressed (typically around 10 Hz; Hari et al., 2006) or 11 Hz (Pfurtscheller et al., 2006) during action execution and observation over the primary motor and somatosensory cortex.

Conflict of interest

Acknowledgements

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