

Stimulus-driven changes in the direction of neural priming during visual word recognition



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ABSTRACT

Visual object recognition is generally known to be facilitated when targets are preceded by the same or relevant stimuli. For written words, however, the beneficial effect of priming can be reversed when primes and targets share initial syllables (e.g., “boca” and “bono”). Using fMRI, the present study explored neuroanatomical correlates of this negative syllabic priming. In each trial, participants made semantic judgment about a centrally presented target, which was preceded by a masked prime flashed either to the left or right visual field. We observed that the inhibitory priming during reading was associated with a left-lateralized effect of repetition enhancement in the inferior frontal gyrus (IFG), rather than repetition suppression in the ventral visual region previously associated with facilitatory behavioral priming. We further performed a second fMRI experiment using a classical whole-word repetition priming paradigm with the same hemifield procedure and task instruction, and obtained well-known effects of repetition suppression in the left occipito-temporal cortex. These results therefore suggest that the left IFG constitutes a fast word processing system distinct from the posterior visual word-form system and that the directions of repetition effects can change with intrinsic properties of stimuli even when participants' cognitive and attentional states are kept constant.

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Introduction

As a general rule, vocabulary size of a language exceeds by far the number of letters used in the same language. In English, for example, more than 300,000 entries in a standard dictionary (<http://www.oed.com/>) are written with only 26 alphabet letters. This fact naturally suggests that many similar combinations of letters should co-exist as different words in almost any written language in the world. An important step for fluent reading is therefore fast and effective analysis of letter-strings for distinguishing a word (e.g., “spice”) from other, visually similar “neighbor” words (e.g., “spite”, “space”, “slice”, “spike” and so on). This early stage of word processing is often challenging for non-skilled readers, such as children and dyslexics (Goulandris, 2006) and can be also a common source of reading errors even for fully literate adults (Grainger et al., 1992). In fact, previous behavioral studies have shown that orthographic similarity of letter-strings strongly influences participants' behavioral response to written words. For instance, visual recognition of a target word (e.g., “diva”) is known to be accelerated when it is preceded by a pseudoword prime sharing the same consonant structure (e.g., “duva”) (New et al., 2008).

Interestingly, however, it is also known that prime–target orthographic overlap can produce an opposite pattern of behavioral effects

in other circumstances. That is, unlike the facilitatory effect of consonantal priming produced by pseudoword primes (New et al., 2008), behavioral response to targets (e.g., “char”) is known to be slowed down when they are preceded by real word primes having shared initial segments (e.g., “chat”) than when preceded by primes without such sublexical overlap. Similar inhibitory modulation of visual word processing seems to occur across different languages when prime and target share a set of initial letters (De Moor et al., 2007; Segui and Grainger, 1990) or a first syllable (Carreiras and Perea, 2002; Mathey et al., 2006; Nakamura et al., 2012a; Nakayama et al., 2011). This negative effect of neighbor priming, occurring only for real word primes, has been thought to arise from a word-level lateral inhibition mechanism, whereby orthographically overlapping primes activate multiple lexical codes which would compete and interfere with targets during visual word recognition (Grainger and Jacobs, 1996). Such lateral inhibition among orthographic neighbors seems to be greater in the left hemisphere than in the right hemisphere, since some previous studies show that orthographic neighbors flashed to the right visual hemifield (RVF) produce greater inhibitory effects relative to those to the left visual hemifield (LVF) (Nakamura et al., 2012a; Perea et al., 2008). The possible hemispheric difference in inhibitory effects may reflect the well-known left-hemisphere advantage in fine-grained analysis of local visual features (Beeman et al., 1994; Ivry and Robertson, 1998).

Indeed, several event-related potential (ERP) studies have shown that neural response associated with those inhibitory effects appears at 250–350 ms after target onset and tends to be lateralized to the

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left-hemisphere (Friedrich, 2005; Friedrich et al., 2013; Massol et al., 2010). To date, however, little is known about specific neuroanatomical structures involved in inhibitory priming during reading. It is nonetheless possible to predict some candidate brain regions from the lexical competition hypothesis as described above. That is, while lateral inhibition among lexical neighbors is thought to be the main source of negative priming effects, lexical activation in itself should rely on bottom-up signals from sublexical levels, either orthographic or phonological (Alvarez et al., 2004; Carreiras and Perea, 2002; Segui and Grainger, 1990). Thus, it is likely that cognitive loci of syllabic priming encompass lexical, orthographic and phonological codes of written words. At the neural level, previous brain imaging studies have identified neural correlates of lexico-semantic memory in the left lateral temporal cortex (LTC) (Campanella et al., 2009; Vandenbulcke et al., 2007). This region is located downstream of the left posterior occipito-temporal sulcus (pOTS) involved in abstract orthographic codes of written words (Dehaene et al., 2005) and seems to play a multimodal role in word processing (Chertkow et al., 1997; Cohen et al., 2004; Vandenberghe et al., 1996). On the other hand, phonological computation of words is known to be a fast and robust cognitive component of fluent reading (Frost, 2003) and thus may play a role in the generation of masked syllabic priming. Recent brain imaging data suggest that such rapid activation of phonological codes is mediated by the left inferior frontal area involved in speech production (Cornelissen et al., 2009; Klein et al., 2015; Pammer et al., 2004; Wheat et al., 2010).

In addition, it is also possible that the inhibitory effects arise at later processing stages involved in behavioral response, such as decision

masking and motor planning, because most of the effects reported seem to appear only during categorical judgment tasks and not during other language tasks without decision making (e.g., word naming) (Carreiras et al., 2005; Schiller, 2004; You et al., 2012). Such motor response stage of word processing has been thought to rely on the premotor region involved in motor preparation and execution (Nakamura et al., 2007; Rissman et al., 2003).

Using functional magnetic resonance imaging (fMRI), the present study investigated how these neural components contribute to the generation of inhibitory priming (Experiment 1). In each trial, participants made natural/artificial judgment about a centrally presented target, which was preceded by a masked prime flashed either to the left or right visual field (Fig. 1A). Consistent with previous behavioral studies, participants responded more slowly when primes and targets shared initial syllables than when not. This behavioral effect of syllabic priming was independent of motor response bias during semantic judgment (see *Methods* section). At the neural level, we observed that the effect of inhibitory priming was associated with a robust effect of repetition enhancement in the left inferior frontal gyrus (IFG). On the other hand, the left dorsal premotor area (PMd) and LTC, although showing activation increase associated with motor response, exhibited no significant priming associated with syllabic overlap.

Therefore, the observed neural priming in the left IFG clearly differed from repetition suppression in the pOTS and its adjacent regions that has been associated with facilitatory behavioral priming during visual word recognition (Dehaene et al., 2005). In fact, however, it is known that behavioral priming can depart from repetition suppression

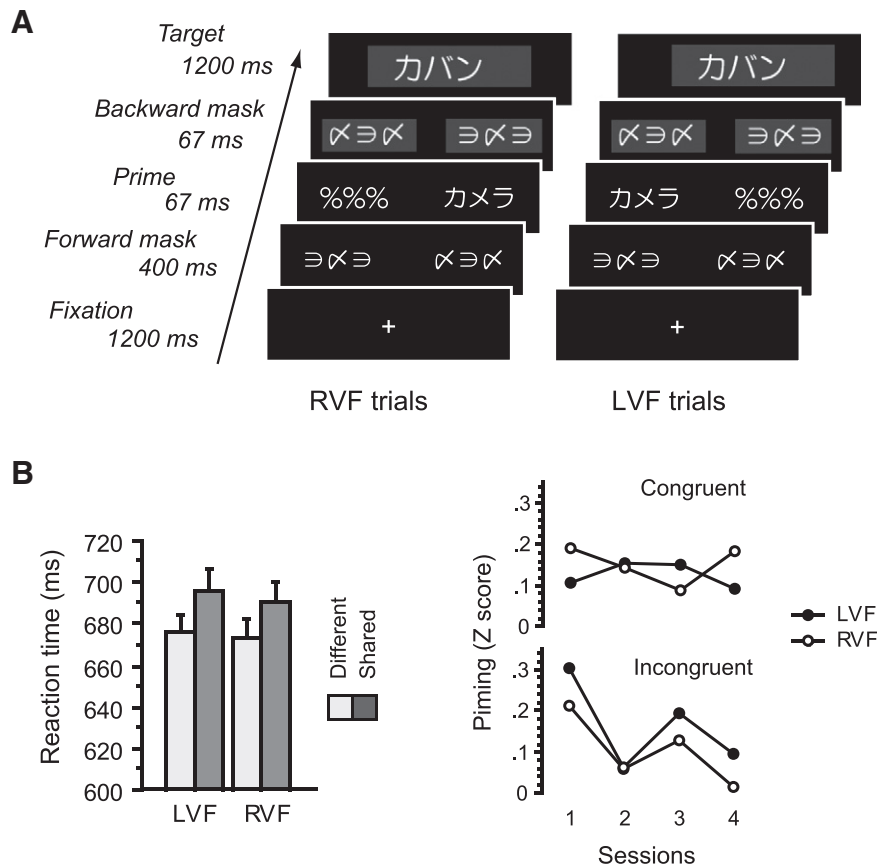


Fig. 1. Experimental paradigm and behavioral data for Experiment 1. (A) Each trial consisted of a forward mask, a prime and a visual foil, a backward masks and a target. We manipulated the visual hemifield of masked primes (LVF or RVF) and prime–target syllabic overlap at word-onset (shared or different). Primes and targets belonged either to the same category or to different categories. Participants made natural/artificial judgment by key-press with their right index and middle fingers. (B) Mean reaction time during semantic categorization (left) and temporal evolution of priming effects (in Z score units) separated by response congruency (right). Participants responded more slowly when primes and targets shared the same syllables at word onset than when they did not. The overall effect-size of this negative priming did not differ between the two hemifields. However, when restricted to congruent trials, the magnitude of syllabic priming tended to be larger in RVF trials than in LVF trials during the first session (see *Results* section).

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