

Through the looking-glass: Mirror reading

Jon Andoni Duñabeitia¹, Nicola Molinaro¹ and Manuel Carreiras^{1,2,3}

¹ Basque Center on Cognition, Brain and Language (BCBL); Donostia, Spain.

² IKERBASQUE. Basque Foundation for Science; Bilbao, Spain.

³ University of the Basque Country; Vitoria-Gasteiz, Spain.

Address for correspondence:

Jon Andoni Duñabeitia

BCBL: Basque Center on Cognition, Brain and Language

Paseo Mikeletegi 69

20009, Donostia (Spain)

phone: +34 678635223

email: j.dunabeitia@bcbl.eu

Abstract

At early stages of object identification we process correctly-oriented and mirrored versions of an object similarly. However, in letter and word perception, such tolerance to mirror reversals is harmful for efficient reading. Do readers successfully develop blindness mechanisms for mirror-letters and words? We conducted two masked priming experiments while recording participants' electrophysiological brain responses to briefly presented primes including mirror-letters (Experiment 1) or to shortly presented mirror-words (Experiment 2). Results showed that the human visual word recognition system is not totally blind to mirror-letters and mirror-words, since at early stages of processing mirror-letters and mirror-words produced effects on target word recognition that were highly similar to the effects produced by identical primes (N250 component). In a posterior stage of processing (N400 epoch), the effect of mirror-letters and mirror-words were different from the effect of identical primes, even though reversed primes still elicited N400 priming effects different from unrelated primes. These results demonstrate that readers perceive mirror-letters and words as correct at initial stages of word recognition, and that the visual word recognition system's neural representation is grounded on basic principles that govern object perception.

Keywords: masked priming; mirror-words; reading; visual word recognition.

Through the looking-glass: Mirror reading

1. Introduction

Object and word recognition seem to rely on overlapping visual brain pathways (Dehaene, Cohen, Sigman, & Vinckier, 2005; Logothetis & Sheinberg, 1996; Nobre, Allison, & McCarthy, 1994). The “recycling hypothesis” proposed by Stanislas Dehaene and collaborators (Dehaene et al., 2005, 2010) suggests that the areas involved in object recognition are recycled for visual word recognition, under the premise that it is hardly plausible that relatively recent milestones in the human evolutionary process like reading and writing have led to the creation of domain-specific neural networks. However, this “one for all” characterization of a unique visual system dedicated to the perception and processing of a large number of units from a different nature (e.g., pictures, faces, words) poses a clear problem which stems from the way in which the brain responds to enantiomorphs (i.e., lateral mirror clones). While object orientation is irrelevant at critical moments during the recognition process (Walsh, 1996), letter and word orientation are crucial for efficient visual word recognition (Caramazza & Hillis, 1990).

Reduced populations of neurons at the inferotemporal cortex of monkeys and the human lateral occipital complex are selective for image orientation (Gross, Bender, & Rocha-Miranda, 1969; Rubin, 2001), and respond to both the original and the lateral mirror versions of an image (Rollenhagen & Olson, 2000; Tomasino, Borroni, Isaja, & Rumiati, 2005). From a phylogenetic perspective this mirror-image generalization has been very useful for primate survival (“*a tiger is equally threatening when seen in right*

or left profile”, Rollenhagen & Olson, p. 1506). Thus, mirror generalization is an adaptive mode of processing visual information (Bornstein, Gross, & Wolf, 1978) grounded in an intrinsic property of the primate visual system. However, this generalization is disadvantageous when the object to be recognized is a word or letter, since letter enantiomorphs might change the canonical representation of the letter (Caramazza & Hillis, 1990). Consequently, it has been proposed that mirror generalization must be partially inhibited or unlearned when learning to read (Dehaene et al., 2005, 2010), because visual recognition of word or letter enantiomorphs results in a slowing of the process and a loss of accuracy (e.g., Poldrack et al., 1998). Nonetheless, can an intrinsic property of the visual system which is active for object identification during adulthood be completely “unlearned” or suppressed for a specific accommodation of the visual system to letter or word recognition? Although the human brain must override sensitivity to word or letter enantiomorphs for effective reading, does the human brain become truly irresponsive to them?

According to a number of studies, explicit manifestations of mirror reading and/or writing (i.e., insensitivity to letter or word enantiomorphs) are evident in children only until they start acquiring certain level of proficiency in these skills (e.g., Cornell, 1985). During adulthood this insensitivity might only reappear as a consequence of brain damage, as shown by Pflugshaupt et al. (2007). Thus, explicit mirror-reading behaviour is not present in unharmed competent readers, leading to the conclusion that, as proposed by Dehaene et al. (2005, 2010), mirror generalization is inhibited for efficient reading. However, the critical question that arises at this respect is whether the underlying mechanism that operates in order to eliminate explicit enantiomorph reading or writing is indeed inhibition or whether it is unlearning. If this visual property is constantly exposed to a suppression or inhibition process only when perceivers face

letters and words, then it might be feasible to assume that reminiscences of the “natural” mirror generalization processes could be observed at very early stages of word processing (i.e., within the interface between purely visual processing and pre-orthographic assembly of the letters and words). If, on the contrary, the main operation is based on an unlearning process, this would result in a selective perceptual process by which only correctly oriented letters and words would constitute the valid raw material for the visual word recognition system, consequently implying a total blindness to mirror-letters and mirror-words.

To explore the sensitivity of readers to mirror reversals of readable material the technique and paradigm chosen should allow for fine-grained temporal analysis and be appropriate for tapping into automatic processes of word and letter processing, since we assume that mirror generalization is an automatic process that occurs early in the course of perception. In a recent study Dehaene et al. (2010) explored whether French and Japanese adult expert readers with no brain lesions were sensitive to mirror-words, using high-resolution functional Magnetic Resonance Imaging (fMRI) combined with the masked priming paradigm (which has been shown to be well-suited to explore the underlying automatic processes of word processing; see Kinoshita & Lupker, 2003). Participants were presented with images and words that were shortly preceded (for 50 ms) by themselves (an identity priming condition), by the mirror version of themselves, by an unrelated image or word, or by the mirror version of the unrelated item. Both behavioural and imaging results confirmed that mirror-invariance was only present for pictures (i.e., they obtained mirror priming effects for pictures), while this was not the case for words, for which only identical non-reversed primes effectively affected target processing. These findings led the authors to conclude that “*in the course of learning to*

read, a special interpretation must be given to letters as two-dimensional objects, thus blocking mirror generalization” (Deahene et al., 2010, p. 1845).

-Insert Figure 1 around here-

Here we aimed to probe the existence of a word and letter recognition stage at which readers’ brains do not discriminate between correctly oriented letters and words and their enantiomorphs. But in order to do so, we opted for using Event-Related Potentials (ERPs). The selection of the technique is not a trivial issue. Early short-living activation differences can be overlooked by a technique like fMRI, in which the final by-product of neural activation within large temporal windows is extracted. Thus, the use of a technique like ERPs that allows for discrimination of neural activity with a fine-grained temporal resolution seems highly appropriated. Moreover, if it is indeed the case that readers initially take mirror-letters and mirror-words as the correct ones, and then suppress or block this information in posterior stages, ERPs could unravel the time-course of these processes, while fMRI could be under the risk of neglecting the initial processing stages.

2. Experiment 1

2.1. Method

2.1.1. Participants. Twenty-seven undergraduate students (18 women) from the University of La Laguna took part in the experiment for course credit. All of them were native Spanish speakers, with no history of neurological or psychiatric impairment and

with normal or corrected-to-normal vision. All participants were right handed, as assessed with an abridged Spanish version of the Edinburgh Handedness Inventory (Oldfield 1971). They all signed consent forms and were informed of the procedure of the experiment before starting. They were also told that this experiment was approved by the Ethics Committee of the research group.

2.1.2. Materials. The critical materials consisted of 210 words (mean frequency: 14.2; mean length: 8.6). We selected the letters A, E, R and C as the critical letters that were subject to rotation, and all these words contained at least 3 of these letters, representing 44% ($\pm 9\%$) of the total, on average. None of the words included any of these letters in initial or final position. These words were presented as targets, and could be preceded by 1) identical primes (Identity condition), 2) identical primes containing rotated letters (Mirror condition), or 3) primes in which the critical letters were replaced by other rotated letters (Control condition). None of these words referred to an animal name, and 30 target animal names were selected in order to create the go trials. These 30 animal names were also presented as primes during the experiment, followed by 30 unrelated words that were not animal names. This was used as a prime visibility test in order to confirm that participants were unaware of the existence of the masked primes (note that participants were instructed to respond only to animal names, and responses to these animal primes would demonstrate conscious processing of the masked primes). This is a generalized procedure in electrophysiological or neuroimaging masked priming studies (see Carreiras et al., 2009).

2.1.3. Procedure. The experiment was run in a soundproof room. Participants were presented with the stimuli on a high-resolution monitor that was positioned at eye level

80 cm in front of the participant. Each trial consisted of the presentation of a forward mask created by hash mark symbols for 500 ms, followed by the displaying of the prime for 50 ms, and immediately followed by the presentation of the target. Primes and targets were presented in lowercase. Critically, in order to minimize physical overlap between primes and targets, different font sizes were used for these strings. Target items remained on the screen for 500 ms. The inter-trial interval varied randomly between 700 and 900 ms. After this interval, an asterisk was presented for 1000 ms in order to allow for participants' blinks. Participants performed a go/no-go semantic categorization task: They were instructed to press the spacebar on the keyboard only when the letter string displayed referred to an animal name. Participants were asked to avoid eye movements and blinks during the interval when the row of hash marks or the asterisk was not present. Considering the practice session, the experiment lasted approximately 1 h and 15 min.

2.1.4. EEG Recording and Analyses. Scalp voltages were collected using a BrainAmp recording system from 60 Ag/AgCl electrodes that were mounted in an elastic cap (ElectroCap International, Eaton, USA, 10-10 system). The left earlobe was used as reference. Eye movements and blinks were monitored with 4 further electrodes providing bipolar recordings of the horizontal and vertical electrooculogram. EEG was filtered with an analogue band-pass filter of 0.01--100 Hz, and a digital 30-Hz low-pass filter was off-line applied before analysis. The signals were sampled continuously throughout the experiment with a sampling rate of 256 Hz. Off-line the signal was re-referenced to the averaged signal of the two earlobes. Based on the target word presentation onset, only trials free of artifacts were averaged and analyzed after ocular inspection (more than 95% of the trials). Epochs of the EEG up to 600 ms after the

onset of the target word were the primary data. The baseline correction was performed using the average EEG activity in the 200 ms preceding the target. Separate ERPs were obtained for each of the experimental conditions, each subject, and each electrode.

Statistics were performed on the mean ERP amplitude values in specific time windows. ERPs were evaluated with an overall two-way Greenhouse-Geisser corrected ANOVA in which the critical factors were Condition (three levels: Identity, Mirror, Control) and Cluster (four levels: Frontal, Central, Parietal and Occipital). Each cluster of electrodes was obtained averaging the amplitude values across five contiguous electrodes in representative scalp areas: Frontal (F3, F1, Fz, F2, F4), Central (C3, C1, Cz, C2, C4), Parietal (P3, P1, Pz, P2, P4), Occipital (PO7, O1, Oz, O2, PO8). We did not consider possible hemispherically lateralized effects since no critical evidence in this direction has been reported in the masked priming literature (see Grainger & Holcomb, 2009). We run separate analyses in small time windows every 50 ms starting from the target word onset until 500 ms. This analysis could show both the onset and the latency of a critical ERP effect. Post-hoc comparisons were performed comparing the three critical conditions in a pairwise manner for each cluster of electrodes. Based on the previous literature we critically monitored possible effects around 150-200 ms (N/P150 and N250 components) and around 400 ms (N400).

2.2. Results

2.2.1. Behavioral data. The behavioural results from the go trials showed that participants correctly categorized more than 98% of the animal target words. Contrarily, when they were presented as primes, only 0.3% of the animals were recognized, showing that participants did not consciously process the masked primes.

2.2.2. ERPs. Between 150 and 200 ms a main effect of prime Condition emerged ($F(2,52)=3.77$, $p<0.05$, $\eta^2=.127$). Post-hoc comparisons (see Table 1) showed that the Identity and Mirror conditions did not differ from each other, but in turn, these two conditions differed from the Control condition, which was more negative-going. These differences tended to be more prominent at parietal and occipital Clusters around 200 ms, as shown in Table 1; Nonetheless, the overall ANOVA did not show any interaction between Condition and Cluster ($F(6,156)<1$), the effect. This time window is associated with the early N250 component reported in the masked priming ERP literature (see Grainger, Kiyonaga, & Holcomb, 2006; see also Grainger & Holcomb, 2009, for review).

-Insert Figure 2 and Table 1 around here-

2.3. Interim conclusions

Experiment 1 revealed that at very early stages of word processing, letter identification is subject to the same tolerance to enantiomorphs as object identification, being insensitive to lateral reversals of the processing units (i.e., taking incorrectly oriented letters as correct). In the critical 150-200 ms epoch, that has been typically related to sub-lexical processing of orthographic units (see Grainger & Holcomb, 2009), both masked words including mirror-letters and correctly written masked words were processed similarly, and differently from control primes (strings containing unrelated mirror-letters). This was attested by a general difference in the N250 time window between Identity and Mirror conditions as compared to the Control condition.

Importantly, no significant differences were observed between the Mirror and the Identity conditions.

However, it should be considered that the most stable existing attractor for a mirror-letter will undeniably be the correct letter, due to the high visual overlap between them, and therefore, it could have been the case that the processing advantage observed for related enantiomorphs was a consequence of their greater visual overlap as compared to unrelated enantiomorphs. For this reason, in Experiment 2 we created a new set of materials that included masked primes that were identical to the target, mirror versions of the whole target word or unrelated mirror versions of a completely different string (see Figure 1). This manipulation represents a stronger test of our hypothesis of the existence of an orthographic processing stage that is tolerant to enantiomorphs (as occurs with other visually processed objects). Furthermore, considering that mirror-words do not visually overlap with their correct representation at all, finding similar brain activation for identical and mirror-reversed unconsciously processed primes as compared with unrelated primes would strongly support our initial hypothesis and this could not be accounted for by explanations based on visually overlapping features of the strings.

3. Experiment 2

3.1. Method

3.1.1. Participants. Twenty-seven right-handed undergraduate students (12 women) from the University of La Laguna participated in the experiment in exchange for course credit. All of them were native Spanish speakers, with no history of neurological or

psychiatric impairment and with normal or corrected-to-normal vision. As in Experiment 1, they all were informed about the procedure of the experiment and signed consent forms.

3.1.2. Materials. A new set of 264 Spanish words was selected for this experiment (mean frequency: 36.4; mean length: 4.8). These words did not contain any B, D, P or Q, since the reversal of the lowercase version of each of these letters leads to a different letter. Moreover, symmetric letters (e.g., O, W, V) were avoided to a great extent (more than 80% of the letters were asymmetric). As in the first experiment, none of these words was an animal name. These words were presented as targets, and could be preceded by 1) identical primes (Identity condition), 2) identical primes that had been completely rotated in the vertical axis creating whole-word mirrors (Mirror condition), or 3) unrelated nonword primes made of unrelated letters that had been also fully rotated in the vertical axis (Control condition). As in Experiment 1, a set of animal names was used in order to create the go trials. Also, as in the previous experiment, the set of animal names was presented as masked primes too, followed by unrelated words referring to non-animal names, in order to create the prime visibility test.

3.1.3. Procedure. The same procedure as in Experiment 1 was followed.

3.1.4. EEG Recording and Analyses. The same procedure as in Experiment 1 was followed.

3.2. Results

3.2.1. Behavioral data. The behavioural results from the go trials showed that participants correctly categorized more than 98% of the animal target words. Contrarily, when they were presented as primes, less than 0.2% of the animals were recognized, showing that participants did not consciously process the masked primes.

3.2.2. ERPs. A more complex pattern of ERP effects emerged in this experiment. At occipital electrodes two subsequent peaks were evident (see Figure 2b). An early peak around 140 ms was more negative-going for words preceded by an Identity prime compared to words preceded by a Mirror or Control prime as showed by an interaction between prime Condition and Cluster of electrodes (100-150 ms: $F(6,156)=8.991$, $p<0.01$, $\eta^2=.257$, see post-hoc comparisons in Table 2). This effect can be interpreted as an N/P150 component, sensitive to the retinotopic visual overlap between prime and target, with Identity being the only physically overlapping condition with respect to the target. Similar to the results found in the first experiment, a main effect of Condition emerged around 200-250 ms ($F(2,52)=4.704$, $p<0.05$, $\eta^2=.153$); the negative peak was larger for words preceded by Control primes as compared to the other two conditions (Mirror and Identity, which did not differ from each other). This effect was mainly evident at central, parietal and occipital sites, as suggested by a marginally significant interaction between Cluster and Condition, $F(6,156)=2.818$, $p=0.063$, $\eta^2=.098$ (see pairwise contrasts in Table 2). At around 450 ms, a graded pattern was observed: Words preceded by Control primes elicited a more negative deflection compared to words preceded by Mirror primes, which, in turn, elicited a more negative deflection compared to words preceded by Identity primes; main effect of Condition emerged in the 400-450 ms interval ($F(2,52)=6.634$, $p<0.05$, $\eta^2=.203$) and in the 450-500 ms interval

($F(2,52)=14.532, p<0.01, \eta^2=.359$). This latter component was identified as an N400 (see post-hoc contrasts in Table 2).

-Insert Table 2 around here-

4. Discussion

These results reveal that expert readers perform an implicit, automatic and unconscious mirror reversal generalization of mirror-letters and mirror-words. Furthermore, as shown by Experiment 2, these effects cannot be accounted for by explanations based on pure visual overlap. Hence, at sub-lexical levels of processing, mirror generalization plays an important role: Mirror-letters and words are (mis)identified as the correct ones. Thus, mirror generalization (i.e., tolerance to enantiomorphs) as a principle of the visual system has a significant reflection in visual word recognition despite canonicity constraints.

The critical effects in these Experiments were mainly evident in the N250 component. This component has been proved to be sensitive to the degree of prime-target orthographic overlap (e.g., Carreiras et al., 2009; Duñabeitia et al., 2009; Grainger & Holcomb, 2009). Accordingly, the present results could be interpreted as showing that at sub-lexical level, mirror generalization plays an important role: Mirror-letters and mirror-words are (mis)identified as the correct letters and words, and therefore activate whole-word representations to the same extent as non-mirrored words and letters do. Considering that the N250 responses were not graded for Identity and

Mirror primes, it is plausible to assume that mirror-letters and mirror-words were in fact being processed as the canonical versions.

While the results observed in Experiment 1 are highly suggestive, it should be acknowledged that the similar pattern found in the N250 epoch for Mirror and Identity conditions could have been the consequence of the greater visual similarity existing between a canonically displayed letter and its enantiomorph, as compared to an unrelated letter (Control condition). However, this criticism does not apply to the pattern observed in Experiment 2, where whole words were reversed in order to create the Mirror masked primes, thus limiting the visual similarity between Mirror primes and their corresponding targets.

Importantly, the results of Experiment 2 are very illustrative for understanding how the human visual word recognition system processes word enantiomorphs. As suggested by the significant difference found at occipital sites in the epoch corresponding to the N/P150 component for the Identity condition as compared to both the Mirror and the Control conditions (i.e., the strings with rotated letters), the perceptual system initially takes the canonical materials as known objects, while this is not the case for the mirrored (related and unrelated) strings. Indeed, Identity primes are the only ones that visually match the targets, despite the small physical change induced by the prime-target font size variation used. In a posterior stage of processing, corresponding to the N250 epoch (which has been generally linked to sub-lexical processing; see Carreiras et al., 2009; Grainger & Holcomb, 2009), Mirror masked primes are taken as primes in the Identity condition, on the basis of a fast-acting automatic process of mental rotation of the whole-words, under the assumption that at initial stages of processing, words can be holistically taken as other visual objects, therefore being subject to general visual principles of mirror generalization (Poldrack et

al., 1998). Nonetheless, considering the specific nature of words, a subunit-based decomposition process is then followed for efficient word recognition (note that syllabic and morphemic units are accessed at early staged of word processing; see Duñabeitia, Perea, & Carreiras, 2008). Following the time course of mirror-word perception unravelled in Experiment 2, in a later epoch (characterized as N400) where the visually processed strings are mapped onto mentally stored lexico-semantic representations, the Mirror condition significantly deviates from the Identity condition, evidencing that despite the earlier tolerance to mirror reversals found in the N250 epoch, the human mental lexicon does not store word enantiomorphs, and therefore there's no perfectly matching abstract word representation to be found for mirrored primes. However, most likely as a consequence of the initial activation elicited by reversed related masked primes (Mirror condition), residual target activation of these strings still elicit effects that are different from those obtained for mirror unrelated masked primes (Control condition).

Previous fMRI evidence has suggested that mirror-words do not activate the corresponding correctly oriented words (Dehaene et al., 2010). However, in the present study a masked mirror priming effect has been shown in two experiments using ERPs. As stated before, it should be considered that due to the early nature of this effect, the selection of the appropriate technique which also taps onto the earliest automatic processes of word recognition is clearly needed. We believe that this is the apparent reason for the observed difference between the present study and that of Dehaene et al.

These results are of special relevance for biologically plausible models of word recognition (e.g., Dehaene et al., 2005; Grainger & Van Heuven, 2003; Whitney, 2001). These models assume that letter detectors are invariant to the physical characteristics of letters (such as size and shape), so that minimal variations that do not contravene the

canonical image can be overlooked in order to access abstract letter representations. In the light of the present results, these models should also concede that as a consequence of a general property of the visual system, some variants of a letter that violate the canonical representation (such as mirror-letters) are processed as simple allographs by the letter detectors. In summary, we have shown that a general neural property of the human brain, the outcome of deeply-rooted evolutionary development, cannot be fully suppressed for a recently acquired skill, and that although its effect might not be explicitly evident in daily behaviour, it is implicitly observed at ballistic and automatic stages of processing.

Acknowledgements

This work was partially funded by CONSOLIDER-INGENIO CSD2008-00048 and PSI2009-08889 grants from the Spanish Ministry of Education and Science. The authors are grateful to the anonymous reviewers for their helpful comments on an earlier version of this manuscript.

Table 1. Time course of the priming effects in Experiment 1: Results of tests of significance every 50 ms time window for four groups of Electrodes: Frontal (average activity of F3, F1, Fz, F2, F4), Central (C3, C1, Cz, C2, C4), Parietal (P3, P1, Pz, P2, P4), Occipital (PO7, O1, Oz, O2, PO8). F-values (d.f. 1,26 Greenhouse-Geisser corrected) in bold characters are significant; we reported the relative η^2 between brackets.

Identity versus Control				
<i>Epochs (ms)</i>	<i>Frontal</i>	<i>Central</i>	<i>Parietal</i>	<i>Occipital</i>
0-50	0.866	1.359	1.218	2.907
50-100	0.087	0.002	0.116	1.083
100-150	1.371	0.833	1.062	1.279
150-200	4.769 (0.155)	8.219 (0.240)	6.615 (0.203)	2.890
200-250	0.702	0.799	2.277	4.669 (0.152)
250-300	0.404	0.674	1.238	0.015
300-350	0.962	4.743 (0.154)	4.968 (0.160)	1.565
350-400	1.612	1.787	1.503	4.182
400-450	0.008	0.019	0.050	0.948
450-500	1.283	1.605	0.931	0.726
Identity versus Mirror				
<i>Epochs (ms)</i>	<i>Frontal</i>	<i>Central</i>	<i>Parietal</i>	<i>Occipital</i>
0-50	0.317	0.198	0.045	1.049
50-100	0.429	0.075	0.150	0.331
100-150	0.281	0.001	0.361	1.245
150-200	1.052	0.052	0.409	0.492
200-250	0.142	0.362	0.250	0.032
250-300	0.022	0.013	0.188	1.653
300-350	0.942	1.449	0.792	0.455
350-400	0.001	0.085	0.120	0.152
400-450	0.115	0.242	0.350	0.082
450-500	0.308	0.731	1.658	1.705
Mirror versus Control				
<i>Epochs (ms)</i>	<i>Frontal</i>	<i>Central</i>	<i>Parietal</i>	<i>Occipital</i>
0-50	0.123	0.430	0.806	0.181
50-100	0.033	0.065	0.001	0.216
100-150	3.250	1.075	0.357	0.047
150-200	2.477	4.120	4.870 (0.158)	2.656
200-250	0.257	2.157	3.865	5.583 (0.177)
250-300	0.170	0.288	0.197	2.146

300-350	0.001	2.047	4.064	1.240
350-400	1.123	2.211	1.982	4.079
400-450	0.149	0.573	0.280	0.225
450-500	4.173	3.976	2.512	2.039

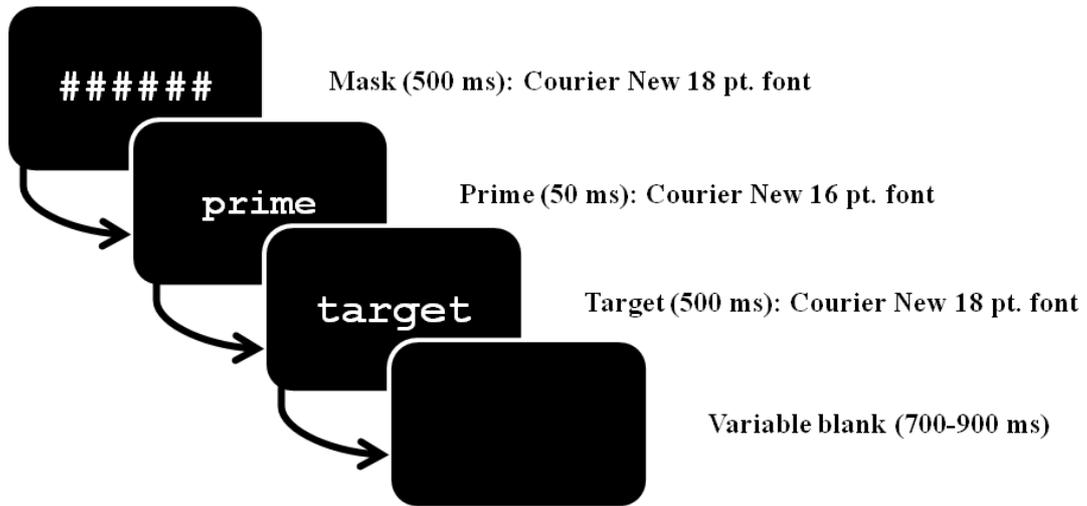
Table 2. Time course of the priming effects in Experiment 2: Results of tests of significance every 50 ms time window for four groups of Electrodes: Frontal (average activity of F3, F1, Fz, F2, F4), Central (C3, C1, Cz, C2, C4), Parietal (P3, P1, Pz, P2, P4), Occipital (PO7, O1, Oz, O2, PO8). F-values (d.f. 1,26 Greenhouse-Geisser corrected) in bold characters are significant; we reported the relative η^2 between brackets.

Identity versus Control				
<i>Epochs (ms)</i>	<i>Frontal</i>	<i>Central</i>	<i>Parietal</i>	<i>Occipital</i>
0-50	0.092	0.001	0.097	0.013
50-100	1.221	2.400	2.197	1.888
100-150	0.099	0.126	1.776	4.946 (0.160)
150-200	1.115	0.048	2.090	2.788
200-250	2.528	5.198 (0.152)	10.784 (0.273)	14.853 (0.341)
250-300	4.539	3.876	4.137	3.651
300-350	1.297	0.127	1.006	2.663
350-400	3.218	3.545	0.036	1.907
400-450	11.634 (0.279)	10.284 (0.258)	6.385 (0.189)	5.645 (0.184)
450-500	11.256 (0.297)	17.405 (0.387)	21.893 (0.427)	18.992 (0.413)
Identity versus Mirror				
<i>Epochs (ms)</i>	<i>Frontal</i>	<i>Central</i>	<i>Parietal</i>	<i>Occipital</i>
0-50	0.505	0.033	0.970	0.607
50-100	0.055	0.003	0.001	0.595
100-150	3.713	1.334	0.743	5.978 (0.187)
150-200	0.094	0.037	0.028	0.396
200-250	0.828	0.024	0.541	1.201
250-300	1.085	0.811	1.071	0.811
300-350	0.160	0.398	3.352	3.098
350-400	1.229	0.263	0.617	3.352
400-450	6.528 (0.167)	2.425	2.377	1.144
450-500	9.954 (0.320)	16.434 (0.388)	13.771 (0.313)	10.949 (0.299)
Mirror versus Control				
<i>Epochs (ms)</i>	<i>Frontal</i>	<i>Central</i>	<i>Parietal</i>	<i>Occipital</i>
0-50	1.909	0.020	0.172	0.240
50-100	2.635	2.622	2.868	0.610
100-150	3.101	1.048	0.007	0.712
150-200	0.970	0.010	2.099	1.100
200-250	4.210	6.563 (0.179)	4.822 (0.163)	6.615 (0.171)
250-300	2.560	2.576	0.937	1.147

300-350	1.071	0.811	0.177	0.112
350-400	3.806	3.935	0.405	0.286
400-450	5.678 (0.248)	5.890 (0.181)	2.859	3.701
450-500	0.241	0.438	0.853	1.401

Figure-1. Procedure and examples of items in Experiments 1 and 2.

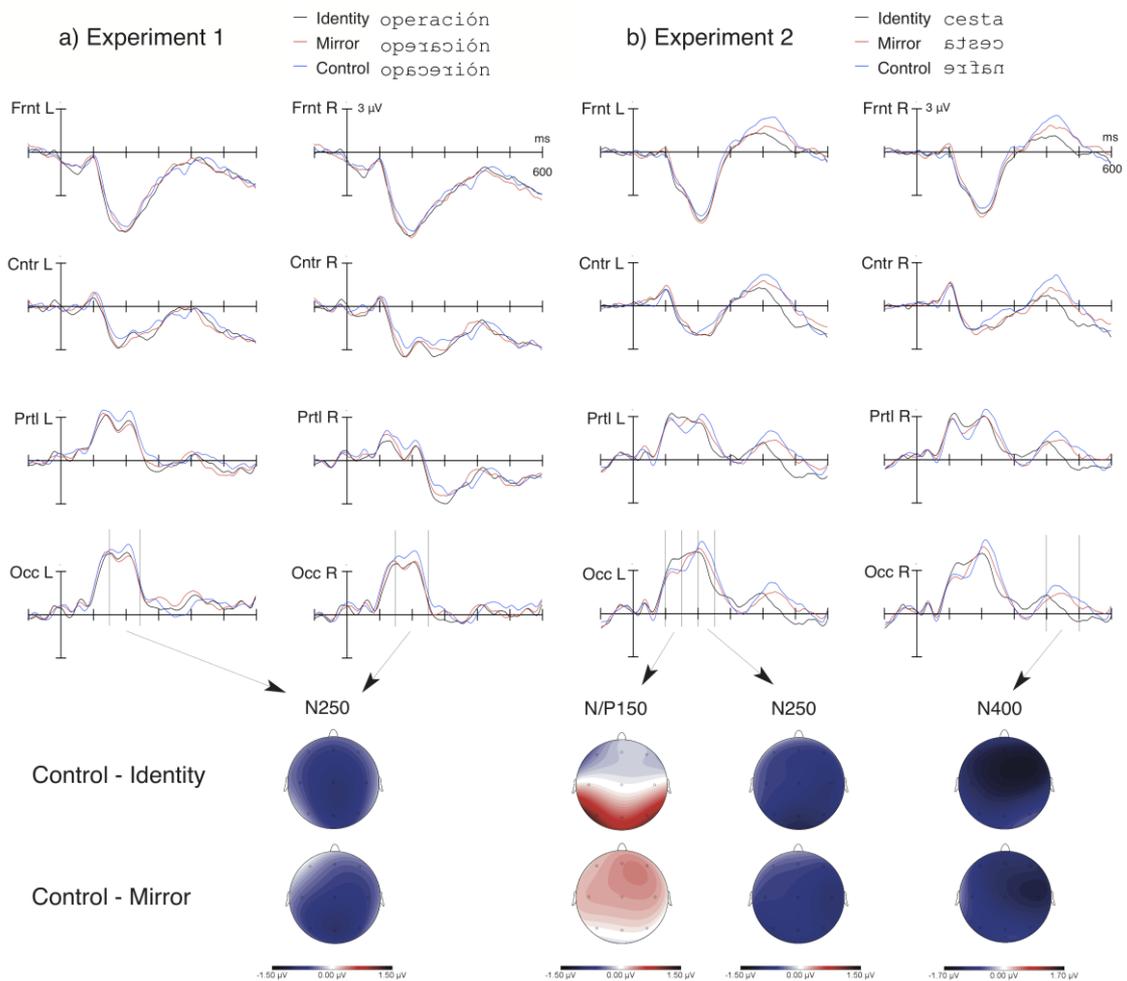
Graph: Procedure followed in Experiments 1 and 2. Table: Examples of items used in Experiments 1 and 2.



Experiment 1			
Conditions	MASK	PRIME	TARGET
Identity	#####	operación	operación
Mirror	#####	operación	operación
Control	#####	opserción	operación
Experiment 2			
Conditions	MASK	PRIME	TARGET
Identity	####	cesta	cesta
Mirror	####	stæc	cesta
Control	####	erīst	cesta

Figure-2: Results in Experiments 1 and 2.

ERPs elicited by the three critical conditions in Experiments 1 (a) and 2 (b). Eight representative electrodes were plotted: FrntL (F5), FrntR (F6), CntrL (C5), CntrR (C6), PrtlL (P5), PrtlR (P6), OccL (O1) and OccR (O2), according to the 10-20 system. Below we report the distribution of each ERP effect over the scalp, relative to the difference between Control and Identity and between Control and Mirror in the two experiments.



References

- Bornstein, M. H., Gross, C. G., & Wolf, J. Z. (1978). Perceptual similarity of mirror images in infancy. *Cognition*, 6, 89-116.
- Caramazza, A., & Hillis, A.E. (1990). Spatial representation of words in the brain implied by studies of a unilateral neglect patient. *Nature*, 346, 267-269.
- Carreiras, M., Duñabeitia, J.A., & Molinaro, N. (2009). Consonants and vowels contribute differently to visual word recognition: ERPs of relative position priming. *Cerebral Cortex*, 19, 2659-2670.
- Cornell, J. (1985). Spontaneous mirror writing in children. *Canadian Journal of Psychology*, 39, 174–179.
- Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: a proposal. *Trends in Cognitive Sciences*, 9, 335-341.
- Dehaene, S., Nakamura, K., Jobert, A., Kuroki, C., Ogawa, S., & Cohen, L. (2010). Why do children make mirror errors in reading? Neural correlates of mirror invariance in the visual word form area. *Neuroimage*, 49(2), 1837-1848.
- Duñabeitia, J.A., Perea, M., & Carreiras, M. (2008). Does darkness lead to happiness? Masked suffix priming effects. *Language and Cognitive Processes*, 23, 1002-1020.
- Duñabeitia, J.A., Molinaro, N., Laka, I., Estévez, A., & Carreiras, M. (2009). N250 effects for letter transpositions depend on lexicality: Casual or causal? *NeuroReport*, 20(4), 381-387.
- Grainger, J. & Van Heuven, W. (2003). Modeling Letter Position Coding in Printed Word Perception. In P. Bonin (Ed.), *The Mental lexicon*. New York : Nova Science Publishers (pp. 1-24).

- Grainger, J., & Holcomb, P. J. (2009). Watching the Word Go by: On the Time-course of Component Processes in Visual Word Recognition. *Language and Linguistics Compass*, 3(1), 128-156.
- Grainger, J., Kiyonaga, K. & Holcomb, P. J. (2006) The Time Course of Orthographic and Phonological Code Activation. *Psychological Science*, 17, 1021-1026.
- Gross, C. G., Bender, D. B., & Rocha-Miranda, C. E. (1969). Visual receptive fields of neurons in inferotemporal cortex of the monkey. *Science*, 166, 1303–1306.
- Kinoshita, S. & Lupker, S. J. (Eds.) (2003). *Masked priming: State of the art*. Hove, UK: Psychology Press.
- Logothetis, N.K., & Sheinberg, D.L. (1996). Visual Object Recognition. *Annual Review of Neuroscience*, 19, 577-621.
- Nobre, A. C., Allison, T., & McCarthy, G. (1994). Word recognition in the human inferior temporal lobe. *Nature*, 372, 260-263.
- Pflugshaupt, T., Nyffeler, T., von Wartburg, R., Wurtz, P., Luthi, M., Hubl, D., Gutbrod, K., Juengling, F.D., Hess, C.W., & Muri, R.M. (2007). When left becomes right and vice versa: mirrored vision after cerebral hypoxia. *Neuropsychologia*, 45, 2078-2091.
- Poldrack, R.A., Desmond, J.E., Glover, G.H., & Gabrieli, J.D.E. (1998). The neural basis of visual skill learning: An fMRI study of mirror reading. *Cerebral Cortex*, 8, 1-10.
- Rollenhagen, J.E., & Olson, C.R. (2000). Mirror image confusion in single neurons of macaque inferotemporal cortex. *Science*, 287, 1506-1508.
- Rubin, N. (2001). Figure and ground in the brain. *Nature Neuroscience*, 4, 857–858.
- Tomasino, B., Borroni P., Isaja, A., & Rumiati, R. (2005). The role of primary motor cortex in mental rotation: A TMS study. *Cognitive Neuropsychology*, 22, 348-363.

- Walsh, V. (1996). Neuropsychology: Reflections on mirror images. *Current Biology*, 6, 1079-1081.
- Whitney, C. (2001). How the brain encodes the order of letters in a printed word: The SERIOL model and selective literature review. *Psychonomic Bulletin & Review*, 8, 221-243.