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On the time course of the tolerance of letter detectors to rotations: A masked priming ERP investigation

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A R T I C L E I N F O

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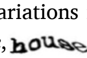
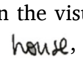
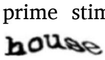
A B S T R A C T

A straightforward prediction of the Local Combination Detectors [LCD] model of word recognition (Dehaene et al., 2005) is that letter rotations above 40–45° should disrupt the mapping of the visual input onto orthographic representations. However, the evidence supporting this claim is scarce and not conclusive. To shed light on this issue, we conducted a masked repetition priming lexical decision experiment while recording the participants' EEG measures. Targets were always presented in the standard horizontal format, and we rotated the individual letters of the identity/unrelated primes (0°, 45°, or 90°). Behavioral and Event-Related Potentials (ERP) results revealed that the identity priming effect decreased as a function of letter rotation. Importantly, the ERP data allowed us to examine in detail the time course of processing of words with rotated letters. Amplitude comparisons showed that identity priming followed the typical course for 0° primes (i.e., it started around 100 ms, in the visual feature encoding stage, and strengthened with processing time). The parallel effect for 45° primes emerged later, at around 175 ms. This pattern strongly suggests that letter rotations at around 45° have a processing cost, thus providing evidence in favor of the LCD model of word recognition (Dehaene et al., 2005).

1. Introduction

Learning to read allows us to become autonomous and self-developing individuals in today's society. On a big scale, becoming literate individuals transforms our knowledge and views about the world. On a smaller personal scale, it changes the very subtle cognitive and brain mechanisms that connect visual forms with meaning. Ultimately, reading acquisition leads to building a flexible and powerful decoding system: despite the multiple variations in the visual form of written words (e.g., house, house, *house*, , , etc.), adult skilled readers can rapidly access their corresponding lexical-semantic representations (see Rayner et al., 2012). Indeed, even briefly shown prime stimuli with heavily distorted letters (e.g., CAPTCHAs like ) produce sizeable masked identity priming effects (see Hannagan et al., 2012). The enormous efficiency of lexical access in adult readers demonstrates that the word recognition system has developed some tolerance to noise and variations in the visual form of the words' constituent letters (see Cohen and Dehaene, 2009; Grainger and Dufau, 2012). However, the empirical evidence on the tolerance of the word recognition system to perceptual distortion is still scarce, probably because it entails many different elements (see Vergara-Martínez et al., 2021, for discussion).

The main goal of the present study is to examine to what degree the visual word recognition system is tolerant to the degradation in the visual form of the letters. Given the drawbacks of investigating the distortion of the visual form of written text due to the many potential factors at play, we focused on a single parameter: letter rotation. Crucially, the examination of the impact of letter rotation in word recognition has an added value: a prominent neural-inspired model of visual word recognition (e.g., Local Combination Detectors [LCD] model, Dehaene et al., 2005) makes an explicit prediction on the influence of rotations in visual word processing: "letter detectors should be disrupted by rotation (>40°)" (Dehaene et al., 2005, p. 340). Specifically, the LCD model assumes that the visual word recognition system shifts from the parallel encoding of letters to an effortful serial

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processing strategy for rotation angles above 40°–45°, thus hampering lexical processing (see Cohen et al., 2008) .[1]

The present research aimed to test this prediction of the LCD model. To that end, we conducted a masked priming lexical decision task in which the individual letters of the primes (that could be identical or unrelated to the target) were rotated in 0°, 45°, or 90°. Importantly, we also recorded the participants' brain electrical activity with an electroencephalogram (EEG) while doing the task. The EEG measures allowed us to characterize the impact of letter rotation during the time-course of lexical access. In the following lines, we first review the relevant background of the effects of letter word rotation effects on lexical processing. Next, we will introduce the experiment along with the predictions.

As indicated above, the tenets from the LCD model set limits to the tolerance of the visual word recognition system regarding letter rotation in 45°, meaning that letter rotations at around 45° or above would interfere with normal visual word recognition. In an event-related potential (ERP) lexical decision experiment, Kim and Straková (2012) examined the impact of letter rotation in visual word recognition. Participants were presented with words (and nonwords) where individual letters were rotated 0°, 22.5°, 45°, 67.5°, or 90°. Behavioral results showed that both response accuracy and speed decreased non-linearly with the eccentricity of letter rotation, with the greatest drop at the 67.6°–90° rotation step. Electrophysiological results revealed early effects of letter rotation in the P1 and N170 ERP components, two ERPs that mark the beginning of word-form analysis during word recognition (i.e. P1 and N170 amplitudes are enhanced in response to letter strings relative to nonlinguistic stimuli; Bentin et al., 1999; Maurer et al., 2005; Rossion et al., 2003). Kim and Straková (2012) found that increasing letter-rotation led to monotonic increases in the P1 and N170 amplitudes up to 67.5°. However, at 90°, P1 and N170 amplitudes decreased substantially. To explain this pattern, they suggested that moderate deviation from preferred stimulus properties (less than 45°) can recruit additional processing resources. However, deviation beyond a certain level (e.g., letter rotations beyond 67.5°) exceeds the resiliency of the processing system, leading to a decrease in the EEG response.

Are these results consistent with LCD predictions? As noted by Kim and Straková (2012), the LCD cannot readily explain why letter rotation *gradually* enhance brain responses to words composed of rotated letters from 0 to 22.5° and 45°. Kim and Straková (2012) suggested that the additional processing resources underlying the enhanced brain responses for these letter rotations could imply top-down feedback (attention-driven amplification; see Qiao et al., 2010; Vergara-Martínez et al., 2021) to low-level form processing when the letters are presented in an unfamiliar format (i.e., rotated). That is, top-down attentional processes would help override the disruptive effect of rotation at an abstract orthographic processing level (see Carreiras et al., 2014). One limitation of the procedure used by Kim and Straková (2012) is that word response times were not collected online but after a signal 800 ms post-target. Thus, it is not clear whether their early ERP effects necessarily reflected a cost on lexical access (see Perea et al., 2015; for discussion).

A more stringent test of the LCD model regarding letter rotation is to block out the attention-driven amplification elicited by distorted stimuli presented in isolation (Qiao et al., 2010; Vergara-Martínez et al., 2021). To that end, we employed a technique that taps the very initial steps of lexical access, while also collecting word response times. Experimental paradigms such as the parafoveal preview technique or masked priming address this issue. Notably, several recent studies with rotated words, using Forster and Davis' (1984) masked priming technique, have questioned the tenet of the LCD model regarding the 45° threshold of the tolerance of letter detectors to rotation (e.g., Benyhe and Csibri, 2021; Perea et al., 2018; Yang and Lupker, 2019). The rationale of these experiments was that if letter rotations above 45° slow down the access to the word's orthographic representations, masked identity rotated primes would no longer facilitate (or only to a minimal extent) target processing. However, Perea et al. (2018) found sizeable masked priming effects with 90° rotated words (both identity priming and transposed-letter priming), similar to those with canonical presented stimuli. Likewise, Yang and Lupker (2019) reported reliable transposed-letter priming effects not only with 90° but also with 180° rotated stimuli. While these findings demonstrate that the word recognition system is tolerant to word rotations, these experiments suffer from an interpretive issue: the prime and the target were rotated. Thus, one might argue that participants could have been accustomed to mentally rotating the stimuli to their canonical disposition and then processing them as usual (see Gomez and Perea, 2014; Whitney, 2002, for discussion).

An excellent strategy to minimize the above issue is to use a paradigm where participants have to process an upright presented stimulus preceded by an identity (or unrelated) stimulus (in various degrees of rotation) that is not consciously perceived. Benyhe and Csibri (2021) followed this strategy in a masked priming experiment in which participants were asked to read aloud target words in their canonical orientation (0°). The targets were preceded by identical or unrelated prime words that could be rotated in 0°, 30°, 60°, 90°, 120°, 150° and 180°. They found significant priming effects for rotation angles until 60° when the prime duration was 50 ms and 90° when the prime duration was 75 ms. Thus, masked priming evidence with word rotations favors the idea that letter detectors are tolerant to rotations >45° even in the first moments of processing.

The robustness of masked priming effects to word rotations is quite revealing. However, in the above-cited experiments, one might argue that the cognitive system rotates the whole stimulus and then process each letter as usual (i.e., a mental rotation; see Gomez and Perea, 2014; Whitney, 2002, for discussion). This scenario is much less disrupting than rotating the letters that make up the words. Keep in mind that, unlike word rotations, the rotation on a letter-by-letter basis involves the disruption of trans-letter features (i.e., features that are larger than letters but smaller than words; Mayall and Humphreys, 1996). Thus, the effect of rotating the individual letters within words is a more stringent test for the invariance-within-limits assumption of the LCD model than the rotation of the whole words. This was the approach followed in a recent study by Fernández-López et al. (2021). They used Rayner's (1975) gaze-contingent boundary change paradigm during sentence reading. The parafoveal preview was either identical or unrelated to the target word, and the letters of the preview were rotated 15°, 30°, 45°, or 60°. Importantly, the letters of the fixated target word and the rest of the sentence were always in the canonical—upright—orientation. Results showed that the advantage of the identity preview condition in eye fixation times on the target word decreased progressively as a function of the rotation angle (i.e., the identity advantage was sizeable for 15° and 30°, weak for 45°, and absent for 60°). Notably, at the critical boundary of the LCD model (i.e., 45°), the advantage of the identity preview was only marginal (i.e., 5, 10, and 7 ms for first fixation duration, gaze duration, and single fixation duration, respectively). Thus, the cost of letter rotation of parafoveal previews during sentence reading increased as a function of rotation angle, being substantial after 45°, thus providing empirical support to the LCD model. One interpretive issue, however, is that in the Fernández-López et al. (2021) experiment, the prime ("preview" in the eye movement literature) was presented in the parafovea, where the quality of the spatial information is lower than in the fovea. Hence, it is difficult to completely ascertain whether the cost of letter rotations at 45° reflects the system bounds on early orthographic processing or whether it reflects structural limitations of parafoveal processing.

[1] This claim was initially inspired by a study on the generalization at recognizing isolated objects at different orientations in macaques (Logothetis and Pauls, 1995). Of note, Cohen et al. (2008) and Vinckier et al. (2006) interpreted their data with adult readers in light of this invariance-within-limits prediction of the model.

To thoroughly characterize the effects of individually rotated letters during word recognition and thus test the tenets of the LCD model, we chose the masked priming technique (Forster and Davis, 1984) in combination with the recording of EEG measures. The reason for selecting this paradigm is twofold: (i) it taps on the very early stages of visual word recognition, and (ii) it reflects only bottom-up processing within the ventral stream, in the absence of attention-driven amplification (Qiao et al., 2010). Furthermore, the invariance-within-limit assumption of the LCD model can be readily tested in masked priming experiments: letter rotations at 45° or higher would slow down feature-letter mapping, decreasing masked identity priming effects. As in the Benyhe and Csibri (2021) experiment, the targets in the present study were *always* presented in the canonical upright position so that participants were unaware of prime identity or prime rotation (Fig. 1).

Thus, the main goal of the present experiment was to examine whether readers can extract abstract orthographic representations of rotated letters during visual-word recognition and, if so, when. Of specific interest was the scrutiny of three ERPs associated with the processing of visual feature representations (N/P150), abstract letter representations (N250), and lexical-semantic representations (N400) in masked priming experiments (see Holcomb and Grainger, 2006, 2007, for review). The N/P150 is a bipolar (positive at frontal scalp areas; negative at occipital scalp areas) ERP that peaks between 125 ms and 175 ms after the target onset. This early ERP reflects the initial mapping of the stimulus' visual features (e.g., size, color, cAsE) onto higher-level orthographic representations. Differences in the ERP waves in this epoch depend on the degree of overlap of coarse-grain visual features at a relatively abstract level, with no impact of lexical factors (e.g., lexicality or word frequency). For instance, the N/P150 component is modulated by letter case, regardless of whether the letters of prime and target match the same orthographic representation (e.g., it is larger for altar-ALTAR than for ALTAR-ALTAR; Vergara-Martínez et al., 2015; see also Petit et al., 2006). The second ERP of interest peaks around 250 ms (N250; 175–300 ms) and shows a slighter widespread distribution than the N/P150 over frontal-central areas. The N250 reflects the mapping of the orthographic units onto orthographic word forms. The N250 component is modulated by the degree of orthographic overlap between prime and target: its amplitude is larger to completely unrelated pairs, moderate to almost-overlapped pairs, and most attenuated for identical pairs (e.g., agenda-SOCIAL > soical-SOCIAL > social-SOCIAL; see Chauncey et al., 2008; Dickson and Federmeier, 2014; Dufau et al., 2008; Pickering and Schweinberger, 2003, for further evidence). Finally, the N400 component is also sensitive to masked priming manipulations. It is obtained between approximately 300 and 450 ms after stimulus onset and shows a widespread distribution peaking at central scalp areas. The N400 reflects the mapping of word representations onto

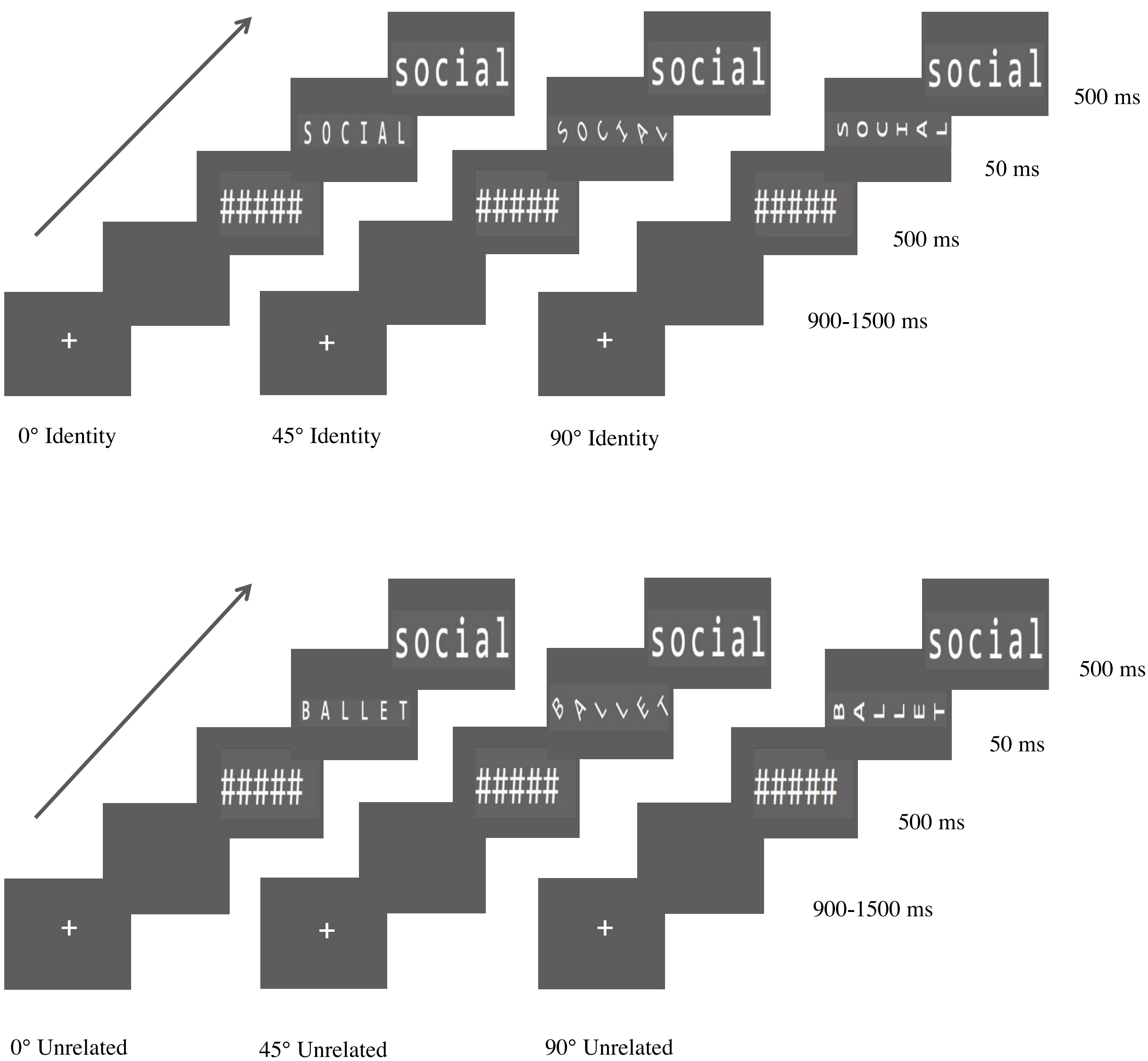

Fig. 1. Depiction of the masked priming task.

semantic representations (i.e., lexical-semantic interactions) in long-term memory. Thus, similarly to the N250, the N400 component is more negative to targets that are completely unrelated to their primes, intermediate to targets that partially overlap their primes, and least negative to targets that are complete repetitions of their primes (e.g., agenda-SOCIAL > soical-SOCIAL > social-SOCIAL). Importantly, unlike the N250, the N400 in masked priming is sensitive to word stimuli (but not nonword stimuli) and has been associated the access to semantics (see Holcomb and Grainger, 2006; Kiyonaga et al., 2007).

In the present experiment, each target stimulus was preceded by a masked prime that could be the same as the target (e.g., social-SOCIAL) or unrelated (e.g., agenda-SOCIAL). Critically, the prime was composed of letters rotated 0°, 45°, or 90° (see Fig. 1). If, as hypothesized by the LCD model (Dehaene et al., 2005), letter rotation above 40°–45° severely hinders the encoding of letter detectors in the first stages of orthographic-lexical processing, we would expect at the behavioral level: i) a sizeable identity priming effect for the canonical 0° primes; ii) a weak/negligible effect for 45° rotated primes, and 3) null priming effects for the more extreme 90° rotated primes. Alternatively, if the orthographic coding system is widely tuned to rapidly process distorted stimuli (Benyhe and Csibri, 2021; Hannagan et al., 2012; Perea et al., 2018, 2020; Yang and Lupker, 2019), one would expect a priming effect at all rotation angles. This latter scenario does not exclude that priming effects could be numerically smaller for the steeper rotations (see Fernández-López et al., 2021).

More importantly, the registration of the participants' ERPs allowed us to track the size and time course of the masked identity priming effect for all rotation angles. The predictions in the framework of the LCD model are the following. We expect the N/P150 to be sensitive to coarse perceptual changes (i.e., letter rotation) between prime and target (see Gutiérrez-Sigut et al., 2019; Vergara-Martínez et al., 2015). In the N250 component, we would expect identity priming effects for the 0° rotation primes. This difference would be substantially weaker for 45° rotated primes, as letter detectors would be at the boundary to automatically encode letter identities (Dehaene et al., 2005), and it would be negligible for 90° rotated primes. For the N400, we can envision two scenarios. On one side, as the N400 is sensitive to the same degree of orthographic overlap as the N250, one could expect the same pattern of results for both components (N250 and N400). On the other side, as the N400 reflects the access to the lexical entry of the target, top-down lexical feedback could override the disruption of prime letter rotation (see Carreiras et al., 2014; Vergara-Martínez et al., 2021). In this latter scenario, one can expect that top-down processes may facilitate the encoding of the rotated primes, thus leading to priming effects also with rotated primes—this may be more pronounced for the less disruptive 45° rotated primes.

The alternative hypothesis to the LCD predictions entails that letter detectors could quickly overcome the constraints imposed by rotation early in processing, similar to the rotation of whole words (Benyhe and Csibri, 2021; Perea et al., 2018, 2020; Yang and Lupker, 2019). In this case, one would expect sizeable identity priming effects in the N250 and N400 components at all rotation angles. This latter outcome would reflect that participants can rapidly integrate the abstract orthographic representations of the primes into the targets regardless of the rotation of the individual letters of the primes.

2. Method

2.1. Participants

A group of 26 (20 females) undergraduate university students participated in the study for course credit. Ages ranged from 19 to 30 years (M = 21.57, SD = 3.42). All participants were native Spanish speakers with no neurological or psychiatric impairment history and normal or corrected-to-normal vision. In addition, all participants were right-handed, as assessed with a Spanish version of the Edinburgh Handedness Inventory (Oldfield, 1971). This study was approved by the Experimental Research Ethics Committee of the University of Valéncia. Before starting the experiment, all participants signed an informed consent form.

2.2. Materials

We selected 240 target words of five and six letters from the EsPal subtitle-based database in Spanish (Duchon et al., 2013). The mean frequency was 122 occurrences per million (range: 0.5–1352)—this corresponded to an average Zipf frequency of 4.83 (range: 2.65–6.13; van Heuven et al., 2014). The mean orthographic Levenshtein distance 20 (OLD20; Yarkoni et al., 2008) was 1.50 (range: 1–2). We also created 240 nonwords as foils using Wuggy (Keuleers and Brysbaert, 2010). To act as primes, we employed the same stimuli selected for targets. Each target stimulus, presented in lowercase, was preceded by an uppercase prime that could be (a) the same as the target, or (b) an unrelated stimulus; the prime could also be rotated clockwise by (a) 0°, (b) 45° and (c) 90°. Of note, previous studies of letter and word recognition have shown no differences between clockwise and anti-clockwise rotations (see Koriat and Norman, 1985a, 1985b; see also Benyhe and Csibri, 2021, for similar evidence with the masked priming technique). As in previous masked priming experiments, the unrelated primes for word targets were words and the unrelated primes for nonword foils were nonwords—note that the lexical status of the unrelated primes does not affect lexical processing (see Fernández-López et al., 2019). Importantly, in the typical scenario of masked priming lexical decision, the prime is presented in lowercase and the target is presented in uppercase. Nevertheless, to avoid binding and mix-up with the rotated letters (i.e., a rotated *b* can be confused with a p or a q), we rotated letters in uppercase words. To include the six priming conditions across all target words, we created six counterbalanced lists of materials in a Latin square manner (i.e., each target appeared once in each list, each time in a different priming condition). Different participants were assigned randomly to each list. To have the participants familiarized with the task, the 480-trial experimental phase (i.e., 40 items per condition) was preceded by a short practice composed of 12 trials (6-word trials and 6-nonword trials) with the same characteristics as the experimental trials. These practice trials were not included in the analyses. The complete list of prime-target pairs is available in the following OSF link https://osf.io/umk3x/?view_only=bd046c06f1054900a865083a612c85d6.

2.3. Procedure

Participants sat comfortably in a dimly lit and sound-attenuated room. All stimuli were presented on a high-resolution monitor positioned slightly below the eye level, 85–90 cm in front of the participant. The size of the stimuli and distance from the screen allowed for a visual angle of fewer than 5° horizontally. Stimuli were presented in white Consolas font against a dark-gray background. The primes were presented in uppercase and 20-pt of size, whereas both targets and the mask were presented in lowercase and 36-pt. Stimulus display was controlled by Presentation software (Neurobehavioral Systems).

In each trial, a pattern mask (i.e., a series of # signs that matched the length of the target item) was displayed for 500 ms in the center of the computer screen. An uppercase prime replaced the mask in the same spatial location for 50 ms, which was replaced by a lowercase target stimulus that remained in the screen for 500 ms. After participants' response (within an interval of 2 s following target presentation), there was a blank screen of random duration between 900 and 1500 ms. Participants were asked to decide whether the target stimulus was a Spanish word or not by pressing the "yes" or the "no" key. Both speed and precision were stressed in the instructions. To minimize participant-generated artifacts in the EEG signal during the presentation of the experimental stimuli, participants were asked to refrain from blinking and moving from the onset of each trial to the set-up period after response. Instructions did not mention the existence of any uppercase stimuli. Every 30 trials, there was a brief pause for resting and impedance checking. The hand used for each response was balanced across participants. Lexical decision times were measured from target onset until the participant's response. Participants did not receive feedback on reaction times or error rates during the experiment. The order of the trials was randomized for each participant. The whole session, including set up, lasted approximately 1 h and 30 min.

2.4. EEG recording analysis

The electroencephalogram (EEG) was recorded from 29 Ag/AgCl electrodes mounted in an elastic cap (EASYCAP GmbH, Herrsching, Germany). These electrodes were referenced to the right mastoid and re-referenced off-line to the averaged signal from two electrodes placed on the left and right mastoids. Eye movements and blinks were monitored with electrodes providing bipolar recordings of the horizontal and vertical (over the left eye) electrooculogram (EOG). The EEG recording was amplified and bandpass filtered between 0.01 and 100 Hz with a sampling rate of 250 Hz by a BrainAmp amplifier (Brain Products, GmbH, Gilching, Germany). An off-line bandpass filter between 0.01 and 20 Hz was applied to the EEG signal. Impedances were kept below 5 kΩ during the recording session. Epochs of the EEG corresponding to 200 ms pre-to 600 ms post-target onset were analyzed. Baseline correction was performed using the average EEG activity in the 200 ms preceding the onset of the target stimuli. Following baseline correction, trials with muscle activity, eye movements, or blink activity were rejected (8.95%). Trials with incorrect lexical decision responses (3.32%) were neither included in the average ERPs. All participants had a minimum of 30 acceptable correct trials per condition [2] (ID-0°: M = 36, SD = 2.6; ID-45°: M = 35, SD = 2.3; ID-90°: M = 35, SD = 2.4; UN-0°: M = 35, SD = 2.3; UN-45°: M = 35, SD = 2.6; UN-90°: M = 35, SD = 2.6). ERPs were averaged separately for each of the experimental conditions, each of the subjects, and each of the electrode sites. We exclusively focused on the word trials because masked priming effects for nonword trials in the lexical decision task tend to be unreliable (see Carreiras et al., 2009; Gutiérrez-Sigut et al., 2019) .[3]

Statistical analyses were performed on the mean amplitude of three contiguous time windows (100–150 ms; 175–300 ms; 300–450 ms). This was done for the six experimental conditions defined by the combination of the factors Prime-Target Relation (identity, unrelated) and Rotation angle (0°, 45°, 90°). The selection of these epochs was motivated by our aim to track the time course of the potential differences between experimental conditions and was based on previous studies (Carreiras et al., 2007; Holcomb and Grainger, 2006; Grainger and Holcomb, 2009; Vergara-Martínez et al., 2015). Following a similar strategy in the related literature (e.g., Vergara-Martínez et al., 2020), we performed a thorough analysis of the spatial dimension of the ERP results in order to better characterize the ERPs under study in the context of masked priming. To carefully assess the topographical distribution of the ERP effects, we averaged the amplitude values across three electrodes of nine representative scalp areas that result from the factorial combination of the Laterality (left, central, right) and Distribution (anterior, medial, posterior): left-anterior (FP1, F7, F3), left-medial (FC5, T7, C3), left-posterior (CP5, P7, P3), central-anterior (FZ, FC1, FC2), central-medial (CZ, CP1, CP2), central-posterior (PZ, O1, O2), right-anterior (FP2, F4, F8), right-medial (FC6, C4, T8); and right-posterior (CP6, P4, P8; Fig. 2). For each time window, a separate repeated-measures analysis of variance (ANOVA) was performed,

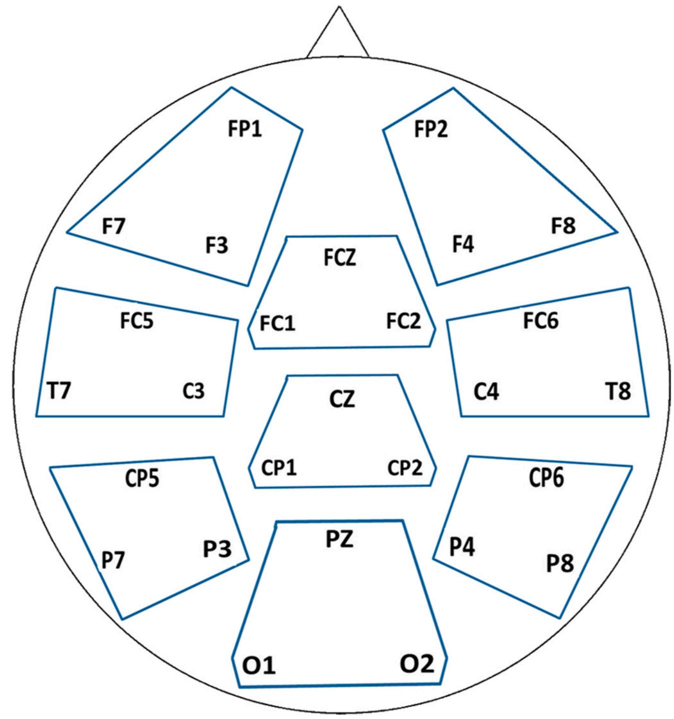

Fig. 2. Schematic representation of the electrode montage and the channels included in statistical analyses.

including the factors Laterality, Distribution, Rotation angle, and prime-target Relation. In all analyses, List (List 1, List 2, List 3, List 4, List 5, and List 6) was included as a between-subjects factor to extract the variance due to the counterbalanced lists (Pollatsek and Well, 1995). Critical values were adjusted using the Greenhouse and Geisser (1959) correction for violation of the assumption of sphericity. The effects of Laterality or Distribution are reported when they interact with the experimental manipulations. Interactions between factors were followed up with simple-effect tests.

3. Results

3.1. Behavioral results

For the inferential analyses, we employed linear mixed-effects (LME) models in R (R Core Team, 2021) using the *lme4* (Bates et al., 2019) *lmerTest* (Kuznetsova et al., 2016) and *car* (Fox and Weisberg, 2019) packages. The models included two fixed factors: (1) prime-target relation (identity, unrelated) and (2) prime rotation angle (0°, 45°, and 90°). Error responses and very short RTs (less than 250 ms: 2 responses) were excluded from the RT analyses. The mean correct RTs and the accuracy in each condition are presented in Table 1. There were 11, 762 observations. Because of the normality assumption required by LME analyses, the raw RTs were inverse-transformed (−1000/RT). For the accuracy analyses, the responses were coded as binary values (1 =

Table 1
Mean correct response times (in ms) and accuracy (in brackets) for words.

		Prime rotation		
		0°	45°	90°
Prime-target relation	Identity	578 (97.8)	597 (96.2)	605 (96.2)
	Unrelated	618 (96.9)	624 (96.4)	613 (96.4)
Priming effect (Unrelated – Identity)		40 (0.9)	27 (0.2)	8 (0.2)

Note: Priming effects for pseudowords were negligible (−6, 1, and 6 ms, for the 0°, 45°, and 90° primes, respectively).

[2] To increase the signal-to-noise ratio in four subjects with a large number of eyeblinks, we applied the independent component analysis procedure to correct eye blinks using the Infomax algorithm (Jung et al., 2000).

[3] Indeed, as shown in Table 1, the size of the behavioral priming effect was minimal (e.g., 6 ms for 0° and 90° primes and 1 ms for 45° primes).

correct, 0 = incorrect), and we used the *glmer* function in the *lme4* package. There were 12,480 observations. For both latency and accuracy analyses, we chose the maximal random effects model whose structure converged .[4] The *p*-values for each main factor and the interactions were calculated using Wald χ^2 tests. In case of a significant interaction, we computed the effect of prime-target relation for each rotation angle with the *emmeans* package (Lenth et al., 2020).

Latency analyses. We found main effects of prime-target relation [$\chi^2(1) = 37.734$, $p < .001$] and angle [$\chi^2(1) = 26.345$, $p < .001$]. More importantly, the two factors interacted significantly [$\chi^2(2) = 31.537$, $p < .001$]. This interaction reflected that identity priming was significant for 0° primes (40 ms; 578 vs. 618 ms for identity and unrelated conditions, respectively; $t = -7.357$, $p < .001$) and 45° primes (27 ms; 597 vs. 624 ms for identity and unrelated conditions, respectively; $t = -4.977$, $p < .001$). In contrast, when the primes were rotated in 90°, there was only a non-significant 8-ms priming effect (8 ms; 605 vs. 613 ms, respectively; $|t| < 1$, $p = .64$).

Accuracy analyses. None of the factors or interactions approached significance (all *ps* > .203).

In sum, the latency data revealed that responses were faster for identity primes than for unrelated primes and, crucially, this difference was modulated by the rotation angle of the prime letters: it decreased as a function of rotations (0° [40 ms] > 45° [27 ms] > 90° [8 ms]).

3.2. ERP results

Fig. 3 shows the ERP waves for related and unrelated prime-target word pairs in six representative electrodes. Around 100 ms post-stimuli and over frontal electrodes, larger positive values are elicited by the 0° primes than for the 45° and 90° primes—this effect is inverted in the occipital electrodes (N/P150). For the 0° primes, differences in amplitude between the identity and unrelated pairs start around 100 ms. This difference increases and peaks maximum of around 400 ms. For the condition with 45° rotation primes, the difference between identity and unrelated primes emerges later, around 200 ms of processing, and reaches its peak around 400 ms. Finally, for the 90° condition, there is no difference in amplitude between the identity and unrelated pairs. The evolution of the masked identity prime for each prime rotation is deployed in Fig. 4. Below, we describe the results of the ANOVA for each time epoch:

100- to 150 ms *epoch.* The ANOVA showed a main effect of rotation angle ($F[2, 40] = 4.37$, $p = .020$) that was modulated by the interaction with distribution ($F[4, 80] = 10.892$, $p < .001$). In frontal areas, larger positive values were observed for the 0° primes compared to 45° primes ($A_{0°} - A_{45°} = 1.246$; $F[1, 20] = 19.94$, $p < .001$) and 90° primes ($A_{0°} - A_{90°} = 1.009$; $F[1, 20] = 9.76$, $p = .005$). In medial areas, we found the same pattern of data: larger positive values were observed for the 0° primes compared to 45° primes ($A_{0°} - A_{45°} = 0.902$; $F[1, 20] = 16.25$, $p = .001$) and 90° primes ($A_{0°} - A_{90°} = 0.725$; $F[1, 20] = 9$, $p = .007$); in both cases, there were no differences between 45° and 90° primes (both *Fs* < 1). The interaction between rotation angle and relation reached significance in frontal and medial regions of the scalp ($F[4, 80] = 3.301$, $p = .050$): we found differences between identity and unrelated pairs that were restricted to 0° primes ($A_{ID0°} - A_{UN0°} = 1.045$ in anterior areas: $F[1, 20] = 8.06$, $p = .010$; $A_{ID0°} - A_{UN0°} = 0.752$ in medial areas: $F[1, 20] = 5.17$, $p = .028$).

175- to 300 ms *epoch.* The ANOVA showed an effect of rotation angle that was modulated by laterality and distribution ($F[8, 160] = 4.62$, $p = .001$), a main effect of relation [$F(1, 20) = 4.90$, $p = .039$] and, more importantly, an interaction between rotation angle and relation ($F[2, 40] = 5.29$, $p = .011$). Regarding rotation, we found differences in amplitude between 0° and 45° primes in right-posterior regions ($F[1, 20] = 5.95$, $p = .024$) and between 45° and 90° primes in central-anterior regions ($F[1, 20] = 5.49$, $p = .029$). Regarding the interaction between rotation angle and relation, for the 0° primes, we found larger positive values for identity than for unrelated pairs ($A_{ID0°} - A_{UN0°} = 1.142$; $F[1, 20] = 12.90$, $p = .002$). The difference between identity and unrelated pairs decreased for 45° primes ($A_{ID45°} - A_{UN45°} = 0.768$; $F[1, 20] = 5.03$, $p = .036$) and was absent for 90° primes ($A_{ID90°} - A_{UN90°} = -0.354$; $F < 1$).

300- to 450-ms *epoch.* The ANOVA showed a main effect of rotation angle ($F[2, 40] = 7.91$, $p = .002$), a main effect of relation ($F[1, 20] = 11.74$, $p = .003$), and an interaction between relation and rotation angle ($F[2, 40] = 5.337$, $p = .010$). Regarding rotation angle, follow-up analyses showed significant differences, restricted to identity pairs between 0° and 90° primes ($F[1, 20] = 21.61$, $p < .001$), and between 45° and 90° primes ($F[1, 20] = 26.69$, $p < .001$)—we did not find any differences between 0° and 45° primes ($F < 1$). Regarding the interaction between rotation angle and relation, the largest difference in amplitude between identity and unrelated pairs was obtained for the 0° primes ($A_{ID0°} - A_{UN0°} = 1.345$; $F[1, 20] = 17.672$, $p < .001$). This difference was attenuated for the 45° primes ($A_{ID45°} - A_{UN45°} = 0.920$; $F[1, 20] = 7.343$, $p = .013$), and absent for 90° primes ($A_{ID90°} - A_{UN90°} = 0.202$; $F < 1$]).

The time-course and size of the effects under study can be summarized as follows. First, the largest impact of rotation angle was observed in the 100–150 ms epoch and over frontal electrodes (N/P150), with the standard 0° prime orientation diverging from each two consecutive rotation angles. Importantly, the identity priming effect for 0° primes followed the natural course: it began around 100–150 ms in frontal areas and strengthened in the following processing stages, including a widespread N400 component. In contrast, the emergence of the identity priming effect for 45° primes was delayed, with its size also being reduced (i.e., it emerged around 170–300 and it was weaker than for the 0° primes). For 90° primes, the identity priming effect was absent in all components.

To sum up, the behavioral data showed that the masked identity priming effects were modulated by the rotation angle of the individual letters of the prime: it was strongest at 0° rotation angle (40 ms), decreased at the 45° rotation angle (27 ms), and vanished at the 90° rotation angle (8 ms). The ERP data showed an overall effect of rotation angle in the component associated with visual coarse feature encoding (N/P150): over frontal areas of the scalp, the amplitude was larger for the 0° primes than for the rotated primes (45° and 90°). Regarding masked identity priming, for the 0° primes, we already found effects in the N/P150 that substantially increased in the N250 and N400. For the 45° primes, the priming effect emerged later, in the N250, and increased in the N400—its size was weaker than for the 0° primes. Finally, the 90° primes did not produce identity priming in any ERP components. Thus, the present experiment revealed consistent and complementary findings on how letter-rotation affects masked identity priming in behavioral and electrophysiological measures.

4. Discussion

In the present ERP masked priming study, we examined the tolerance of letter detectors to visual distortion via letter rotation. The LCD model (Dehaene et al., 2005), one of the leading neurally-inspired models of word recognition, posits that the letter detectors that convert the perceptual input into the abstract representation of letters would be severely hindered by letter rotations by around 40–45°. However, recent research using whole word rotations has questioned this claim. To shed light on this prediction with a more stringent scenario, we examined the temporal course of the effect of rotation of the words' constituent letters—instead of the whole words— in a masked identity priming paradigm (i.e., identity vs. unrelated primes; see Fig. 1). The behavioral data showed that masked identity priming was modulated by letter rotation: it was strongest for the 0° primes (40 ms), decreased for the 45° primes

[4] The maximal random effects models that converged were lmer(-1000/RT ~ angle*relation + (1+relation|subject) + (1+relation|item) and glmer(accuracy ~ angle*relation + (1|subject) + (1|item).

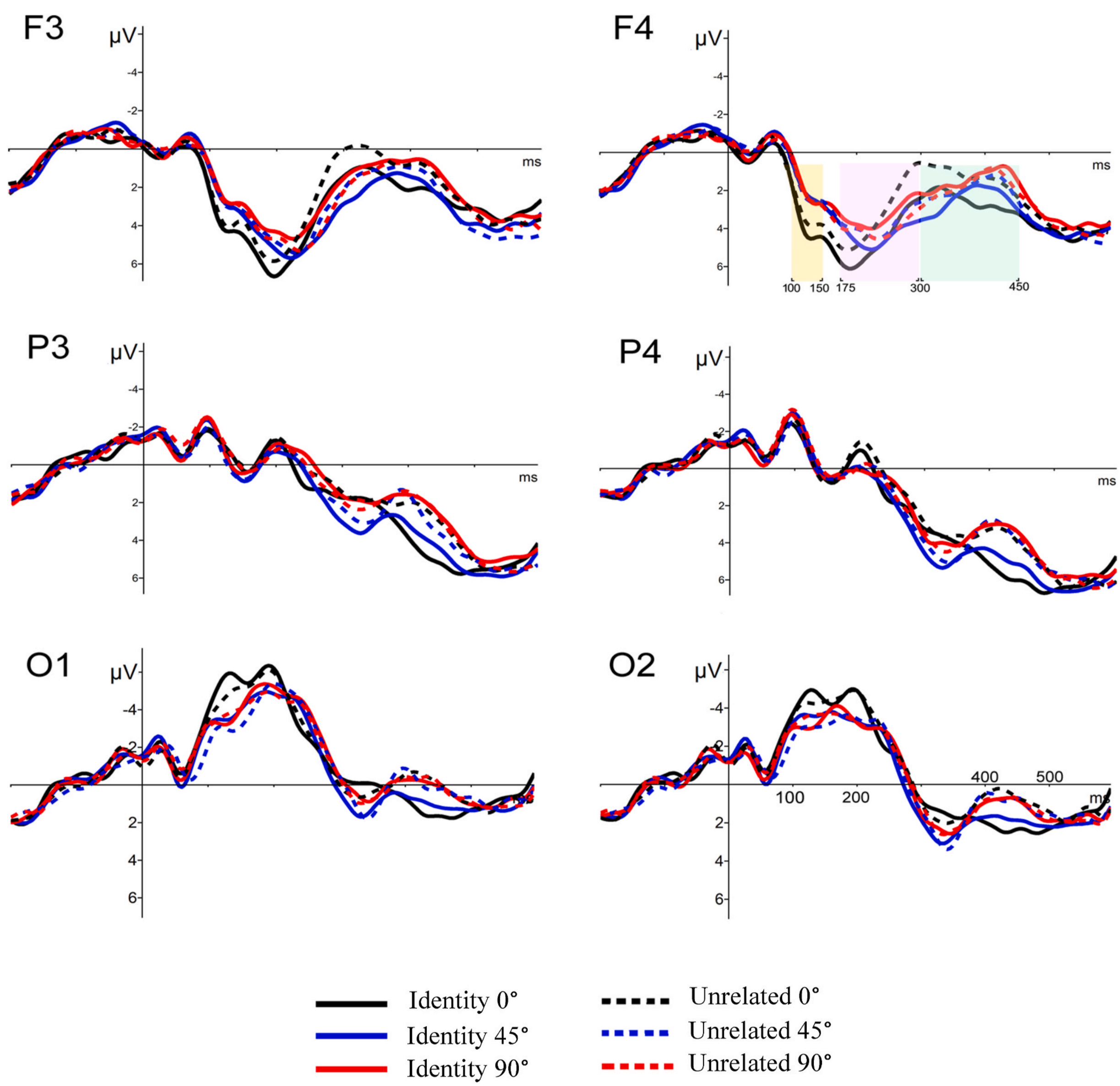

Fig. 3. Grand average event-related potentials to words in the masked priming identity and unrelated conditions, for each word-letter rotation condition, in six representative electrodes of the areas of interest. Electrodes O1 and O2 show the negative counterpart of the N/P150. Color bars indicate the three time epochs under analysis. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(27 ms), and it was negligible for the 90° primes (8 ms). This pattern suggests that letter rotation perturbs feature-letter mapping, with the amount of perturbation determined by the amount of feature overlap. Lower levels of feature overlap slow down the process of letter-level processing, thus leading to smaller priming effects.

More importantly, the ERP data revealed more fine-grained evidence of this pattern. First, in the N/P150, we found an overall effect of rotation consistency between prime and target, a result in line with previous findings (Vergara-Martínez et al., 2015; Gutiérrez-Sigut et al., 2019; Petit et al., 2006)—note that neural activity at this stage of processing mainly deals with coarse physical features for the stimuli. Importantly, we also obtained a prime-target relation effect, but only when prime and target shared orientation (i.e., 0°). This pattern suggests that: (i) letter-form feature detectors are engaged very quickly during word processing, and (ii) the cost of letter rotation occurs very early, in a visual feature encoding stage.

In the N250 time window, we found differences between 0° and 45° primes, and 45° and 90° primes. More importantly, identity priming interacted significantly with prime rotation: The impact of primes on target processing was substantial for 0° primes. Moreover, identity priming effects were significant (although weaker) for 45° primes, whereas they were absent for 90° primes. Thus, at this point of processing, the ERP results were parallel to the behavioral data: identity priming was greatest for the 0° primes, reduced for 45° primes, and null for 90° primes. Importantly, this pattern of ERPs data is consistent with the idea that, at this processing stage, letter size and shape invariance has already been achieved (Chauncey et al., 2008; Grainger and Holcomb, 2009). Nevertheless, the small identity priming effects for the 45° rotated primes (and the absence of priming for the 90° primes) in this time window offer evidence of the limited tolerance of letter detectors to rotation angle. In the first stages of visual-word recognition, the abstract orthographic representations of the primes are integrated with target processing, preferably if a coarse visual feature such as letter orientation is preserved. When the prime stimuli are presented in 0° (i.e., canonical orientation), the letter detectors of the following—identical—target are pre-activated, thus facilitating its processing. However, when the primes are presented in 45° or 90°, and the target in 0°, the pre-activation of the letter detectors decreases as a function of the orientation inconsistency

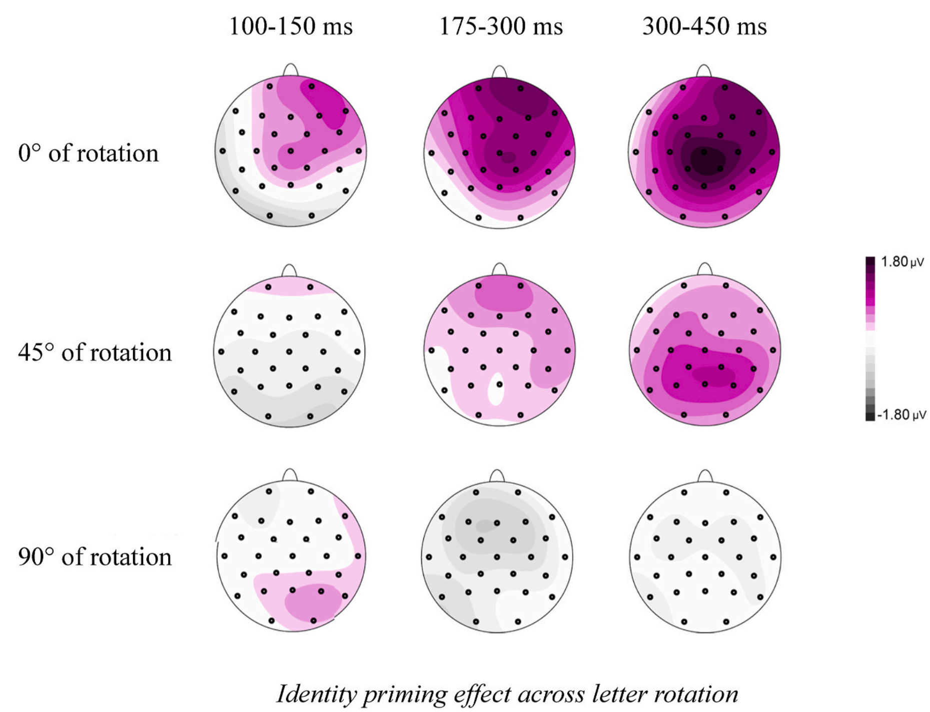

Fig. 4. Topographic distribution of the masked identity priming effect, calculated as the difference in voltage amplitude between the event-related potential responses to identity vs. unrelated priming, for word targets preceded by each type of prime (0° rotation, 45° rotation, 90° rotation) in the three time windows of the analysis.

between the prime and target letters. Thus, in this scenario, the processing of the identical target would be hindered.

Notably, the picture changes by 300–400 ms post-stimuli. We found no overall differences between 0° and 45° primes, but we found differences between 0° vs. 90° and 45° vs. 90°. More importantly, in the N400 window, larger identity priming occurred not only when the letters of the prime were presented at 0° but also—although to a lesser degree—when they were rotated 45°. This pattern suggests that the processing of the stimuli when the primes were presented at 0° followed the typical course (e.g., Vergara-Martínez et al., 2015). In contrast, the integration of orthographic information with 45° primes emerges later in processing. Thus, ≈45° rotated letters may need additional processing resources, such as top-down lexical mechanisms to help integrate the representations of primes and targets (see Benyhe and Csibri, 2021; Kim and Straková, 2012; Vergara-Martínez et al., 2021). [5]

These findings are consistent with the findings reported by Kim and Straková (2012) in an unprimed lexical decision experiment. They obtained increased amplitudes in early time windows (P1 and N170) for 45° words relative to the canonical 0°, thus suggesting a cost in the initial moments of word-form analyses. Moreover, the present findings extend the results from the study conducted by Fernández-López et al. (2021) with parafoveal primes during sentence reading. They showed that skilled readers can efficiently convert parafoveal words composed of rotated letters to a stable orthographic code *only* when the rotation is ≤ 45°. Altogether, this pattern of results offers empirical support to the assumption of the LCD model (Dehaene et al., 2005) that letter detectors are hindered by letter rotation during the initial moments of processing for angles around 45°. Importantly, although it is beyond the scope of the present study, further work should directly examine the apparent discrepancies between the effects from the rotations of words as a whole (e.g., see Benyhe & Csibri, 2021) and the rotations of the individual letters within words.

In sum, the present masked priming study is the first to assess the electrophysiological brain signature of distortion in one single parameter, namely, letter orientation, during the early stages of word processing. Our results suggest that, during visual word recognition, participants can integrate the information from the primes composed of rotated letters up to 45°. However, this comes with a cost: the magnitude of the masked identity priming effects with 45° primes was noticeably smaller than with 0° primes in behavioral and ERP measures. Moreover, the fact that identity priming for 45° primes was weak in the N250 component suggests that rotations hampered the initial letter encoding and access to abstract representations (i.e., letter rotation impeded the automatic integration of the orthographic representation of the masked primes with the targets). Hence, our findings strongly suggest that the word processing system cannot easily handle letter rotations at around 45° or above, thus providing evidence supporting the predictions of the LCD model of word recognition (Dehaene et al., 2005).

Credit author statement

Maria Fernández-López: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Manuel Perea**: Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition. **Marta Vergara-Martínez**: Conceptualization, Methodology, Formal analysis, Writing – review & editing, Supervision, Project administration.

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[5] Parallel ANOVAs run on the ERPs for pseudoword targets revealed similar N/P150 effects of letter rotation to word targets ($F[2, 50] = 4.78$, $p = .018$; Distribution x Rotation: $F[2, 50] = 14.6317.83$, $p < .001$). Simple comparisons revealed significant differences between 0° and 45° over frontal ($F[2, 40] = 12.35$, $p = .002$) and central scalp areas ($F[2, 40] = 6.12$, $p = .022$). However, no effects of identity priming were observed in the time-epochs under study.

laboratory experiment.

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