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Brain responses to handwritten and printed letters differentially depend on the activation state of the primary motor cortex

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ABSTRACT

Previous studies demonstrated that visual perception of handwritten letters activates the left primary motor cortex more strongly than printed letters. Here, we used EEG to record cortical responses evoked by single letters to directly test if their visual processing is actually influenced by their motor content. We manipulated the "motor familiarity" of letters that we considered high for letters written by the observers themselves, medium for letters written by other individuals, and low for printed, machine designed letters. In order to relate the effects of motor familiarity to the activation of the primary motor cortex, we also directly manipulated its availability during the visual task: we computed Event-Related Potentials (ERPs) over the posterior cortex during a dual task where participants had to observe the letters while performing unrelated self-paced brief movements of the right hand approximately every 5 s (allowing the primary motor cortex to successively activate and "idle"). At 300–350 ms and 500–600 ms after stimulus onset, the amplitude of the ERP components markedly reflected the level of motor familiarity of the observed letter. Nonetheless, this was true only when the primary motor cortex was in an "idling" state: when the motor cortex was in an activation state, this motor familiarity effect was dropped. This clearly indicates that, at these latencies, the motor information embedded in letters is processed in the brain and that this processing depends on the activation state of the left primary motor cortex.

Introduction

Nowadays, despite an extensive use of word digitization, handwritten style is still widely present in our environment, for instance in arts or advertising (such as dance patterns, Mosbæk-Johannessen, 2010). Visual recognition of handwritten traces remains a critical and fascinating feat of the perceptual system. Yet, it has received little attention in the cognitive neurosciences. The sparse data in the literature indicate that visual processing of handwritten characters is qualitatively not similar to visual processing of printed letters (Corcoran and Rouse, 1970; van Atteveldt et al., 2002; Williams, 1984).

Recently, we have suggested that differences in the visual processing of handwritten and printed letters may pertain to the fact that only handwritten exemplars carry movement-related information (Longcamp et al., 2006, 2011). Several psychophysical studies demonstrated that the visual system is sensitive to the way the trace is produced, so that the rules we follow to write a symbol constrain the way we perceive it (Babcock and Freyd, 1988; Kandel et al., 2000; Orliaguet et al., 1997; Tse and Cavanagh, 2000; Yeh and Li, 2003). Consistent with this idea, neuroimaging experiments showed that visual observation of handwritten letters involve the participant's own motor system: during visual observation of handwritten letters compared to printed letters, a greater activation of the left primary motor cortex (Longcamp et al., 2011) and a stronger and left-lateralized modulation of ~20 Hz oscillations known to arise from the motor cortex (Longcamp et al., 2006) were observed. Taken together, these results suggest that the brain actually discriminates the motor content of the visual stimulus, and that this discrimination relies on the input of the primary motor cortex. However, properly investigating this question requires manipulating both the motor content of the stimulus and the activation of the primary motor cortex. This was the aim of the present study, in which we assessed the cortical responses evoked by visually presented single letters with EEG during activation or "idling" of the motor cortex.

In order to vary the motor content of the stimuli, we manipulated the "motor familiarity" of the letters. In fact, several recent studies show that motor knowledge resonates more with visual perception when the observed action corresponds to the observer's motor repertoire. This is especially striking in sports where observers proved to be more sensitive to the action they are the most trained with (Calvo-Merino et al., 2005, 2006, 2010). In the domain of handwriting perception, motor familiarity is directly dependent of the observer's motor capacity to produce the perceived letter. Knoblich et al. have shown an authorship effect in the perception of handwritten traces: when handwritten symbols were presented dynamically, the motor information they contained was used more efficiently in a visual discrimination task when the traces were produced by the observers themselves (Knoblich and Prinz, 2001;

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Knoblich et al., 2002). Therefore, we can consider that motor familiarity is maximum when observers perceive their own production and minimum when they perceive printed letters that is letters which cannot be produced by humans. In this context, traces produced by someone else can be considered as intermediary. They are produced by a human therefore they contain some motor information but these motor information do not match exactly with the observers' motor abilities. We expected that if some components of the visual evoked potential reflect the processing of motor-related information, their amplitude should be graded as a function of the level of motor familiarity of the letters.

In order to manipulate the state of activation of the primary motor cortex while the letters were being processed, we used a dual-task in which the visual perception of letters was performed in parallel with a simple motor task (self-paced extensions of the right wrist). The motor task was designed to provide a dynamical manipulation of the level of oscillatory activity of the left primary motor cortex: the amplitude of the ~20 Hz oscillations arising from the motor cortex successively decreases before and during the movement (~20 Hz suppression; activation state of the motor cortex) and increases after the movement (~20 Hz rebound; “idling” state of the motor cortex; Pfurtscheller and Lopes da Silva, 1999; Salmelin and Hari, 1994). Here, in order to test whether this activity is crucial to the discrimination of motor familiarity of the letters, we presented the letters either during the activated state or during the “idling” state of the motor cortex. We analyzed the interaction between this manipulation and the motor familiarity of the letters on the visual evoked potentials. The rationale was that the effect of motor familiarity should be observable only when the primary motor cortex is "available" (i.e., during the "idling" state) but should be dropped out when the primary motor cortex is unavailable as it is activated by the additional motor task (i.e., during the suppression state).

An advantage of using ERPs to investigate the sensitivity of the brain to motor-related content of the visual stimulus is that ERPs allow to precisely time the influence of the motor cortex in the flow of visual processing. Indeed, if an interaction between motor cortex activation and motor familiarity of letters occurs at some point, then we shall be able to better pinpoint the stage of visual information processing that integrates the input of the motor cortex. Visual processing of letters has already been investigated using the combination of the event-related potentials (ERPs) measurement and a masked priming technique (Grainger and Holcomb, 2009; Holcomb and Grainger, 2006; Kiyonaga et al., 2007; Petit et al., 2006; Rey et al., 2009). The results highlighted that a cascade of ERP components, starting as early as 100 ms post-letter-onset and continuing through as late as 600 ms, is affected by a manipulation of prime-target similarity. For instance, the early ERP components occurring around 100 ms (like P1) are assumed to reflect the processing of low-level features (Di Russo et al., 2002; Petit et al., 2006; Rey et al., 2009), whereas later components occurring after 150 ms, (like N170) are related to abstract letter identification (Grainger and Holcomb, 2009; Grainger et al., 2008; Mitra and Coch, 2009). Among all these components possibly candidates to be affected by the activity of primary motor cortex, we particularly focused on the component around 200–300 ms, known to be related to the observers' expertise in the writing system (Wong et al., 2005). Moreover, we investigated the component around 500 ms, because it corresponds to the activation latency of the motor cortex during visual perception of stimuli implying motion (Nishitani et al., 2004; Papeo et al., 2009; Proverbio et al., 2009).

Finally, the possible lateralization of the effects is of interest: it is now well established that the difference in processing handwritten and printed letters or words relies on a stronger involvement of visual regions of the right hemisphere (Barton et al., 2010a, 2010b; Hellige and Adamson, 2007; Longcamp et al., 2011; Qiao et al., 2010). This right-hemispheric involvement has been related to the handling of visual complexity that is inherent to handwritten traces (Hellige and Adamson, 2007) and to the analysis of script style (Barton et al., 2010a). On this basis, we expected to find larger effects in the right hemisphere.

Methods

Participants

Sixteen adults (mean age 25.3; age range 20–39; 7 women) participated in the experiment. One of the participants was removed from the final statistical analysis due to head motion artifacts. The fifteen remaining participants were right-handed (handedness quotients 62–100%; mean 87%; (Oldfield, 1971), and they consistently used their right hand to write. All participants had normal or corrected-to-normal visual acuity. None of the participants reported history of dyslexia or any neurological diseases. The experimental procedure was approved by the ethics committee of the Paul Sabatier University in accordance with the Helsinki declaration. All participants signed an informed consent form prior to their participation.

Stimuli and materials

Fourteen lower case letters (a, c, e, f, g, h, j, k, l, r, s, t, y and z) were used as stimuli because they were not ambiguous with their mirror image. Among these stimuli, three Types of Letters were presented to the participants: printed letters (Nosuka font style), participant's own handwritten letters and letters handwritten by one of the other participants. Handwritten letters were collected from each participant before the experimental session. One independent observer paired participants whose handwritten letters differed most, so that within a pair their handwritten letters served as "other" letters for each other. The letters, matched in size, luminance (mean luminance = 66.56 cd/m^2), contrast and stroke thickness, were displayed as black symbols against grey background. The letters were displayed within a 400 × 400 pixels area in the middle of a black screen. Stimulus presentation was controlled by Presentation software version 0.81 (Neurobehavioral Systems Inc., Albany, CA) run on a PC.

Participants were seated in front of a computer screen (1280 × 1024, 100 Hz) in a dimly illuminated room with their right arm attached on the table. They were instructed to keep their gaze fixated to the middle of the screen. A magnet was fixed on the second phalanx of the middle and third right fingers in order to activate a magnetic switch when participants produce one hand extension. Besides, two response switches, placed under participants' feet, were connected to an analogic acquisition card (NI PCI-6503) which allowed a temporal precision of 1 ms.

Procedure

Motor cortex activity was manipulated by a simple motor task performed with the right (dominant) hand during a letter visual discrimination task. Motor cortex activity related to hand extension was quantified by the ~20 Hz oscillations around the motor cortex exhibits two particular periods: an activation and a “idling” state of the motor cortex (respectively associated with the Suppression and the Rebound of the ~20 Hz oscillations; for more details see (Pfurtscheller and Lopes da Silva, 1999; Salmelin and Hari, 1994). Because these periods were relatively variable between participants, we determined their latency for each participant during a preliminary independent session (simple motor task). The dual-task session was systematically performed after this session (a range of 1–6 days in average 2 days).

Single motor task to determine the individual suppression/rebound ~20 Hz oscillations periods

Participants had to perform 2 blocks of 50 self-paced extensions of the right hand at intervals of ~5 s. In order to help participants to respect the 5 s interval between each movement, this task was preceded by a familiarization session in which participants had to synchronize the extension of their fingers to an auditory metronome pacing each 5 s. After familiarization (2 min in average), feedback on their regularity performance was given at each participant. Then, in the following task, no auditory stimuli were given and participant had to produce spontaneously extension–flexion of the right wrist and fingers at intervals of ~5 s.

Dual-task

Participants had to simultaneously discriminate the orientation of letters (either Self-handwritten or Non-self handwritten or Printed, 200 ms stimulus duration), and produce spontaneous self-paced brief movements of extension-flexion of the right wrist and fingers at intervals of ~5 s (Fig. 1). The visual task was chosen in order to maintain attention of the participants on the letter presentation. Participants were asked to respond with their left foot by depressing a response switch every time a mirror letter was presented (~8% of all stimuli). The response's foot (right or left) was counterbalanced across participants. The 3 types of letters were presented in a random order during 2 periods previously determined for each individual on the basis of the simple motor task: either (1) during the Suppression of the ~20 Hz oscillations (associated with an activation state of the motor cortex) or (2) during the Rebound of the ~20 Hz oscillations (associated with "idling" state of the motor cortex). During the inter-stimuli interval, varying randomly between 2.25 and 4 s, a fixation cross appeared. Dual-task was composed of 12 blocks of 72 trials (9 for each Type of Letter × 2 Periods of stimuli presentation, 6 mirror letters and 10 trials without any presented image). Mirror trials were not included in the EEG analysis.

Data acquisition and analysis

The EEG was recorded continuously during the two sessions through the Active Two Biosemi system from 64 active electrodes mounted on an elastic cap (10–20 International system Electro-Cap Inc). The impedance of all electrodes was kept below 5 kΩ. Two additional electrodes were used to monitor eye movements and blinks (one placed at lateral canthi and one below the eyes).

Single motor task

Continuous EEG was digitized at 512 Hz and filtered offline (1–45 Hz) using EEGLAB software (Delorme and Makeig, 2004) and recalculated to average reference. Epochs consisting of 1000 ms pre-movement and 3500 ms post movement were processed (whole window as baseline). Epochs contaminated by behavioral excessive deflection (±100 μV) were excluded from the analysis. Event-related changes in the oscillatory activity were quantified using a time–frequency wavelet decomposition of the continuous EEG signals between 1 and 45 Hz (complex Morlet's wavelets, ratio $fo/\sigma f = 7$) implemented in a Matlab toolbox (Fieldtrip software; for a complete description of this method, see (Tallon-Baudry et al., 1996). The resulting time–frequency representations (TFRs) of the spectral power of the signal were averaged for the time window. The mean spectral power of the pre-event period (from −900 to −500 ms) was considered as a baseline level and subtracted from each time point for a given frequency.

For each participant, we selected from the rolandic sensorimotor region, the sensor where the TFRs showed a strong ~20 Hz reactivity (Suppression followed by Rebound; C3 for 13 participants and CP3 for 2 participants). Then, for this sensor, we averaged the spectral power of the signal around 20 Hz (between 13 and 30 Hz) for the whole time window. Based on this average, two Periods were defined for each participant (Fig. 1): the ~20 Hz oscillations suppression period between 50 and 550 ms after the movement onset and the ~20 Hz oscillations rebound period lasted for 500 ms and centered on the maximum of the spectral power of the signal around 20 Hz.

Dual-task

Continuous EEG was digitized at 512 Hz and filtered offline (1–20 Hz) using EEGLAB software (Delorme and Makeig, 2004) and recalculated to average reference. ICA-based artifact correction was used in order to correct blink artifacts (Delorme et al., 2007). Epochs consisting of 100 ms pre-stimulus and 800 ms post stimulus were processed separately for each Type of Letter, with the 100 ms pre-stimulus used as baseline. Epochs contaminated by muscular contractions or an excessive deflection (±75 μV) were detected by a visual inspection of the data, and excluded from the averaged ERP waveforms (i.e., on average 8.5% of the trials). ERPs were computed for each condition using the 100 ms pre-stimuli as baseline. Based on visual inspection of the scalp maps distribution averaged for the 3 conditions, we collapsed ERPs across PO7/P7/P9 and PO8/P8/P10 to represent maximal left and right posterior activity for P100 and N170 components respectively (Fig. 2).

Peak latency for P100 component was defined (for each condition and each participant) as the time of maximum positivity occurring between 75 and 150 ms from stimulus onset. Peak latency for the

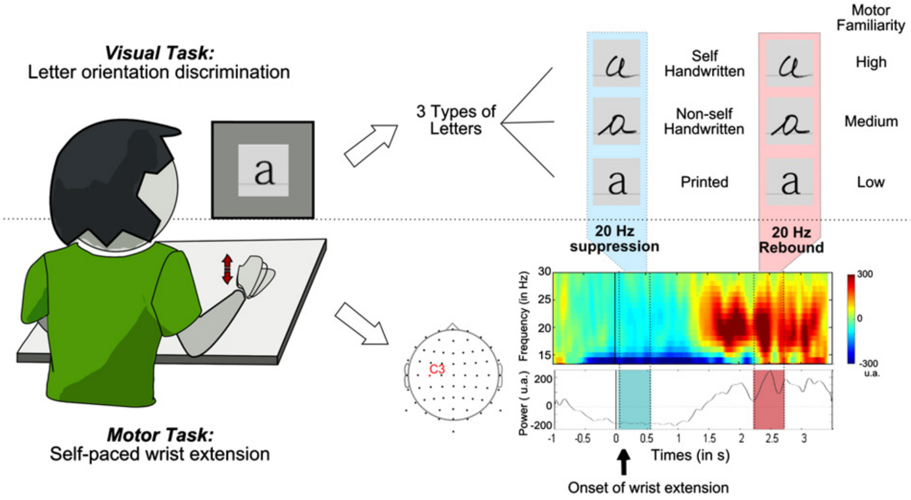

Fig. 1. Description of the dual-task procedure: participants had to perform simultaneously a letter orientation discrimination task (correct or mirror orientation) and a self-paced wrist extension at 5 s interval (left panel of the figure). When a wrist extension was produced, two particular periods of the activation state of the motor cortex could be recorded under the C3 electrode: an activation state (associated with a ~20 Hz oscillations Suppression, blue region in the time–frequency representations in the right bottom panel of the figure) and an "idling" state (associated with a ~20 Hz oscillations Rebound, red region). During the dual-task procedure, three Types of Letter (Self-handwritten, Non-self handwritten and Printed), related to three different levels of motor familiarity, were presented to each participant. Letters' presentation was synchronized with these two particular periods (left top panel of the figure).

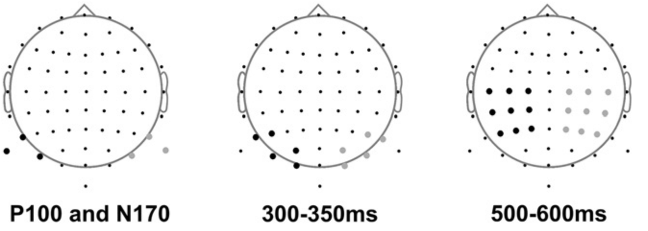

Fig. 2. Regions of interest for each component of interest: For the P100/N170 components, activity recorded under the PO7/P7/P9 (black) and PO8/P8/P10 (grey) electrodes was merged in order to respectively represent the left/right maximal posterior activity at these latencies. For the 300–350 ms time-window, averaged activity from the left/right posterior regions was computed on the basis of PO7/PO3/P5/P7/O1 (black) and PO8/PO4/P6/P8/O2 (grey) signal electrodes. Concerning the left/right maximal parietal activity, occurring around 500–600 ms, the C1/C3/C5/CP1/CP3/CP5/P1/P3/P5 (black) and C2/C4/C6/CP2/CP4/CP6/P2/P4/P6 (grey) was merged.

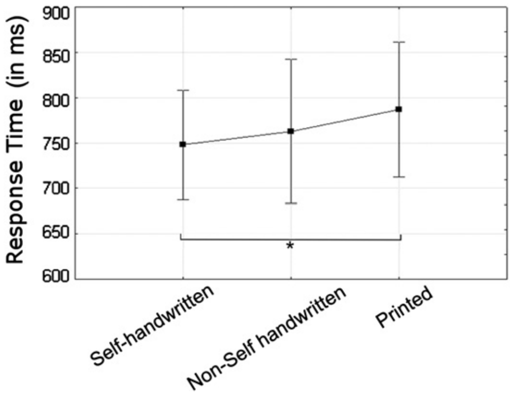

Fig. 3. Response-time (RT) for mirror letter presentation as a function of the Type of Letter presented (Self-handwritten, Non-self handwritten and Printed). Error bars represent the 95% confidence intervals. (*) Indicates that planned comparison is statistically significant at $P<0.05$.

N170 was defined as the time of maximum negativity occurring between 140 and 250 ms from stimulus onset. Mean peak amplitudes of these two components were calculated over a 20 ms window centered at the peak latency. Recordings across PO7/PO3/P5/P7/O1 and across PO8/PO4/P6/P8/O2 were collapsed to respectively represent maximal left and right posterior positive activity between 300 and 350 ms (Fig. 2). Besides, recordings were also collapsed for C1/C3/C5/CP1/CP3/CP5/P1/P3/P5 and C2/C4/C6/CP2/CP4/CP6/P2/P4/P6 to represent maximal parietal (respectively left and right) activity between 500 and 600 ms (Fig. 2). Mean amplitude of these two time-windows was respectively computed by averaging data between 300–350 ms and 500–600 ms.

An ROI (Right vs. Left) × Type of Letter (Self-handwritten and Non-self handwritten, Printed letters) × Period (the ~20 Hz oscillations Suppression or Rebound) ANOVA was computed on the mean amplitude and peak Latency of the P100, N170. A similar ANOVA was computed for the mean amplitude of the 300–350 ms and the 500–600 ms time-window.

Besides, response time was computed for each Type of Letter and submitted to an ANOVA with the Type of Letter as repeated measures. Planned comparisons between relevant condition pairs were used to specify the effects.

Results

Behavioral data

The percentage of correct responses in the mirror discrimination task was on average 91.5% (SD: 8.04). Because no response was recorded on critical trials, the fact that participants had a high level of performance on mirror trials was a guarantee that they adequately perceived and identified the stimuli. Moreover, the ANOVA on the response time for mirror responses revealed a significant effect of the Type of Letter ($F_{2,28}=3.86$, $P<0.05$; Fig. 3). Planned comparisons only revealed that the response time to identify Printed letters in mirror orientation was longer than those necessary to identify mirror Self-handwritten letter ($F_{1,14}=5.72$, $P<0.05$).

ERP data

P100 component

The ANOVA revealed significant effects of the Type of Letter ($F_{2,28}=5.17$, $P<0.05$) and the Period ($F_{1,14}=11.59$, $P<0.005$) on the P100 peak amplitude. Planned comparisons only revealed that the P100 peak amplitude evoked by Printed letters differed significantly from those evoked by Self-handwritten letters ($F_{1,14}=13.03$, $P<0.005$) or by Non-self handwritten letters ($F_{1,14}=4.92$, $P<0.05$) (Fig. 4). There were no significant differences between the peak amplitude of the P100 as a function of the laterality of region considered. Neither effects nor interaction were significant on the peak latency of the P100.

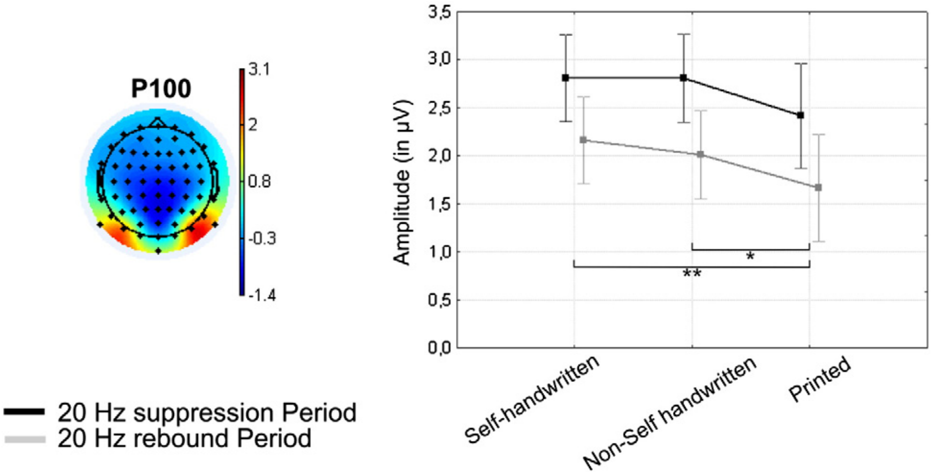

Fig. 4. (a) Scalp map distribution of the ERPs occurring 100 ms after the onset of the letter presentation (for the 3 conditions averaged). (b) P100 amplitude component (in µV) as a function of the Type of Letter presented (Self-handwritten, Non-self handwritten and Printed) and the Period of presentation (~20 Hz oscillations Suppression in black and ~20 Hz oscillations Rebound in grey). Each participant score was normalized by subtracting the participant's deviation score from the original score (for more details see Loftus and Masson, 1994). Error bars represent the 95% confidence intervals. (*) and (**) indicate that planned comparison is respectively statistically significant at $P<0.05$ and $P<0.01$.

N170 component

Mean peak amplitude and latency of the N170 did not differ as function of either the Type of letter or the Period of presentation. The interaction was not significant. Moreover, the ANOVA did not reveal any difference on the mean peak amplitude or latency of the N170 as function of the ROI considered.

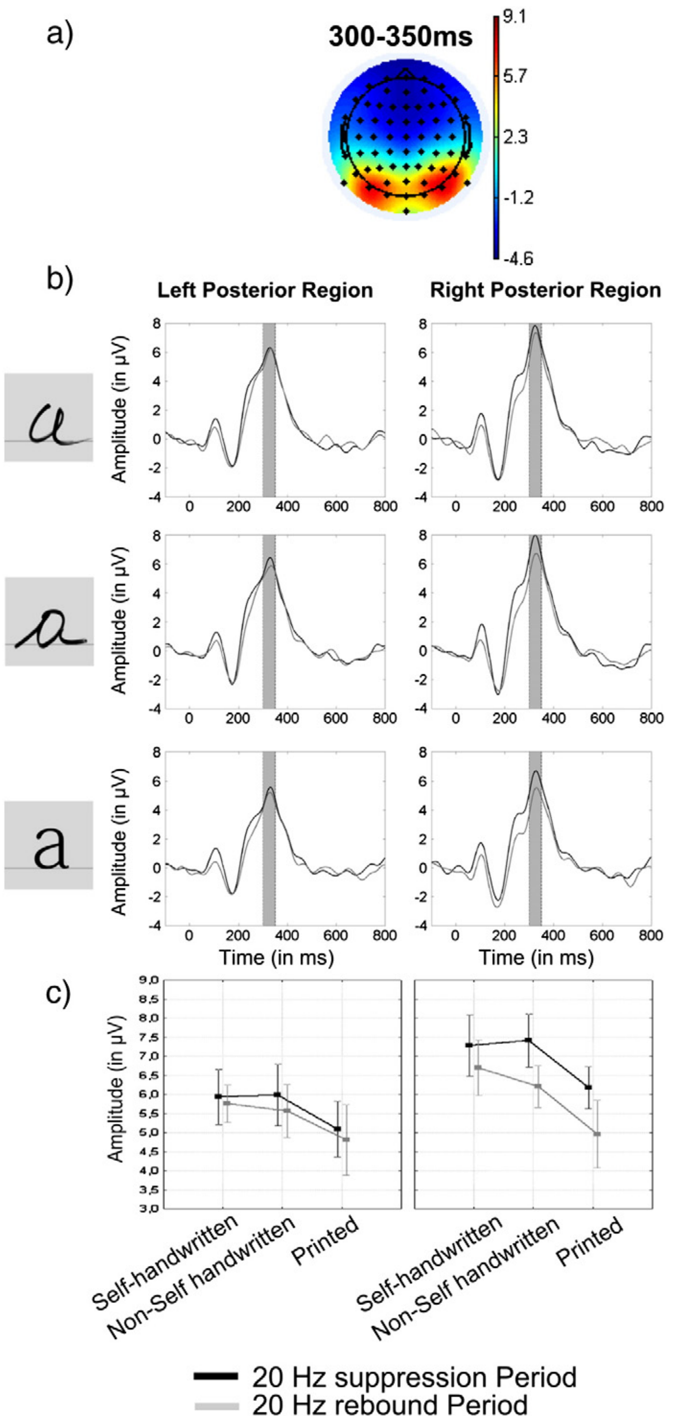

Fig. 5. (a) Scalp map distribution of the ERPs for the 300–350 ms time-window (for the 3 conditions averaged). (b) ERP waveforms recorded over left and right posterior region as a function of the Type of Letter and Period of presentation. The grey area represents the time-window of interest. (c) Mean amplitude of the 300–350 ms time-window (in μV) for the left and right posterior region as a function of the Type of Letter (Self-handwritten, Non-self handwritten and Printed) and the Period of presentation (~20 Hz oscillations Suppression in black and ~20 Hz oscillations Rebound in grey). Each participant score was normalized by subtracting from the original score, a participant deviation score (for more details see Loftus and Masson, 1994). Error bars represent the 95% confidence intervals. Significance of the effects is summarized in Table 1.

300–350 ms

The ANOVA revealed a main effect of the Type of Letter on the mean amplitude of the 300–350 ms time-window ($F_{2,28}=13.85$, $P<0.001$; Fig. 5). The ANOVA also revealed three significant interactions: ROI × Type of Letter interaction ($F_{2,28}=4.31$, $P<0.05$), ROI × Period interaction ($F_{1,14}=6.30$, $P<0.05$) and ROI × Type of Letter × Period interaction ($F_{2,28}=4.10$, $P<0.05$). During the Rebound, in the right posterior site, the potential showed a clear gradation of amplitude according to the motor familiarity of the stimuli. As presented in the Table 1, planned comparisons revealed that the amplitude of the positivity evoked by Self-handwritten letters in the right posterior region, was significantly greater than those evoked by Non-self handwritten letters ($F_{1,14}=4.72$, $P<0.05$) which, in turn, was significantly greater than the positivity evoked by Printed letters ($F_{1,14}=20.20$, $P<0.01$). The gradation of amplitude according to the motor familiarity of the letter was dropped (Fig. 5) during the Suppression. Indeed, during the Suppression, planned comparisons only revealed that the amplitude of the positivity evoked by Printed letters in the right posterior region differed significantly from those evoked by Self-handwritten letters ($F_{1,14}=8.44$, $P<0.05$) or by Non-self handwritten letters ($F_{1,14}=11.31$, $P<0.01$).

500–600 ms

The ANOVA revealed significant effects of the Type of Letter ($F_{2,28}=9.73$, $P<0.001$) and the Period ($F_{1,14}=7.74$, $P<0.05$) on the mean amplitude of the 500-600 ms time-window (Fig. 6). The ANOVA also revealed a significant Type of Letter × Period interaction ($F_{2,28}=4.21$, $P<0.05$). As presented in the Table 1, planned comparisons indicated that the amplitude of the positivity evoked by Self-handwritten letters, was significantly greater than those evoked by Non-self handwritten letters ($F_{1,14}=4.72$, $P<0.05$) which, in turn, was significantly greater than the positivity evoked by Printed letters ($F_{1,14}=20.20$, $P<0.01$). During the Rebound, the potential showed a clear gradation of amplitude according to the motor familiarity of the letters, whereas during the Suppression, this effect was dropped (Fig. 6). Indeed, during the Suppression, planned comparisons only revealed that amplitude of the positivity evoked by Printed letters in the parietal region differed significantly from those evoked by Self-handwritten letters ($F_{1,14}=4.65$, $P<0.01$) or by Non-self handwritten letters ($F_{1,14}=9.37$, $P<0.01$).

Discussion

In this experiment, we examined the modulation of the visual ERPs evoked by letters of different levels of motor familiarity as a function of the activation/"idling" state of the left primary motor cortex. Guided by the idea that visual observation of handwritten letters recruits the motor cortex more strongly than printed letters (Longcamp et al., 2006, 2011) and that action's authorships increases this effect (Knoblich and Flach, 2001; Knoblich et al., 2002), we hypothesized that some of the components of the visual evoked potentials would be related to the letter's level of motor familiarity. Even more, this motor familiarity effect would be impacted by the state of activation of the motor cortex.

Motor familiarity effects on ERPs

The main result of our study is that the amplitude of some components of the visual ERPs markedly reflected the letter's motor familiarity. This suggests that the motor information embedded in letters presented in static condition is processed in the brain: the more the letter corresponds to what the observers prefer produce, the higher the amplitude of the visual ERPs. This result is in line with behavioral data obtained during the observation of various motor skills suggesting that visual

Table 1
Summary of the planned comparisons computed between the three Types of Letter (Self-handwritten, Non-self handwritten and Printed) and the two Periods (~20 Hz oscillations Suppression and Rebound) and their corresponding regions (left and right posterior regions and parietal region) on the mean amplitude of the 300–350 ms and 500–600 ms time-windows. "Significant" indicates that planned comparison is statistically significant at $P<0.05$ whereas "NS" indicates $P>0.05$.

	300–350 ms Time window				500–600 ms Time window	
	Left posterior region		Right posterior region		Parietal region	
	~20 Hz suppression	~20 Hz rebound	~20 Hz suppression	~20 Hz rebound	~20 Hz suppression	~20 Hz rebound
Self-handwritten vs. Non-self handwritten	NS	NS	NS	Significant	NS	Significant
Non-self handwritten vs. Printed	Significant	Significant	Significant	Significant	Significant	Significant
Self-handwritten vs. Printed	Significant	Significant	Significant	Significant	Significant	Significant

recognition depends on the motor familiarity of the action observed (Calvo-Merino et al., 2010; Casile and Giese, 2006; Knoblich and Flach, 2001; Martel et al., 2011). This result fits the classical common coding models for action perception, in which representations of external visual input overlap with the observer's own motor representations of the same actions (Schutz-Bosbach and Prinz, 2007).

The motor familiarity effects are dropped when the primary motor cortex is activated

More interestingly, our paradigm allows to directly relate this effect of motor familiarity to the state of the motor cortex at the time when the letter is presented. Indeed, the gradation of amplitude as a function of the motor familiarity of the letter was dropped when the letter was presented during the period of activation of the primary motor cortex. During this period, the amplitude of the ERPs to both types of handwritten letters was similar, and only the difference between printed and both types of handwritten letters was significant. This means that when the primary motor cortex is not available for the visual task, the brain is still able to discriminate between printed and handwritten letters in general (possibly because handwritten letters are visually more complex; see below the discussion of a similar complexity effect on the P100), but does no longer finely distinguish the motor content of the stimulus. This suggests that visual processing of the motor related information is dependent of the "availability" of the left primary motor cortex. These neurophysiological observations extend previous behavioral results observed with a comparable dual-task paradigm, during visual observation of traces of biological motion (Wamain et al., 2011). Indeed, in this study, we revealed that when the primary motor cortex was activated by the execution of a dominant hand movement, the concurrent visual discrimination of graphic traces containing relevant motor information was impaired. Taken together, our results demonstrate that visual processing of graphic traces is dependent on the input of the primary motor cortex.

Possible role of the primary motor cortex activation during visual processing of letters

Importantly, our data provide crucial information on the timing of the interaction between visual processing of the letters of distinct motor familiarities and activation of the primary motor cortex. An interaction occurred at 300–350 ms and 500–600 ms.

At 300–350 ms, the effect was restricted to the right posterior region, consistent with several recent studies showing a stronger involvement of right hemispheric occipital regions for the processing of handwritten letters (Barton et al., 2010b; Heckmann et al., 2001; Hellige and Adamson, 2007; Longcamp et al., 2011; Qiao et al., 2010). This right-sided effect has been hypothesized to be related to the processing of shape properties that are necessary for script style identification (Barton et al., 2010b). Our result therefore raises the possibility that when handwritten letters are observed, an implicit processing of script style is carried out through an interaction between the left primary motor cortex and the right-hemispheric visual cortices, and that script style identification is dependent on the motor content of the stimulus. The most likely substrate for this interaction in the posterior region is the right-homologue of the visual word form area (Barton et al., 2010a; Qiao et al., 2010). Nonetheless, neural populations involved in biological motion perception might also play a role, since handwritten letters are traces of biological motion and biological motion analyses are carried out at similar latencies (between 260 and 360 ms) in the right posterior region (Jokisch et al., 2005; Krakowski et al., 2011). The timing of this effect nicely fits recent data by Nakatsuka et al. (2012) who used single pulse TMS to show that at 300–400 ms after visual stimulus onset, the cortico-spinal excitability decreased more when participants viewed handwritten than printed letters.

The interaction observed in the 500–600 ms time window is also consistent with the known latency of the motor cortex activation during visual perception of stimuli implying actions (Nishitani et al., 2004; Papeo et al., 2009; Proverbio et al., 2009). In addition, in visual recognition tasks, components of the evoked potentials at around 500–600 ms are also known to be responsible for recollection (for review Friedman and Johnson, 2000), their amplitude being related to the amount of knowledge of the observed stimulus (Smith, 1993; Touryan et al., 2011). It is therefore possible that the information coded by the primary motor cortex participates in the recollection process, probably because the knowledge related to the movement is necessary to produce the letter is critical. Behavioral data exhibit a greater response time to printed letters than to self-handwritten letters. Because the response time for Non-self-handwritten letters was intermediate, the relative advantage of self-handwritten compared to printed letters can also be interpreted as a function motor familiarity. However, the absence of an interaction between the type of letter and the activation state of the motor cortex in these behavioral data makes it difficult to conclude that the motor cortex has an actual influence on the behavioral responses.

Other results

Other results suggest that neither the type of letter nor the state of the motor cortex affected the amplitude of the N170 component, known to reflect abstract letter identification (Rey et al., 2009). This corroborates that processes occurring at this latency are independent from the script style observed.

Our results revealed a mean effect of the type of letters on the amplitude of the P100 component, related to a global difference between handwritten and printed letters, independent of motor familiarity. This effect is not really surprising since the P100 component, known to reflect processing dedicated to low-level (feature-based) analysis (Grainger et al., 2008; Rey et al., 2009), is smaller for printed letters which are, by definition, visually less complex (Babcock and Freyd, 1988; Corcoran and Rouse, 1970; Hellige and Adamson, 2007; Wagner and Harris, 1994). This effect was compatible with the visual complexity of the letter on the amplitude of the component P100. It appeared also on the two time windows 300–350 ms and 500–600 ms when the letter was presented during the period of activation of the primary motor cortex (~20 Hz oscillation suppression).

Finally, a main effect of the period of presentation was found on the amplitude of the P100 component revealing a larger component when the letter was presented during the ~20 Hz oscillations suppression

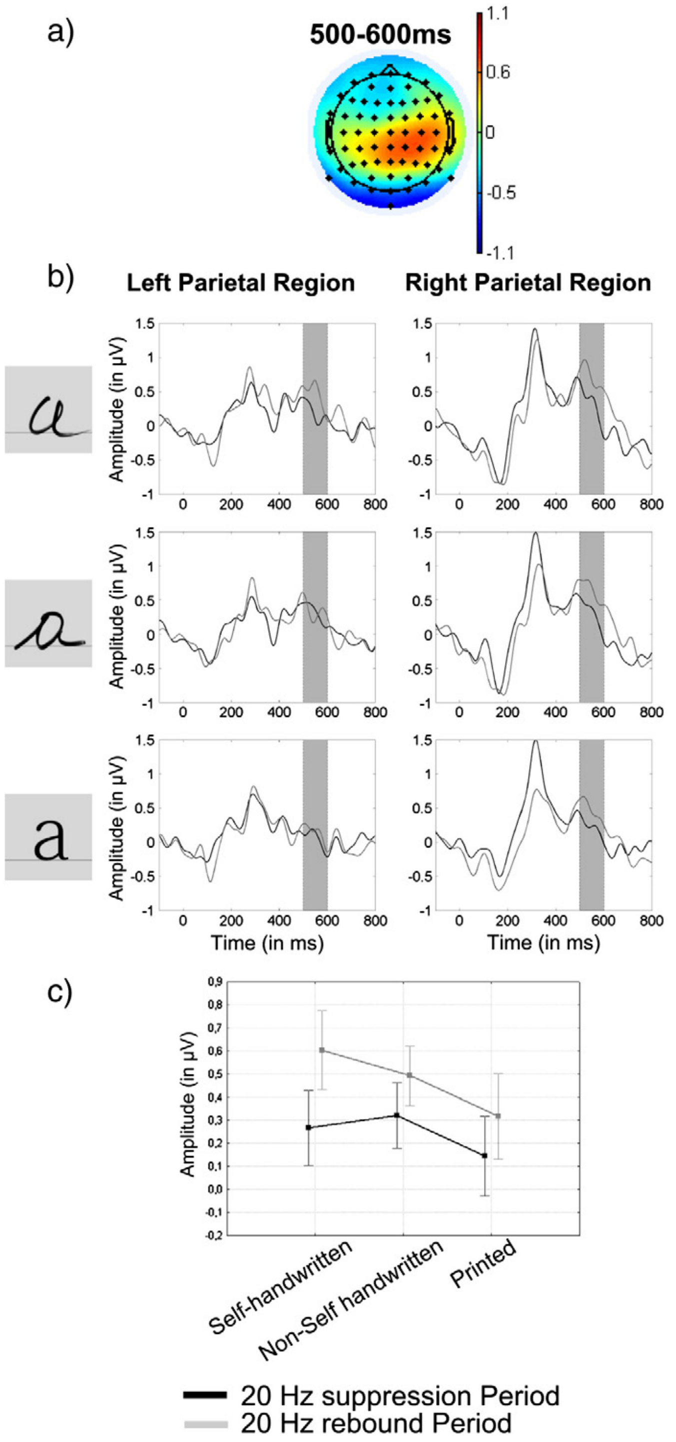

Fig. 6. (a) Scalp map distribution of the ERPs for the 500–600 ms time-window (for the 3 conditions averaged). (b) ERP waveforms recorded over left and right parietal region as a function of the Type of Letter and Period of presentation. The grey area represents the time-window of interest. (c) Mean amplitude of the 500–600 ms time-window (in μV) for the left and right parietal region as a function of the Type of Letter (Self-handwritten, Non-self handwritten and Printed) and the Period of presentation (~20 Hz oscillations Suppression in black and ~20 Hz oscillations Rebound in grey). Each participant score was normalized by subtracting from the original score, a participant deviation score (for more details see Loftus and Masson, 1994). Error bars represent the 95% confidence intervals. Significance of the effects is summarized in Table 1.

period compared to ~20 Hz oscillation rebound period. This global effect on early visual processing of letters is possibly related to more general attentional factors associated with the dual task. First, it is possible that when the stimulus occurs close to the onset of the wrist extension, participants are monitoring their movement and has less attentional resources to allocate to the visual signal. However, it is known that decreases in attention are related to lower amplitude P100 components (Mangun and Hillyard, 1991). However, our results show the inverse pattern of results: during movements, the amplitude of the occipital P100 increased. Alternatively, the effect of period on the amplitude of the P100 component is compatible with observations by Correa's team suggesting that the onset of the wrist extension could be a signal which induces a greater "temporal attention" (i.e., expectation) of the participant to visual stimuli, and consequently an increase of the P100 amplitude (Correa et al., 2006).

Conclusion

In summary, our data indicate that the activation of the left primary motor cortex has a functional impact on the visual processing of handwritten letters as early as 300 ms post-stimulus-onset. This impact is most important for the letters in which the motor-related information is the most relevant, that is, the letters produced by the observers themselves. The relative earliness of this effect, compared to the estimated latency of activation of the motor cortex in such tasks (Nishitani et al., 2004; Proverbio et al., 2009), strongly suggests that the oscillatory state of the motor cortex exerts a top-down influence on the posterior regions responsible of visual processes such as script style analysis. Further work is required to establish the exact nature of this influence.

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