The imprint of action: Motor cortex involvement in visual perception of handwritten letters

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Introduction

Humans are able to recognize handwritten texts accurately despite the extreme variability of scripts from one writer to another. This skill has been suggested to rely on the observer’s own knowledge about implicit motor rules involved in writing. To investigate the possible neural correlates of such an ability, we monitored with magnetoencephalography (MEG) the −20-Hz oscillations originating from the motor cortex. The oscillations were more suppressed after visual presentation of handwritten than printed letters, indicating stronger excitation of the motor cortex. The oscillations were more suppressed after visual presentation of handwritten than printed letters, indicating stronger excitation of the motor cortex. These results support the idea of embodied visual perception of handwritten scripts and the involvement of the motor cortex in the underlying action–perception link.

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To study the potential implication of cortical motor networks in the perception of handwritten traces, we probed the functional state of the primary motor cortex by monitoring the reactivity of the rolandic ∼20-Hz oscillations that are known to depend on motor behavior (for reviews, see Hari and Salenius, 1999; Pfurtscheller and Lopes da Silva, 1999). Jasper and Penfield in their intracranial recordings already in 1949 noted generation of such oscillations in a restricted part of the precentral motor cortex. This observation is supported by later studies of the generators of the MEG ∼20-Hz oscillations estimated using various methods (Salmelin and Hari, 1994; Taniguchi et al., 2000; Liljestrom et al., 2005) and by the existence and behavior of cortex–muscle coherence within this same frequency band (Salenius et al., 1997; Mäkelä et al., 2001).

The ∼20-Hz activity displays a typical behavior in relation to movements: preparation and execution of a voluntary movement are associated with a suppression of the ∼20-Hz activity followed within 1 s by a rebound above the resting level (Salmelin and Hari, 1994; Pfurtscheller and Lopes da Silva, 1999). The suppression is therefore clearly associated with activation of the motor cortex, whereas the rebound can be interpreted as an inhibitory state (Jasper and Penfield, 1949; Salmelin and Hari, 1994; Chen et al., 1999). Interestingly, already Gastaut et al. (1952) observed that the rolandic oscillations recorded with scalp electroencephalography (EEG) are also blocked during mental imagery of a movement, and this finding is supported by later MEG recordings (Schnitzler et al., 1997). More recently, recording of the ∼20-Hz MEG oscillations has been informative in showing that the primary motor cortex reacts during observation of movements in a variety of situations (Hari et al., 1998; Järveläinen et al., 2001, 2004). Overall, these data point out that the ∼20-Hz oscillations provide a tool to assess the involvement of the motor cortex in the perception of visually presented handwritten letters.

Materials and methods

Subjects

We studied 11 adults (5 females, 6 males; mean age 27 years, range 22–31; normal or corrected-to-normal visual acuity). Ten subjects were right-handed and 1 was ambidextrous according to the Edinburgh handedness inventory (Oldfield, 1971); all used their right hand to write. None of subjects had history of dyslexia or any neurological disorders. The participants gave their informed written consent, and the recordings had a prior approval by the Ethics Committee of the Helsinki and Uusimaa Hospital District.

Stimuli and procedure

Visual stimuli

The printed and handwritten letters used as stimuli were matched in size and stroke thickness. Stimulus presentation was controlled by Presentation® software (http://www.neurobs.com) run on a PC computer. The stimuli were displayed through a data projector (VistaPro™, Christie Digital Systems Inc., Cypress, CA, USA) onto a rear projection screen ~1 m in front of the subject. The background was gray, with a white 5.5 cm × 5.5 cm presentation area in the middle. The subjects were asked to keep their gaze fixated to the middle of this square. The letters were 2.2–4.0 cm in height, depending on their shape. The mean luminance was 7.2 cd/m² (black) for the stimuli, 81 cd/m² for the presentation area (white) and 76 cd/m² for the background. The two categories of stimuli were presented in a random order, with an interstimulus interval varying randomly between 2.5 and 3.5 s. Each stimulus was displayed for 400 ms. The subjects were asked to respond by lifting the left index finger every time the letter “a”, handwritten or printed, was presented. Target trials (6% of all) were not included in the MEG analysis. Finger lifts to pinpoint the motor cortex

Finger lifts were performed in a block separate from the visual conditions. The subjects made about 20 self-paced brisk extensions of the right index finger at intervals of ~4 s; optical fibers were used to detect the movement (and to provide a trigger for signal analysis). During the movements, the subjects kept their eyes open and were instructed to avoid looking at the moving finger.

Behavioral tests

After the MEG recordings, the subjects’ recognition performance was tested behaviorally by presenting a stimulus sequence similar to that in the actual experiment and asking the subjects to respond as rapidly and accurately as possible by pressing a button with either the left or right index finger, depending on whether the displayed letter was a vowel or a consonant. Both response times and error rates were measured to check for any differences in the difficulty of processing handwritten vs. printed letters and to establish correlations with possible modulations at the brain level.

The subjects’ writing speed was quantified by measuring the time needed to write down from memory the 4 first verses of the Finnish (for one subject, Portuguese) national anthem, at normal speed, after careful reading of the text and practice to make sure that the subjects were able to write the verses from memory without hesitation. This procedure did not provide any absolute values of the writing speed, but it allowed a relative comparison between the 11 subjects so that possible modulations at the brain level could be correlated with individual measures of writing ability.

MEG recording

Whole-scalp neuromagnetic signals were measured in a magnetically shielded room, while the subject was sitting with the head surrounded by the helmet-shaped Vectorview™ 306-channel neuromagnetometer (Neuromag Ltd., Helsinki, Finland). The detector array comprises 102 identical triple sensor units, each housing two planar first-order SQUID (Superconducting QUantum Interference Device) gradiometers and one magnetometer. The two gradiometers of each unit measure orthogonal tangential derivatives of the magnetic field component normal to the head surface. Planar gradiometers pick up the strongest signals just above a local current, and thereby the locations of the sensors detecting the strongest signals can be readily used as the first guesses of the activated brain areas (for details, see Hämäläinen et al., 1993). MEG signals were bandpass filtered at 0.1–173 Hz and sampled at 600 Hz. Horizontal and vertical electro-oculograms were recorded for subsequent off-line rejection of MEG epochs contaminated by eye blinks or eye movements.

Data analysis

Event-related changes in oscillatory MEG activity

Only signals from the 204 gradiometers, downsampled to 300 Hz, were analyzed. For both the letter and finger lift conditions, event-related changes in the oscillatory activity were quantified using a time–frequency wavelet decomposition of the
continuous MEG signals between 5 and 30 Hz (complex Morlet’s wavelets, ratio $f_0/\sigma_f=7$) implemented in a Matlab toolbox (Ole Jensen’s 4D toolbox, http://neuro.hut.fi/~tanzer/d4d/); for a complete description of this method, see Tallon-Baudry et al. (1996). The resulting time–frequency representations (TFRs) of the energy of the signal were averaged for time windows starting 0.5 s before and ending 1.5 s after the onset of the event (visual stimulus or finger lift). Epochs coinciding with electro-oculographic signals $>250 \mu$V were discarded from the average. About 100 epochs were averaged for each of the 2 categories.

The mean energy of the pre-event period (from $-400$ to $-20$ ms for the letter conditions and from $-500$ to $-300$ ms for finger lift conditions) was considered as a baseline level and subtracted from each time point for a given frequency.

**Statistical analysis of the $\sim 20$-Hz oscillations**

For each subject and condition, we thus had data on the location, frequency and timing of the MEG signals. Because systematic statistical testing of such a large data set would involve multiple comparisons, we focused our analysis on the region of the primary motor cortex using the results of the finger lift task to define for each individual the sensors and frequency bands of interest. Thus, the whole-scalp TFRs (from 204 sensors) were reduced to a set of statistically testable values as follows.

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**Fig. 1.** Whole-head data from Subject 7 during the right finger lift condition. The time–frequency representations (TFRs), illustrating the level of oscillatory activity at different frequencies as a function of time, are shown from 5 to 30 Hz and from $-500$ to 2000 ms, where time 0 represents the onset of the lift (102 gradiometers pairs, head viewed from the top; the power values with respect to a baseline from $-500$ to $-300$ ms are given in arbitrary units). Enlarged TFRs are shown from one representative gradiometer pair from the left rolandic region (indicated by rectangle in the top illustration). On the bottom right, the mean current dipole source of the oscillations between 18 and 22 Hz is displayed on a coronal and an axial view of the subject’s magnetic resonance image (MRI). The yellow circle marks one standard deviation of the dipole density plot, and the line indicates current orientation. Below the MRI, the single-trial time courses of the dipole strengths are displayed from 1 s before to 2 s after the onset of the finger lift; altogether, 43 single trials are superimposed.
**Signal location.** For each subject, we first selected from the rolandic sensorimotor region 4 such sensors where the TFRs showed a strong ∼20-Hz reactivity (suppression followed by rebound) to finger lifts; the sensors were mostly located in the left rolandic region (see Fig. 3, helmet view). As a control, we then selected 4 sensors from the occipital region, where clear averaged evoked responses were elicited by the visual stimuli (“letter-string response” at ∼150 ms, Tarkiainen et al., 1999). The 4 TFRs of each of these 2 subsets (“rolandic” and “occipital”) were then averaged for the finger lift and the 2 visual conditions. Fig. 4 (top) indicates the location of the channels taken into account in the two regions for all the subjects.

**Signal frequency.** The frequency band of interest was individually defined as the dominant frequency ±2 Hz of the post-movement rebound of the rolandic TFR during the motor condition. The energy was then averaged over this band for the 2 visual conditions, providing 4 time-traces per subject (i.e. 2 per region).

**Signal timing.** For each subject, we first identified at 0–1500 ms the time point of absolute maximum difference between the 2 curves originating from the rolandic region. The mean activity was computed within a ±50 ms time window around the selected time point. The same procedure was applied for the traces originating from the occipital region. We therefore obtained 4 values per subject (2 conditions × 2 regions), which were finally entered into a 2×2 repeated-measures ANOVA.

**Control analysis of the ∼10-Hz oscillations**

To evaluate the specificity of the effects to the ∼20-Hz frequency band, we applied the same statistical analysis to the

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Fig. 2. Whole-head data from Subject 7: TFRs for printed letters have been subtracted from TFRs for handwritten letters. Time 0 represents the onset of the visual stimulus. Other details as in Fig. 1; the baseline was from −400 to −20 ms. The letters used as stimuli are shown on the bottom right.
oscillatory activity averaged across frequencies from 8 to 12 Hz for the two regions and the two conditions.

Source modeling of the \(~20\text{-Hz oscillations}\)

To replicate the previously reported motor cortex origin of the \(~20\text{-Hz activity}, we modeled the sources of these oscillations as current dipoles for one subject’s data recorded during the finger lift task. A detailed description of the procedure used can be found in Hari et al. (1998).

Results

Event-related changes in the MEG oscillatory activity

Fig. 1 displays whole-head TFRs from Subject 7 in the finger lift condition, used to pinpoint the location of the primary motor cortex. The 102 pairs of sensors of the MEG helmet are viewed from the top. Finger lifts were associated with reactivity in well-restricted rolandic recording sites, mostly in the left hemisphere, contralateral to the moving finger. The typical behavior of the oscillatory activity in such a movement task (suppression around time zero, i.e. the button release, and rebound starting after 0.5 s; Salmelin and Hari, 1994) is well evident in the enlarged TFR.

The insert (bottom right) shows, on the subject’s magnetic resonance image (MRI), the mean location and direction of the 107 current dipoles used to model the \(~20\text{-Hz oscillations}. The Talairach coordinates \((-32, -23, 54)\) of the mean location agree with activation of the primary motor cortex (Rademacher et al., 2001; Yousry et al., 1997). The traces below the MRIs illustrate the strength of the mean current dipole as a function of time during 43 successive single trials. In agreement with previous findings (Salmelin and Hari, 1994), the signals are clearly suppressed during the movement and increased afterwards.

Fig. 2 shows the difference in the reactivity to handwritten vs. printed letters (TFRs for printed letters were subtracted from TFRs for handwritten letters). In the upper frequency band (around 20 Hz), the difference is restricted mostly to the rolandic region and is largest at the same recording sites where the reactivity was prevalent during finger lifts. Qualitatively, the difference is negative, meaning that the level of \(~20\text{-Hz activity is lower for handwritten than printed letters.}

The 3 top rows in Fig. 3 show the rolandic and occipital TFRs for 2 representative subjects. In both of them, the visual stimuli suppressed the oscillations, more strongly and for a longer time for handwritten than printed letters. This reactivity and pattern of difference were present only in the rolandic region. The traces at the lowest panels show the level of the \(~20\text{-Hz activity for printed and handwritten letters: the differences are clearly larger in rolandic than occipital areas.}

The individual dominant \(~20\text{-Hz} frequencies of the 11 subjects varied from 15 to 23 Hz (mean 18 Hz). Group-level statistical analysis was performed on the values of the \(~20\text{-Hz level at the absolute maximum difference between the 2 curves (illustrated by shaded vertical bands for two subjects in Fig. 3, bottom traces), which arose on average 0.83 s (range 0.53–1.15 s) after stimulus onset in the rolandic region and 0.96 s (range 0.55–1.49 s) in the occipital region. The times of maximum differences between the two regions did not correlate \((r=-0.19, \text{n.s.})\).
Fig. 4 shows that in the rolandic region the ~20-Hz level was higher for the printed letters in 9 subjects out of 11 (p=0.065, sign test) but in the occipital region only in 4 subjects out of 11 (n.s.). Results of an ANOVA showed a main effect of condition (F(1,10)=6.89; p<0.026) and an interaction between condition and region (F(1,10)=13.76; p<0.005), with no main effect of area (F(1,10)=0.01, n.s.). In the rolandic region, the level was positive for the printed letters and negative for the handwritten letters (planned comparison F(1,10)=12.08; p<0.006), whereas in the occipital region, the level was close to zero for both conditions (planned comparison F(1,10)=1.03; n.s.). The coloring in the sensor arrays at top refers to the channels chosen for analysis in individual subjects.

To ensure that the results were not due to the time window selection, we repeated the statistical analysis, with the ~20-Hz level averaged over the whole (0–1500 ms) time window as the dependant variable. Again, this analysis revealed a main effect of condition (F(1,10)=5.84; p<0.04), the same interaction between condition and region (F(1,10)=10.13; p<0.01), and regional differences (planned comparisons F(1,10)=8.53 p<0.02 for the rolandic region and F(1,10)=1.64, n.s. for the occipital region).

To scrutinize the laterality of the effects, Fig. 5 shows values from two sets of 6 gradiometer pairs from the left and right rolandic regions. The mean activity in the ~20-Hz frequency band over the whole (0–1500 ms) time window was statistically significantly different between the handwritten and printed letter conditions in the left hemisphere (p<0.02, Scheffé's post hoc test), with a similar nonsignificant trend in the right hemisphere (p<0.29, Scheffé's post hoc test).

The amplitude of the difference between the two conditions in the rolandic region was positively correlated with the handedness laterality quotient of the subjects, assessed by the Edinburgh inventory (Oldfield, 1971), but the result was statistically nonsignificant (r=0.48; n.s.).

The control ANOVA performed on the ~10-Hz levels at the time of maximum difference between the two conditions failed to show any statistically significant main effect (condition: F(1,10)=1.92, n.s.; region: F(1,10)=1.77, n.s.) nor interaction between the two factors (F(1,10)=2.24, n.s.). This result was not due to the selection of the time window because also the analysis of the ~10-Hz level averaged over the whole (0–1500 ms) time window revealed neither main effects (region: F(1,10)=0.32, n.s.; condition: F(1,10)=0.48, n.s.) nor interaction between the two factors (F(1,10)=2.87, n.s.).

In addition, a correlation matrix calculated between the values in the ~20-Hz and in the ~10-Hz bands for the 2 conditions and the 2 regions showed no significant relationships between the ~10-Hz and ~20-Hz signals.

To summarize, the analysis of the MEG signals indicated stronger suppression of the motor cortex ~20-Hz activity by visual presentation of handwritten than printed letters; the effect was seen in the left hemisphere, with no similar difference in the occipital region.

**Behavioral measures**

Behavioral recognition performance and reaction times in a vowel/consonant classification task, tested after the MEG recordings, were similar for both conditions: the mean ± SEM
studies have already posited strong links between perception and conditions were positively correlated with the subject’s writing (Järveläinen et al., 2004).

The writing speed and the difference in recognition times between right hand for writing. Similarly, the observed correlation between the action–perception link. Accordingly, some earlier behavioral studies have already posited strong links between perception and production of handwriting (Freyd, 1983; Babcock and Freyd, 1988; Orliaguet et al., 1997; Knoblich et al., 2002; Li and Yeh, 2003). This interpretation is further supported by the left-hemisphere dominance of the effect in our subjects who all used their right hand for writing. Similarly, the observed correlation between the writing speed and the difference in recognition times between the two conditions agrees with internal motor simulation during recognition of handwritten letters, and the finding is in line with a previous MEG study that indicated the importance of motor experience for motor cortex modulation during action observation (Järveläinen et al., 2004).

Although letters may automatically trigger phonological processing and associated articulation movements (Paulesu et al., 1993), any contamination of our results by such activity seems highly unlikely because the observed 20-Hz reactivity, on the basis of source analysis (see Fig. 1, bottom right), was centered in the hand knob of the motor cortex (Yousry et al., 1997) and not in the more lateral mouth representation area. Moreover, it is difficult to envision why only handwritten and not printed letters would cause such an activation.

Contamination by attentional effects also seems unlikely because of the clear lateralization of the difference between handwritten and printed letters and because the effects were strongly dissociated between the rolandic and occipital regions. Furthermore, the equal behavioral performance for both types of letters indicates equal processing difficulty, and the randomized presentation order of stimuli precludes any long-lasting differences in the attentive state. Finally, the control analysis of the ~10-Hz oscillations did not demonstrate any difference between the two types of letters. Since the ~10-Hz frequency band is typically modulated by the attentional state of the subject (for a review, see Niedermeyer, 1993), this result argues against different attentional processing of the two types of letters.

Seeing manipulable objects can activate parts of the motor system (Chao and Martin, 2000; Mecklinger et al., 2002). In our study, both handwritten and printed letters could be objects of motor processing because they both afford potential writing actions (Longcamp et al., 2003). Nevertheless, only handwritten letters intrinsically carry production-related information. Our finding of a greater activation of the motor cortex during the perception of handwritten letters therefore implies that a part of the system underlying action observation is specifically involved in that case.

The observed effect needs not be writing-specific but could also arise for printed vs. hand-drawn non-meaningful signs and figures. However, it is likely to be stronger for movements more frequently practiced by the viewer.

Interestingly, because handwritten letters are static stimuli in which the movement is ascribed to the actor long time after the action has taken place, our data confirm that the brain is able to “reconstruct” the action a posteriori on the basis of static information. Previously, human brain areas involved in movement processing have been reported to be activated by still photographs that only imply actions (Kourtzi and Kanwisher, 2000; Nishitani and Hari, 2002; Johnson-Frey et al., 2003). Compared with the above studies, the present results go one step further by showing that the primary motor cortex, which is downstream from the inferior frontal gyrus, the core area of the MNS, also reacts to the sensory consequences of somebody else's action, although this action is neither directly visible nor currently executed. In handwriting, similarly as in speech perception (Wilson et al., 2004), the knowledge of a common production process, shared by both the perceiver and the producer, would help recognition and therefore communication (Liberman and Mattingly, 1985; Wada, 1995; Wilson et al., 2004; Nishitani et al., 2005).

Overall, our results can be considered to support internal motor simulation associated with visual perception of handwritten letters. These processes underline the involvement of the human primary motor cortex in the continuous action–perception link of an individual interacting with her environment.

Acknowledgments

This research was supported by the Academy of Finland (National Center of Excellence Program), Fyssen foundation (France), the Finnish Cultural Foundation, and Sigrid Jusélius foundation. We thank Mia Illman for expert help in data recording.

References


