

BRIEF REPORT

Masked repetition priming and event-related brain potentials: A new approach for tracking the time-course of object perception

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Abstract

This study reports a new approach to studying the time-course of the perceptual processing of objects by combining for the first time the masked repetition priming technique with the recording of event-related potentials (ERPs). In a semantic categorization task ERPs were recorded to repeated and unrelated target pictures of common objects that were immediately preceded by briefly presented pattern masked prime objects. Three sequential ERP effects were found between 100 and 650 ms post-target onset. These effects included an early posterior positivity/anterior negativity (N/P190) that was suggested to reflect early feature processing in visual cortex. This early effect was followed by an anterior negativity (N300) that was suggested to reflect processing of object-specific representations and finally by a widely distributed negativity (N400) that was argued to reflect more domain general semantic processing.

Descriptors: ERP, N400, N300, Masked priming, Object recognition

It is widely accepted that the sequence of neural events underlying the recognition of visual objects occurs rapidly and with little effort (e.g., Biederman, 1987; Tanaka, 1996). Although studies in nonhuman primates have revealed much about the sequence and timing of the mechanisms involved in processing visual stimuli (e.g., Schroeder, Mehta, & Givre, 1998), relatively little is known about comparable mechanisms in humans. The current study examined the time-course of visual object processing in the human brain using a novel combination of techniques: event-related brain potentials (ERPs), a noninvasive electrophysiological procedure with excellent temporal resolution (e.g., Rugg & Coles, 1995), and rapid masked repetition priming, a paradigm that has been used successfully in the behavioral literature to examine the time-course of visual word recognition (e.g., Forster & Davis, 1984).

The basic effect reported in numerous masked repetition priming studies is that manipulating the similarity of a briefly presented, pattern masked “prime” word and an immediately following and clearly visible “target” word produces systematic differences in target reaction time (RT; greater overlap = faster RTs). Such effects have typically been interpreted as reflecting processing that is started by the masked prime and then modified when the ensuing target is similar to or different from the prime

along some dimension of interest (e.g., orthographic, lexical, or semantic). Because subjects are usually unaware of the identity of the prime, it is widely believed that this type of priming is predominantly sensitive to the fast feed-forward (automatic) components of word recognition (Forster, Mohan, & Hector, 2003; Lamme, Zipser, & Spekreijse, 2002).

Recently, several masked priming studies have reported that certain measures of neural activity are also sensitive to processes involved in visual letter and word processing (e.g., Dehaene et al., 2004; Grossi & Coch, 2005; Holcomb & Grainger, 2006; Petit, Grainger, Midgley, & Holcomb, in press). Most relevant here are a handful of studies using electrophysiological measures that have reported a sequence of effects starting as early as 100 ms and continuing through to 500 ms post-target onset (Holcomb & Grainger, 2006; Kiyonaga, Midgley, Holcomb, & Grainger, 2006; Petit et al., in press). Importantly, each of these effects has been shown to be dissociable as a function of prime–target similarity at different levels of representation of words (e.g., feature, orthographic, lexical, and semantic; Holcomb & Grainger, 2006) when word stimuli have been used. This degree of temporal sensitivity suggests that the ERP masked priming technique may be well suited for dissecting the time-course of neural processes in other domains of visual processing as well.

In the current study we sought to determine if ERPs recorded to pictures of common objects presented in a masked priming paradigm would prove sensitive to the sequence of neural events hypothesized to underlie visual object processing. Several studies have examined processing of visual objects using behavioral

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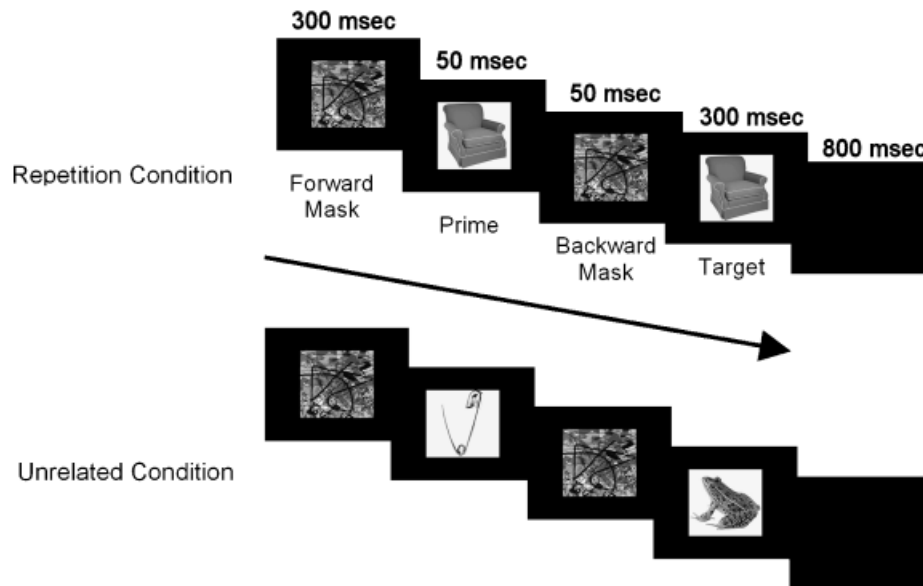


Figure 1. Examples of typical trials and their timing.

paradigms (e.g., Bar & Biederman, 1998, Dell'Acqua & Grainger, 1999), demonstrating that semantic and repetition priming effects are observed even when the prime is not consciously available to the subject. Also, using an implicit memory repetition priming paradigm, Zhang et al. (1997) found electrophysiological indices of object processing when primes were followed by the same or different target objects between 180 and 240 ms later. Another set of ERP studies using unmasked picture primes (Hamm et al., 2002; McPherson & Holcomb, 1999) in semantic priming paradigms has reported a frontally distributed negativity, the N300, which has been suggested to reflect object-specific processing (because a similar component has not been reported for words). In these studies the N300 is followed by the more central-parietally distributed N400, which has been argued to reflect semantic processing at an amodal level of representation (because a comparable component is found for words). More recently, an effect in an earlier epoch, overlapping the time range of the exogenous N1 component and focused over occipital electrodes, has been reported in two studies using the rapid masked priming paradigm (Holcomb & Grainger, 2006; Petit et al., in press).¹ Although these studies did not use pictures of objects (letters and words were used as stimuli), the scalp distribution and early time-course lead the authors to speculate that the effect reflects initial feature processing in visual cortex.

The current experiment used the same rapid repetition priming paradigm as that employed in our previous word and letter studies (Holcomb & Grainger, 2006; Petit et al., in press) and included two types of target objects, those that were completely unrelated to and those that were identical repetitions of the immediately preceding masked prime object (*rapid* refers to the use of a very brief prime–target interval). These were presented in a semantic categorization task in which participants detected

occasional probe objects belonging to a particular semantic category (food items). ERPs were time-locked to the presentation of critical nonfood target objects (see Figure 1). We predicted that the ERPs recorded to unrelated and repeated target objects, which differ at the feature, object, and semantic levels of representation, would produce (1) an early effect peaking in the time range of the exogenous N1 component and thought to reflect differences in low-level feature processes over visual cortical areas, (2) effects on the N300 component reflecting differences in the processing of object-specific representations over anterior brain regions, and (3) effects on the N400 component reflecting differences in the processing of domain-general semantic representations over more central-posterior brain regions.

Methods

Participants

Sixteen (7 men, 9 women, mean age = 20, range 18–24 years) right-handed Tufts University undergraduates participated for monetary compensation.

Stimuli and Procedure

Color photographs of 260 common objects taken from conventional views were displayed on a white background (each 256×256 pixels) on a 19-in. display (visual angle 2°) time-locked to the vertical refresh signal of the video card (100 Hz resolution). Each subject viewed 130 pseudorandomly arranged trials composed of a unique prime–target pair of objects. In the 80 critical trials (those used to form the ERPs of interest), 40 pairs of stimuli presented the same picture of an object in the prime and target positions (repeated) and another 40 pairs presented pictures of different unrelated objects in the prime and target positions (unrelated; see Figure 1). The remaining 50 trials contained a “probe” object (food item) paired with a nonfood object (25 in the prime position and 25 in the target position). Eight counterbalanced lists resulted in each repeated and unrelated object being presented an equal number of times across participants, but each object being presented in only one trial for each

¹The rapid masked priming paradigm refers to priming when the duration of the prime is brief (50 ms or less) and, most importantly, the onset of the prime and target are separated by a very short interval (100 ms or less). When the prime–target interval is longer (e.g., 500 ms), many of the effects of behavioral repetition priming that are seen at short intervals are refractory (Ferrand, 1996).

participant. Figure 1 depicts examples of the two types of critical trials and their timing. Participants were instructed to attend to the screen and rapidly press a button whenever they detected an object depicting a food item. All other items, including the critical items, were to be viewed passively.

EEG Recording

A 32-channel electrode cap (Electro-cap International) was used to collect the electroencephalogram (EEG; see Figure 2A for electrode locations). All electrodes, including one over the right mastoid, were referenced to an electrode over the left mastoid (the right mastoid was used to monitor differential left mastoid activity; none was found). Horizontal and vertical eye movements/blinks were detected from electrodes placed below and to the side of the eyes (scalp impedances $< 2 \text{ k}\Omega$). The EEG (200 Hz sampling rate, bandpass 0.01 and 40 Hz) was recorded continuously and ERPs averaged time-locked to the onset of targets. Trials with blinks, eye movements, and muscle artifact were rejected prior to averaging (approximately 10% of trials).

Data Analyses

Mean amplitude measurements were made in three time windows (early region = 100–250 ms; N300 region = 250–350 ms, and N400 region = 350–650 ms). ANOVAs were performed with Repetition, Electrode, and Hemisphere (except midline) as within-subject factors in four separate columnar analyses (e.g., Holcomb, Reder, Misra, & Grainger, 2005; see Figure 2 for four columns). Because two previous rapid masked repetition priming ERP studies (Holcomb & Grainger, 2006; Petit et al., in press) have reported early posterior effects of priming, a more fine-grained temporal analysis was also used to better characterize the time-course of the earliest effects of repetition. This involved separate ANOVAs run on successive 20-ms epochs between 40 and 400 ms at the two most posterior sites (O1 and O2), which were shown in a previous study to be the focus of the earliest effects of masked priming (Petit et al., in press).

Results

The average d' for probe items in the prime position was 0.81 and for probes in the target position it was 3.15, suggesting that participants were processing the targets for meaning but that the masking manipulation effectively blocked detection of the semantic properties of the primes on the great majority of trials.²

For all statistical analyses a Geisser–Greenhouse correction was applied to all comparisons with more than 1 degree of freedom. Figures 2B and 3 reveal that between 100 and 250 ms, an anterior negativity (N190) and focal posterior positivity (P190) were apparent when comparing ERPs to unrelated and repeated target objects (100–250 ms epoch, Repetition \times Electrode interaction, midline: $F[4,60] = 31.71$, $p = .00000001$, $\epsilon = .549$; Column 1: $F[2,30] = 7.30$, $p = .01$, $\epsilon = .626$; Column 2: $F[3,45] = 19.11$, $p = .0001$, $\epsilon = .445$; Column 3: $F[4,60] = 46.02$, $p = .00000001$, $\epsilon = .426$). To better characterize the time-course of the posterior aspect of this effect, successive 20-ms bins between

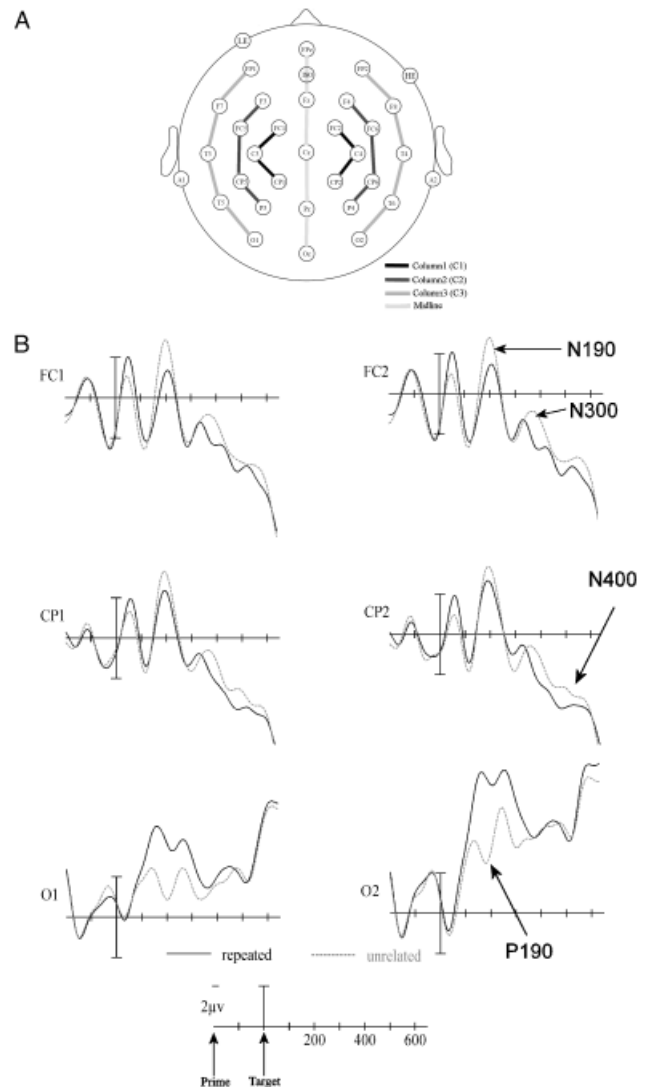


Figure 2. A: Electrode montage and analysis columns for ANOVAs. B: Repeated targets versus unrelated targets at six scalp sites, high-pass filtered at 10 Hz.

40 and 400 ms were analyzed at O1 and O2. There were significant repetition effects starting at 100 ms that continued on through each successive 20-ms epoch up to 400 ms (all $ps < .05$).

There were also significant priming effects apparent in the 250–350-ms window. These effects tended to be of negative polarity at more anterior sites (interaction of Repetition \times Electrode, midline: $F[4,60] = 3.917$, $p = .049$, $\epsilon = .374$; Column 3: $F[4,60] = 5.524$, $p = .024$, $\epsilon = .307$) as can be seen in the voltage maps in Figure 3B. This anterior priming effect took the form of unrelated targets being more negative than repeated targets, although at the most posterior sites the ERPs were more positive-going for unrelated compared to repeated items (note in Figure 2B that at the most posterior sites this effect appears to be continuous with the earlier P190 effect).

In the final window (350–650 ms) there was a broadly distributed effect of repetition with a central/parietal focus (see Figure 3C). Consistent with this being an N400 effect, unrelated targets produced more negative-going ERPs than repeated targets (main effect of repetition, midline: $F[1,15] = 7.37$, $p = .016$;

²Although the conclusion that participants did not consciously process the vast majority of prime pictures is supported by the very low number of probe primes detected, it is not critical to the claims of this study that all primes were processed completely outside of awareness. This is because the point of using the rapid masked priming technique is not to study unconsciousness, but rather to track the time-course of prime–target interactivity at short interstimulus intervals.

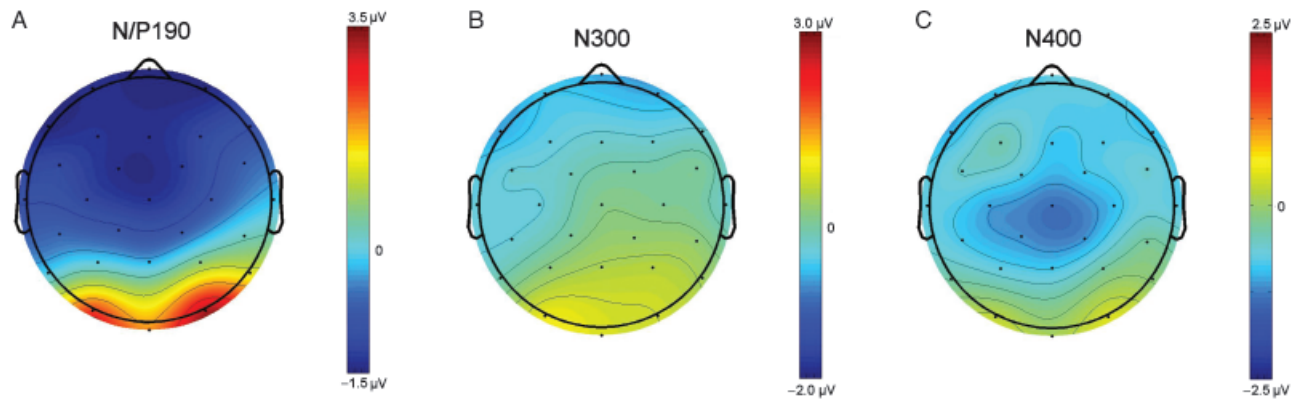


Figure 3. Voltage maps of the N/P190 (A), N300 (B), and N400 (C) at the peak of the effects.

Column 1: $F[1,15] = 8.59$, $p = .01$; Column 2: $F[1,15] = 10.94$, $p = .005$; Column 3: $F[1,15] = 12.35$, $p = .003$; see voltage map in Figure 3C).

Discussion

Studies in infrahuman species have demonstrated that visual perceptual processing involves a rapid set of cascaded information processes in classic visual areas of the brain (e.g., Schroeder, et al., 1998). Because complementary chronometric data do not exist for humans, the goal of the current experiment was to determine if an ERP adaptation of the rapid masked priming paradigm could be used to study the time-course of neural events underlying object perception in humans. In this regard we found evidence for three sequential ERP effects that began as early as 100 ms after target and continued on through 650 ms. All three of these effects differentiated target objects that were identical to the immediately preceding masked-prime object from targets that were different/unrelated to the prime at the feature, object, and semantic levels of representation. Consistent with the conclusions from numerous behavioral studies using the masked priming paradigm with word stimuli, it seems reasonable to propose that these effects reflect interactions between representations activated by the prime in the initial sweep of fast feed-forward processing in the visual and semantic systems (Forster et al., 2003; Lamme et al., 2002).³

The first of the ERP effects was a focal posterior positivity that was slightly larger over the right hemisphere and a more widespread anterior negativity. One possibility for these seemingly complementary effects is that they reflect a polarity inversion due to activity in a single neural source. This effect started around 100 ms post-target onset and peaked at about 190 ms and produced a polarity inversion where larger amplitudes (frontal negativities and posterior positivities) were observed for unrelated than repeated targets. Previous methodologically similar masked priming studies using single letters and words have reported a remarkably similar posterior positivity with a compar-

able time-course, right larger than left distribution, and complementary anterior negativity (Holcomb & Grainger, 2006; Petit et al., in press). One possibility is that all of these effects reflect activity in early visual extrastriate cortex that is involved in the initial phases of visual feature processing. Consistent with this view, Petit et al. reported that this positivity was substantially larger when prime and target letters had fewer elementary letter features in common (e.g., a-A vs. A-A) than when there was greater feature overlap (e.g., c-C vs. C-C). In a recent fMRI study with masked words, Dehaene et al. (2001) reported a right hemisphere effect that they attributed to extrastriate feature processing. One interesting prediction based on Dehaene's fMRI data is that if the N/P190 priming effect reflects this same or a similar early feature process, then it should be more sensitive than later postfeature object and semantic processes to changes in the relative location of primes and targets. This is because feature processes have been shown to have relatively small (and numerous) receptive fields compared to later higher level processes, which tend to be field size/location invariant (Dehaene et al., 2004).

The second component found in this study was an anterior negative-going effect that was maximal near 330 ms. Like previous unmasked priming studies using pictures of objects, this negativity, which has been referred to as the N300 in unmasked priming studies (e.g., Hamm et al., 2002), was larger for unprimed than primed target objects. Also, like at least one previous study, this effect inverted in polarity at the most posterior sites (McPherson & Holcomb, 1999). Previously it has been suggested that the N300 reflects an object-specific process (e.g., the effort involved in processing object specific representations; McPherson & Holcomb, 1999), as a similar component has not been reported in studies using words. This hypothesis could be tested in future masked priming studies by contrasting priming of target pictures when the prime is a word versus a picture. If the N300 reflects an object-specific process, then word-picture priming should not produce changes in this component.

Like earlier word studies using masking (e.g., Holcomb & Grainger, 2006) and previous unmasked picture studies (e.g., Hamm et al., 2002), masked picture priming also produced a widely distributed repetition effect in the N400 time window (350–650 ms) with target objects that were unrelated to the prior masked prime object producing more negative-going ERPs than targets that were repetitions of their masked primes. Consistent with the N400 literature, it seems most likely that this negativity

³Although the initial feed-forward sweep in monkey unit studies is largely complete in the 100–200-ms time frame (Lamme et al., 2002), it seems reasonable that the time-course of human feed-forward processing (especially any semantic component), would have a considerably longer time-course.

reflects processing at the level of meaning and is larger when integration of the semantic properties of the prime and target are relatively more difficult (i.e., for unrelated prime–target pairs). It will be important in future masked picture priming studies to determine if similar semantic effects can be obtained when primes and targets are only semantically related and not full repetitions. This is because N400 repetition priming effects may be relatively more sensitive to interactions between form and meaning, whereas semantic priming arguably involves interactions primarily at the level of meaning (Grainger & Holcomb, in press). A recent

study using the masked semantic priming has shown that the N400 is sensitive to semantic overlap with words in the rapid masked priming paradigm (Grossi, 2006).

Overall, the results of this study suggest that combining masked picture priming with the recording of ERPs is good way to dissect the time-course of object processing. In future studies it will be important to more directly test hierarchy of object processing proposed here by systematically manipulating the overlap in features across different levels of representation thought to underlie the perception of objects.

REFERENCES

- Bar, M., & Biederman, I. (1998). Subliminal visual priming. *Psychological Science*, 9, 464–469.
- Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review*, 94, 115–147.
- Dehaene, S., Jobert, A., Naccache, L., Ciuciu, P., Poline, J., Le Bihan, D., et al. (2004). Letter binding and invariant recognition of masked words behavioral and neuroimaging evidence. *Psychological Science*, 15, 307–313.
- Dehaene, S., Naccache, L., Cohen, L., Le Bihan, D., Mangin, J., Poline, J., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience*, 4, 752–758.
- Dell'Acqua, R., & Grainger, J. (1999). Unconscious semantic priming from pictures. *Cognition*, 73, B1–B15.
- Ferrand, L. (1996). The masked repetition priming effect dissipates when increasing the interstimulus interval: Evidence from word naming. *Acta Psychologica*, 91, 15–25.
- Forster, K. I., & Davis, C. (1984). Repetition priming and frequency attenuation in lexical access. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 10, 680–698.
- Forster, K. I., Mohan, K., & Hector, J. (2003). The mechanics of masked priming. In S. Kinoshita & S. J. Lupker (Eds.), *Masked priming: State of the art* (pp. 3–37). Hove, UK: Psychology Press.
- Grainger, J., & Holcomb, P. J. (in press). Neural constraints on a functional architecture for word recognition. In P. Cornelissen, P. Hansen, M. Kringlebach, & K. Pugh (Eds.), *The neural basis of reading*. Oxford: Oxford University Press.
- Grossi, G. (2006). Relatedness proportion effects on masked associative priming: An ERP study. *Psychophysiology*, 43, 21–30.
- Grossi, G., & Coch, D. (2005). Automatic word form processing in masked priming: An ERP study. *Psychophysiology*, 42, 343–355.
- Hamm, J. P., Johnson, B. W., & Kirk, I. J. (2002). Comparison of the N300 and N400 ERPs to picture stimuli in congruent and incongruent contexts. *Clinical Neurophysiology*, 113, 1339–1350.
- Holcomb, P. J., & Grainger, J. (2006). On the time course of visual word recognition: An event-related potential investigation using masked repetition priming. *Journal of Cognitive Neuroscience*, 18, 1631–1643.
- Holcomb, P. J., Reder, L., Misra, M., & Grainger, J. (2005). Masked priming: An event-related brain potential study of repetition and semantic effects. *Cognitive Brain Research*, 24, 155–172.
- Kiyonaga, K., Midgley, K. J., Holcomb, P. J., & Grainger, J. (2006). Masked cross-modal repetition priming: An ERP investigation. *Language and Cognitive Processes*.
- Lamme, V. A., Zipser, K., & Spekreijse, H. (2002). Masking interrupts figure-ground signals in V1. *Journal of Cognitive Neuroscience*, 14, 1044–1053.
- McPherson, W. B., & Holcomb, P. J. (1999). An electrophysiological investigation of semantic priming with pictures of real objects. *Psychophysiology*, 36, 53–65.
- Petit, J., Grainger, J., Midgley, K. J., & Holcomb, P. J. (in press). On the time-course of processing in letter perception: A masked priming ERP investigation. *Psychonomic Bulletin and Review*.
- Rugg, M. D., & Coles, M. G. H. (1995). The ERP and cognitive psychology: Conceptual issues. In M. D. Rugg & M. G. H. Coles (Eds.), *Electrophysiology of mind* (pp. 27–39). Oxford: Oxford University Press.
- Schroeder, C., Mehta, A., & Givre, S. (1998). A spatial-temporal profile of visual system activation revealed by current source density analysis of the awake macaque. *Cerebral Cortex*, 8, 575–592.
- Tanaka, K. (1996). Inferotemporal cortex and object vision. *Annual Review of Neuroscience*, 19, 109–139.
- Zhang, X. L., Begleiter, H., Porjesz, B., & Litke, A. (1997). Visual object priming differs from visual word priming: An ERP study. *Electroencephalography and Clinical Neurophysiology*, 102, 200–215.

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