

Cerebral Bases of Subliminal and Supraliminal Priming during Reading

Sid Kouider^{1,2}, Stanislas Dehaene^{1,3}, Antoinette Jobert¹ and Denis Le Bihan⁴

¹Cognitive Neuroimaging Unit, INSERM U562, SHFJ, CEA/DSV, Orsay, France, ²Laboratoire des Sciences Cognitives et Psycholinguistique (EHESS/CNRS/DEC-ENS), Paris, France, ³Collège de France, Paris, France and ⁴Anatomical and Functional Neuroimaging Unit, SHFJ, CEA/DSV, Orsay, France

Several studies have investigated the neural correlates of conscious perception by contrasting functional magnetic resonance imaging (fMRI) activation to conscious and nonconscious visual stimuli. The results often reveal an amplification of posterior occipito-temporal activation and its extension into a parieto-frontal network. However, some of these effects might be due to a greater deployment of attentional or strategic processes in the conscious condition. Here, we examined the brain activity evoked by visible and invisible stimuli, both of which were irrelevant to the task. We collected fMRI data in a masking paradigm in which subliminal versus supraliminal letter strings were presented as primes while subjects focused attention on another subsequent, highly visible target word. Under those conditions, prime visibility was associated with greater activity confined to bilateral posterior occipito-temporal cortices, without extension into frontal and parietal cortices. However, supraliminal primes, compared with subliminal primes, evoked more extensive repetition suppression in a widely distributed set of parieto-frontal areas. Furthermore, only supraliminal primes caused phonological repetition enhancement in left inferior frontal and anterior insular cortex. Those results suggest a 2-stage view of conscious access: Relative to masked stimuli, unmasked stimuli elicit increased occipito-temporal activity, thus allowing them to compete for global conscious access and to induce priming in multiple distant areas. In the absence of attention, however, their access to a second stage of distributed parieto-frontal processing may remain blocked.

Keywords: consciousness, fMRI, priming, reading, subliminal

Introduction

Much controversy surrounds the issue of the differences in brain activity associated with conscious and unconscious perception. In the last years, a number of experimental paradigms have been used to contrast the processing of conscious and nonconscious stimuli while collecting brain-activation data with functional magnetic resonance imaging (fMRI), electroencephalography, or magnetoencephalography (Dehaene et al. 2001; Rees, Wojciulik et al. 2002; Koivisto and Revonsuo 2003; Pins and Ffytche 2003; Ress and Heeger 2003; Gross et al. 2004). A major difficulty confronting this research, however, is that the visibility of a stimulus is frequently confounded with the consequences of becoming aware of that stimulus (Frith et al. 1999; Rees 2001; Pessoa and Ungerleider 2004). Indeed, one may wonder whether it is ever possible to dissociate the “pure” act of becoming aware of a stimulus, from its cognitive consequences on subsequent information processing. A conscious stimulus, by the very fact that it is seen, can be recognized, reported, evaluated, or memorized much better than an invisible stimulus. Thus, those

processes will be frequently if not always confounded with conscious perception.

This methodological problem affects the interpretation of most current neuroimaging findings. In many experiments, conscious perception has been associated with an amplification of activation in posterior perceptual regions as well as a late synchronous activation of parietal, prefrontal, and cingulate association cortices (Beck et al. 2001; Koivisto and Revonsuo 2003; Gross et al. 2004). Such coordinated parieto-fronto-cingulate activity has been proposed as the neuronal mechanism of access to conscious report in the global neuronal workspace theory (Dehaene, Kerszberg et al. 1998; Dehaene and Naccache 2001), as well as in several related accounts (Shallice 1988; Posner 1994; Desimone and Duncan 1995; Miller and Cohen 2001; Rees, Kreiman et al. 2002). Yet, as an alternative, these extensive activations might be attributed, in large part, to the additional cognitive processes afforded by conscious access rather than to conscious perception per se.

In view of this possibility, several researchers have considered the alternative possibility that conscious perception is, in fact, associated with a much narrower set of brain regions, perhaps confined solely to posterior cortices specifically involved in encoding the relevant sensory attributes. Zeki (2003) has argued that such early and focal stimulus-specific activation is associated with a form of “microconsciousness,” whereas Lamme (2003) has argued that local recurrent loops in the visual system suffice to create “phenomenal consciousness.” Empirically, a number of paradigms have observed early and low-level correlates of conscious visual perception (Grill-Spector et al. 2000; Bar et al. 2001; Moutoussis and Zeki 2002; Ress and Heeger 2003), such as a correlation with the amplitude of the P1 waveform of the visual event-related potential (Pins and Ffytche 2003), a posterior negativity peaking around 200 ms (Koivisto and Revonsuo 2003), or an increase in occipito-temporal activation and functional connectivity (Ress and Heeger 2003; Haynes et al. 2005; Tse et al. 2005). It is noteworthy, however, that the vast majority of these studies have also observed late distributed parieto-frontal correlates, thus making it difficult to decide which of the early or late events, if any, are causally related to conscious perception.

In the present study, we attempted to address this issue by measuring the brain activity evoked by visible and invisible stimuli, which were irrelevant for the task and therefore did not receive task-related attention. To manipulate visibility, we contrasted the subliminal presentation of briefly flashed (43 ms) and masked lower-case letter strings with the presentation of the same strings under a supraliminal condition obtained by removing the surrounding masks (Fig. 1). Previous experiments have used this paradigm to demonstrate that subliminal word

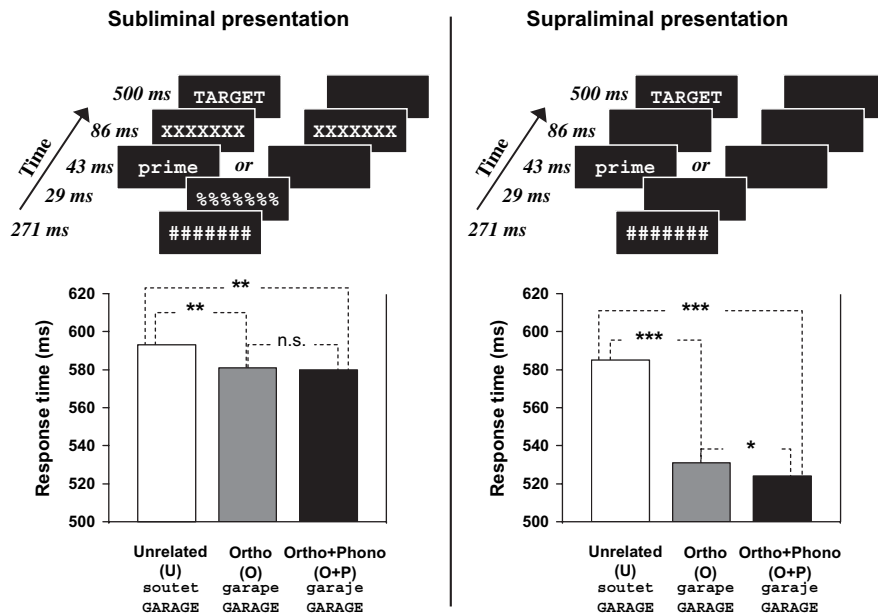


Figure 1. Experimental procedure and behavioral results for the subliminal (left part) and supraliminal presentation (right part) (n.s. = nonsignificant; * $P < 0.02$; ** $P < 0.002$; *** $P < 0.0002$).

processing is associated with detectable activity in occipital and temporal cortices, and that supraliminal presentation yields additional parieto-prefrontal activity (Dehaene et al. 2001). Crucially, however, relative to those previous designs, here the task required neglecting those initial lower-case stimuli (hereafter termed the “primes”) in order to perform a semantic decision task on other highly visible “target” words presented subsequently in upper case and at the same screen location. In this manner, we could study the neural correlates of prime visibility, that is, the fate of subliminal or supraliminal stimuli, which did not receive task-related attention.

Naturally, the status of such brief stimuli in relation to consciousness may be debated. Although the unmasked primes were, *visible*, in the sense that they could be reported by subjects when told to do so, it does not necessarily imply that they were consciously *seen* on every trial of the main task performed on target stimuli. Research on the attentional blink and inattention blindness (Mack and Rock 1998; Sergent et al. 2005) suggests that unattended stimuli may completely fail to be registered into consciousness. Indeed, in the present design it could be advantageous for subjects to actively withdraw attention from the primes, in order to avoid interference with the main target word. Thus, it has been argued that the present design merely studies a “preconscious” level of processing where stimuli are potentially accessible but not consciously accessed (Dehaene et al. 2006). We will return to whether attention is necessary for consciousness and how the pre-conscious level is specified in the Discussion.

In addition to allowing us to contrast visible versus invisible stimuli, our design allowed us to study the effect of those stimuli on the subsequent processing of another conscious target. To this end, we exploited the phenomenon of fMRI adaptation (Grill-Spector and Malach 2001), a reduction of brain activity when some properties are shared between the prime and target, compared with a situation in which they fully differ (Naccache and Dehaene 2001; Henson 2003). We studied whether this

repetition suppression phenomenon differs in the subliminal and supraliminal conditions.

We contrasted 3 conditions (see Fig. 1): The prime could be unrelated to the target, it could be orthographically similar to the target, or it could be orthographically similar and also homophonic with the target, and thus related at both the orthographic and phonological levels. Behavioral studies of visual word recognition have suggested that although masked orthographic priming obtains easily, this is not the case for phonological priming, especially when using brief prime durations (e.g., below 50 ms). Indeed, priming at the phonological level necessitates longer prime durations (Ferrand and Grainger 1992, 1993). However, because longer durations induce higher visibility, phonological effects also correlate with prime visibility (Kouider and Dupoux 2001). As both factors were confounded in previous studies, it is still a matter of debate whether phonological effects are driven by prime duration (Grainger et al. 2003) or, as we previously suggested, by prime visibility (Kouider and Dupoux 2001). In the present study, we addressed this issue by taking advantage of the fact that visible and invisible primes were contrasted while the prime duration was kept constant (i.e., 43 ms). Under these conditions, we expected orthographic, but no phonological priming in the subliminal condition. By contrast, we expected phonological effects to emerge with visible primes, even when using the same short prime duration.

The emergence of phonological priming as a function of prime visibility can be taken, in itself, as an indication that supraliminal primes are able to invade a much larger set of brain regions than subliminal primes. If stimulus visibility relates to the recurrent activation of a broad network of regions, then in the unmasked condition we should see an extension of the fMRI repetition suppression effect into a broad set of areas distant from visual cortex, some of which should show specific phonological effects.

A final difficulty is that fMRI lacks temporal resolution and therefore lumps together the activation evoked by the masks,

primes, and targets. In order to isolate the activation evoked by primes and targets, we added to the experimental design 2 *mask-only* baselines. On such trials, the primes and targets were replaced by blank screens, and the subject therefore did not perform the task but the sequence of masks was exactly identical, respectively, to the supraliminal or subliminal conditions (Fig. 1). All contrasts and activation levels were computed relative to the relevant mask-only baseline, which corrects for the different masking context in which the visible and invisible primes were presented. After this subtraction, we could directly compare the activity and the priming effects evoked by the same strings, presented for the same short duration (43 ms), under conditions in which they were invisible (masked) or visible (unmasked).

In summary, our experiment implemented a factorial design, which manipulated orthogonally the visibility of the primes (visible or invisible, alternating across fMRI runs) and the prime-target relation (3 trial types, pseudorandomly varied across trials: unrelated [U], orthographic [O], or orthographic + phonological [O + P]). Based on the past literature, our predictions were as follows. First, for the visibility contrast (visible minus invisible primes), we expected to observe either the same large network of posterior occipito-temporal and fronto-parieto-cingulate areas as in our previous work (Dehaene et al. 2001) or, if the latter areas are associated with conscious access rather than visibility, we expected visibility to be associated with a restricted set of posterior areas. Regarding orthographic subliminal priming, we expected subliminal repetition suppression effects to be restricted to occipito-temporal cortex, particularly the left “visual word form” area (VWFA) (Dehaene et al. 2001; Devlin et al. 2004). By contrast, we expected supraliminal repetition suppression effects to extend into a much broader set of cortical regions including parietal and frontal regions. We further expected that phonological priming would show behavioral and neural effects only for visible primes, and these effects would appear within regions classically associated with phonological processing, such as the left superior temporal, supramarginal, inferior frontal, and anterior insular regions (e.g., Booth et al. 2002; Burton et al. 2005; Dehaene-Lambertz et al. 2005).

Methods

Participants

Fifteen right-handed native French speakers (8 females; mean age 23.5 year, range 21–28 year) gave written informed consent to take part in this study. The protocol was approved by the French Regional Ethical Committee for Biomedical Research (Hôpital de Bicêtre).

Stimuli

Forty 4 to 6 letters French nouns served as target stimuli (mean frequency = 14.1 per million; mean length = 5.5 letters). Half of them denoted natural objects (e.g., “CACTUS”) and the other half, matched in length and frequency, represented artifacts (e.g., “GARAGE”). For each target word, 3 types of pronounceable pseudowords primes were constructed by changing one letter from real words. For the orthographic (O) condition, the prime shared all but one letter with the target (e.g., garape-GARAGE); for the phonological (O + P) condition, one letter of the prime also varied (at the same position) but the prime was also homophonic with the target (e.g., garaje-GARAGE); for the unrelated (U) condition, the prime did not share any letter at the same position with the target (e.g., soutet-GARAGE). Because masked priming tends to be stronger for words with low neighborhood density (i.e., the number of words that can be created by changing one letter of the stimulus word, preserving letter positions) (Forster 1998; Perea and

Rosa 2000), only stimuli with a few neighbors were used here (mean = 1.1 neighbor for target words and 1.6 for each of the 3 types of prime stimuli).

Procedure

Each trial consisted of a precisely timed sequence of a prime presented in lowercase letters for 43 ms and a target presented in uppercase letters for 500 ms (Fig. 1). The presentation of the prime could be subliminal or supraliminal depending on the masking conditions. On subliminal blocks, the prime was preceded by a first forward mask (i.e., “#####”) for 271 ms and a second forward mask (i.e., “%%%%%%%%”) for 29 ms, and followed by a backward mask (i.e., “XXXXXXX”) presented for 86 ms and prior to the target. On supraliminal blocks, the 2 masks surrounding the prime (i.e., the second forward mask and the backward mask) were replaced by blank screens. All stimuli covered up the central area of the screen and appeared with the same nonproportional font (i.e., courier). There was a new trial every 2.4 s (which corresponded to the fMRI time repetition [TR]). A fixation cross was continuously displayed in between the offset of the target and the onset of the first forward mask on the next trial. Participants were asked to decide as quickly and as accurately as possible whether target words denoted natural objects or artifacts. They were asked to pay attention solely to uppercase stimuli (i.e., targets) and to ignore any other displayed event (i.e., primes and masks). Each block was constituted of 164 trials: 4 initial trials that were later discarded and 40 targets × 3 priming conditions randomly mixed with 40 mask-only trials. The latter trials comprised sequences with blank screens replacing primes and targets. There were thus 2 baselines, one for the subliminal blocks and the other for the supraliminal blocks, in each case measuring the activation evoked by the masks only (see Fig. 1). Importantly regarding the subliminal versus supraliminal contrast, such mask-only baselines allowed us to image only the activation evoked by the prime-target pair, while subtracting away the distinct activity patterns induced by the 2 types of masking. Participants were told to avoid pressing a button for these mask-only trials.

The first 4 participants received 6 blocks, whereas for the remaining 11 participants we extended the experiment to 8 blocks. They received either half the blocks with supraliminal primes first, or half the blocks with subliminal primes first. The block order (subliminal first or supraliminal first) was systematically alternated from one participant to the other. In addition, separate small blocks of 8 training trials were presented prior to the subliminal blocks and prior to the supraliminal blocks.

Immediately after the imaging sessions, while lying inside the scanner, participants performed a forced-choice test designed to evaluate the visibility of primes. They were told to focus only on the lowercase letter strings and to ignore the uppercase words. To maximize the possibility of prime perception, participants initially received 16 training trials with primes presented for 300 ms, then 60 trials in each of the masking presentation conditions at normal speed (43 ms primes). Each trial comprised the same sequence of masks and stimuli as in the priming experiment and, in addition, a pair of choices presented simultaneously after the target. One alternative appeared on left of fixation, whereas the other appeared on the right side. One of the 2 alternatives always corresponded to the prime and could appear on the left or right side with the same probability. Participants were asked to determine which of the 2 items corresponded to the prime within the preceding event sequence. They responded by pressing the left button if the correct alternative was on the left side, and with the right button if it was on the right side. They were told that only response accuracy, not response speed was important. The 2 alternatives remained on the screen until a response was made. They were orthographically dissimilar (“garaje” vs. “soutet”) on 67% of the trials, and similar on the remaining trials (“garaje” vs. “garape”). This distinction was made to obtain indexes of partial versus full awareness of the primes, and to control for their influence on priming effects (Kouider and Dupoux 2004). Indeed, orthographic priming could potentially result from seeing one or a few letters and could thus be induced by partial awareness (seeing “ga_a_e” provides an advantage as opposed to “so_t_t” when preceding the target “GARAGE”). Thus, it was important to show that, in the subliminal condition, orthographic priming obtains in the absence of even partial

awareness of the primes. If phonological priming (as measured by a difference between the orthographic and phonological conditions) obtains only under conditions of full prime awareness, that is awareness of all the word constituents, then partial awareness would not suffice (seeing “ga_a_e” preceding the target GARAGE would not provide a specific phonological advantage as it can occur either in the orthographic or in the phonological condition). Thus, it was critical to assess whether participants in the supraliminal condition were able to identify the whole prime, not just fragments of it.

fMRI Analysis

We used a 3-Tesla whole-body system (Bruker, Germany) using a standard head coil optimized for a gradient echo-echo planar imaging sequence (40 contiguous axial slices, thickness 3 mm with 0.5 mm gap, TR = 2400 ms, time echo = 40 ms, flip angle = 90°, field-of-view = 192 × 256 mm², 64 × 64 pixels). High-resolution anatomical images were obtained following the priming experiment.

After image reconstruction, the functional images were processed using the SPM2 software (Wellcome Department of Cognitive Neurology, London, UK). Four initial volumes were discarded to eliminate nonequilibrium effects of magnetization. Images were corrected for head motion, resampled every 4 mm using sinc interpolation, normalized to the standard brain space (Friston et al. 1995), and spatially smoothed with an isotropic Gaussian filter (8-mm full width at half maximum). These images were then high-pass filtered at 120 s and smoothed with a 4 s Gaussian kernel. For each participant, a weighted-mean image for each contrast was computed by fitting each voxel time-series with the known time-series of the 8 event types convolved with a canonical hemodynamic response function and its time derivative. Group-based statistical inferences were then made using a random effect model (Friston et al. 1999), with voxelwise $P < 0.001$ and cluster-level $P < 0.05$ corrected across the entire brain volume. However, for repetition suppression only (activation reduction in related trials relative to unrelated trials), in order to maximize detectability, we first calculated the set of regions activated during the semantic decision task relative to the mask-only baseline (voxelwise $P < 0.001$, cluster-level $P < 0.05$ corrected across the entire brain volume), and then searched for repetition suppression within this active network (voxelwise $P < 0.001$, cluster-level $P < 0.05$ corrected for multiple comparisons over the smaller volume of 42 804 voxels activated voxels). We also report whenever additional regions showed repetition suppression or enhancement effects in a whole-brain search (voxelwise $P < 0.001$, cluster-level $P < 0.05$ corrected across the entire brain volume).

Results

Prime Visibility

Data from the forced-choice prime identification task were used to evaluate prime visibility. Measures of d' values for each subject confirmed that they were unable to consciously perceive the primes in the subliminal condition (53.2% correct; $d' = 0.19$, $t(14) = 1.63$, $P > 0.13$), whereas they could do so in the supraliminal condition (82.4% correct; $d' = 2.21$, $t(14) = 7.111$, $P < 0.0001$), resulting in a significant difference ($t(14) = 7.113$, $P < 0.0001$). When considered separately, indices of partial and full awareness in the subliminal condition did not differ from each other (respectively $d' = 0.27$ and $d' = 0.18$; $t < 1$) and none was significantly above 0 (both P s > 0.12). Thus, the primes in the subliminal condition were genuinely invisible even when considering awareness of letters or word fragments. By contrast, in the supraliminal condition, both partial and full awareness measures were significantly above 0 (respectively, $d' = 2.79$, $t(14) = 7.07$, $P > 0.001$; and $d' = 1.71$, $t(14) = 6.70$, $P > 0.001$). Not surprisingly, partial awareness trial led to better discrimination than full awareness trials ($t(14) = 3.02$, $P < 0.01$). Nevertheless, the highly positive d' in the full awareness condition shows that even details of the prime constituents could be identified in the

supraliminal condition, such that participants were able to discriminate between the similar orthographic and phonological primes (“garaje” vs. “garape”).

Behavioral Priming

An analysis of variance (ANOVA) on mean correct response times during the semantic categorization task revealed a main effect of Presentation Type (subliminal vs. supraliminal; [$F_{1,14} = 45.66$, $P < 0.0001$]): Responses were 38 ms faster overall in the supraliminal condition, presumably because removal of the masks rendered the target easier to process. There was also a main effect of Prime Type (phonological, orthographic, or unrelated primes; [$F_{2,28} = 112.56$, $P < 0.0001$]). A strong interaction ($F_{2,28} = 7.44$, $P < 0.002$) indicated greater priming in the supraliminal compared with the subliminal condition (Fig. 1). Planned contrasts revealed an overall orthographic priming effect (unrelated minus orthographic primes) ($F_{1,14} = 100.17$, $P < 0.0001$), which was significantly larger in the supraliminal condition ($F_{1,28} = 10.17$, $P < 0.0005$), as well as an overall phonological priming effect (orthographic minus phonological primes) ($F_{1,14} = 7.41$, $P < 0.02$), which did not interact significantly with presentation type ($F < 1$). Further comparisons revealed the presence of orthographic priming under supraliminal presentation (54 ms; $F_{1,14} = 128.42$, $P < 0.0001$) as well as under subliminal presentation (12 ms; $F_{1,14} = 15.079$, $P < 0.002$). By contrast, phonological priming obtained under supraliminal presentation (7 ms; $F_{1,14} = 7.40$, $P < 0.02$) but not under subliminal presentation (1 ms; $F < 1$).

Overall error rates were low (subliminal presentation: O = 5.0%, O + P = 5.7%, U = 5.7%; supraliminal presentation: O = 4.8%, O + P = 4.3%, U = 5.9%). A similar ANOVA performed on error rates did not reveal any significant orthographic or phonological priming, either under subliminal or supraliminal presentation (all P s > 0.12).

In summary, in agreement with previous results (Kouider and Dupoux 2001, 2004, 2005), behavioral priming was observed in response times but not error rates, with a strengthening and broadening of priming effects when the prime stimuli were unmasked. We then turned to fMRI to identify the cerebral mechanisms of this increase in priming.

Imaging Results

Relative to the baseline mask-only trials, performance of the semantic decision task led to overall task-related activation in a broad bilateral network including ventral occipito-temporal, posterior superior parietal, supramarginal, primary motor, supplementary motor, dorsal anterior cingulate and cerebellar cortices, the thalamus, putamen, cerebellum, as well as left-lateralized activations of the anterior insula, inferior frontal, and dorsolateral prefrontal cortices. Deactivation was observed in the right parieto-occipito-temporal junction, posterior cingulate, and ventral anterior cingulate.

We examined how these activations were modulated by prime visibility (main effect of supraliminal minus subliminal trials, see the Methods section). Greater activation to supraliminal primes was seen only in the left and right ventral occipito-temporal regions (Fig. 2, top). The peak difference was observed in the left occipito-temporal gyrus (Montreal Neurological Institute [MNI] coordinates: -44, -70, -12; $Z = 5.55$) but in fact extensive bilateral differences were found, extending from the occipital pole ($y = -102$) to the anterior fusiform ($y = -38$). No

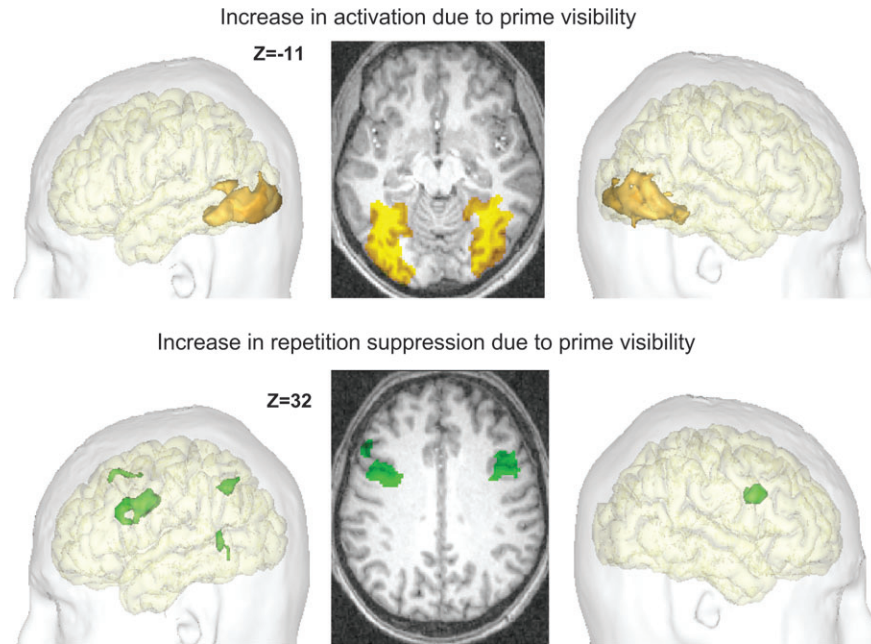


Figure 2. Neural correlates of prime visibility. The top images show the brain regions with more activity for visible primes (supraliminal minus supraliminal trials). The bottom images show the brain regions where orthographic priming was significantly stronger under supraliminal than under subliminal conditions (i.e., an interaction between orthographic priming and the subliminal vs. supraliminal status of the primes).

other clusters showed a main effect of visibility, even when restricting the search only to active voxels, although a trend was found in left inferior frontal cortex ($-42, 20, 18$; $Z = 3.62$). As expected, there were no regions of greater activation to subliminal than to supraliminal primes.

We then examined the effects of the primes (Fig. 3). A first contrast was designed to maximize the detection of orthographic priming effects, which should be present in both the O and O + P conditions. We therefore searched for more activity in condition U than in the mean of conditions O and O + P (orthographic repetition suppression) as well as the reverse contrast (orthographic repetition enhancement).

In the subliminal condition (Fig. 3A), we observed several regions with orthographic repetition suppression (but no region with repetition enhancement). Repetition suppression reached corrected significance in a right ventral region with both mesial ($16, -56, -8$) and lateral (e.g., $28, -62, -8$) subpeaks, at a location overlapping mostly with the right cerebellum but encroaching partially into the right lingual gyrus. Two symmetrical regions were also observed, just below significance, at a location corresponding to the left and right frontal eye fields (FEF) ($-22, -14, 66$, $Z = 4.56$, corrected $P = 0.055$; and $26, -6, 70$, $Z = 4.09$, corrected $P = 0.081$). Another a priori location of interest, the VWFA previously reported in several studies of subliminal priming during reading (Dehaene et al. 2001, 2004; Devlin et al. 2004), also showed a small repetition suppression effect ($-38, -62, -20$; peak $Z = 3.56$; voxel-level $P = 0.0002$, uncorrected; cluster extent 23 voxels).

When tested in the supraliminal condition (Fig. 3B), orthographic repetition suppression became extensive (still without any region of repetition enhancement). Repetition suppression was significant in the left occipito-temporal sulcus, within a large cluster extended from the posterior occipito-temporal sulcus ($-40, -70, -4$) to the VWFA and the lateral inferotemporal multimodal area (Cohen et al. 2004) ($-50, -58, -10$). There was

also a smaller peak in the right occipito-temporal sulcus ($32, -70, -22$). Outside the ventral visual pathway, repetition suppression was also observed in the left middle temporal gyrus ($-56, -50, 10$), the depth of the left and right precentral sulci ($-36, 4, 30$ and $48, 10, 34$), the left inferior prefrontal cortex ($-50, 40, 8$), the bilateral supplementary motor area (SMA)/preSMA ($12, -10, 54$ and $-14, 8, 52$), the right intraparietal cortex ($40, -58, 42$), and right thalamus ($22, -22, 12$).

The vast majority of these regions showed a strong interaction of orthographic repetition suppression with prime visibility, indicating that they showed more repetition suppression with supraliminal than with subliminal primes (Fig. 2, bottom). The sole exceptions were the left and right ventral occipito-temporal and the lateral inferotemporal cortices, where histograms of percent signal change confirmed that orthographic repetition suppression was approximately as strong for visible than for invisible stimuli (Fig. 4, top left).

A second contrast examined *phonological* priming by comparing conditions O + P and O. No supraliminal repetition suppression was observed ($O + P < O$). In the converse contrast for supraliminal repetition enhancement, although no difference was found at the conventional voxel-level threshold of $P < 0.001$, lowering this threshold to $P < 0.005$ revealed an extended cluster of greater activation for phonologically related trials than for orthographically related trial (corrected cluster-level $P = 0.002$), with subpeaks in the left inferior frontal ($-32, 28, -6$) and left anterior insula ($-34, 12, -6$). No subliminal phonological effect was observed, as either suppression or enhancement, and both of the above peaks showed a small interaction effect suggesting greater priming in the supraliminal compared with the subliminal condition (respectively $Z = 3.61$ and 2.99), although this interaction did not reach significance at the cluster level.

Figure 4 summarizes the major task-related regions and their profile of activity across the 6 conditions. Examination of those

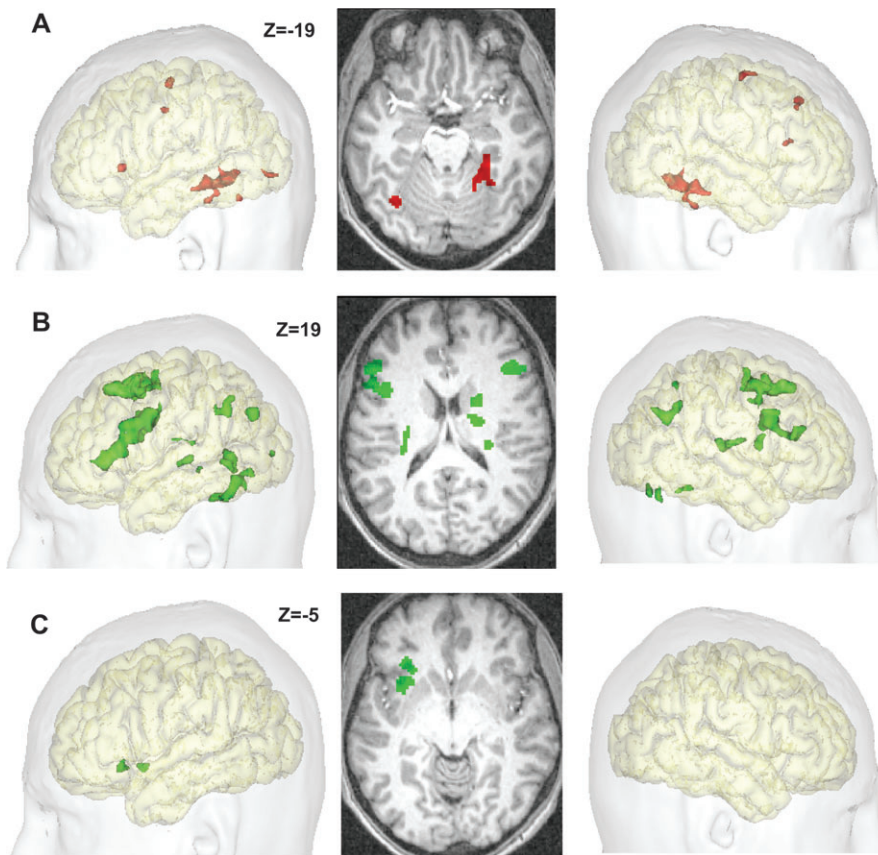


Figure 3. Effects of priming, projected onto left hemispheric, top, and right-hemispheric views of the standard MNI brain. (A) Regions showing subliminal repetition suppression. (B) Regions showing supraliminal repetition suppression. (C) Regions showing repetition enhancement in the supraliminal phonological condition. For illustration purposes, all contrasts are thresholded at $P < 0.001$, cluster size >23 voxels.

profiles shows that, in many regions, the main difference arises from a stronger activation in the unrelated, supraliminal condition compared with all of the others. This is the principal reason underlying the above-described priming by visibility interaction. To demonstrate this effect more directly, we reexamined the visibility contrast (supraliminal minus subliminal trials) as a function of the prime-target relation. When the prime was related (O and O + P conditions), the visibility contrast was entirely confined to bilateral occipito-temporal regions, as described earlier. However, when the prime was unrelated, in addition to this major occipito-temporal difference, an additional increase in activation with visibility was seen in left and right precentral sulci ($-42, 2, 38$ and $54, 2, 30$), the left inferior prefrontal cortex ($-44, 22, 10$), and the bilateral SMA/preSMA ($6, 6, 50$ and $-8, 8, 54$). Thus, when the subject was presented with 2 completely distinct strings, these regions showed more activity when this pair was visible than when it was subliminal.

Discussion

Neural Correlates of Subliminal Priming

In accord with previous studies of masked priming during reading (Dehaene et al. 2001, 2004; Devlin et al. 2004), subliminal priming was associated with repetition suppression in left occipito-temporal cortex, at a location roughly corresponding to the VWFA. In the present study, however, the peak of fMRI adaptation was slightly posterior to the one reported by

Dehaene et al. (2001). Such a difference might be related to the progressive posterior-to-anterior anatomo-functional hierarchy thought to be involved in visual word recognition (Dehaene et al. 2004; Nakamura et al. 2005). Although Dehaene et al. (2001) used word repetition priming, the present study relied on orthographic priming by a pseudoword prime, which shared all but one letter with the target. Such priming may engage only sublexical letter and bigram levels, which are thought to engage the posterior occipito-temporal sulcus (Dehaene et al. 2004; Nakamura et al. 2005). Devlin et al. (2004) also used subliminal orthographic priming with partial letter overlap rather than repetition priming and also observed a posterior peak of repetition suppression very close to the one in the current study (respectively, $-40, -60, -20$ and $-38, -62, -20$).

However, by contrast to previous work, we also observed subliminal orthographic effects in 2 additional regions. First, repetition suppression was observed in the left and right FEF known to be involved in saccadic eye and attention movements (Schall 2004). In spite of their anterior localization, the FEF are increasingly thought of as early visual processing areas with a fast connection to visual cortex (Schmolsky et al. 1998) and a demonstrable activation by subliminal visual stimuli (Thompson and Schall 1999). However, the FEF were not observed in previous studies of subliminal priming during reading. This discrepancy might be explained by the use of pseudoword primes in the present study, whereas only word primes were used in previous work. Pseudowords involve serial rather than parallel reading, as demonstrated by a significant word length

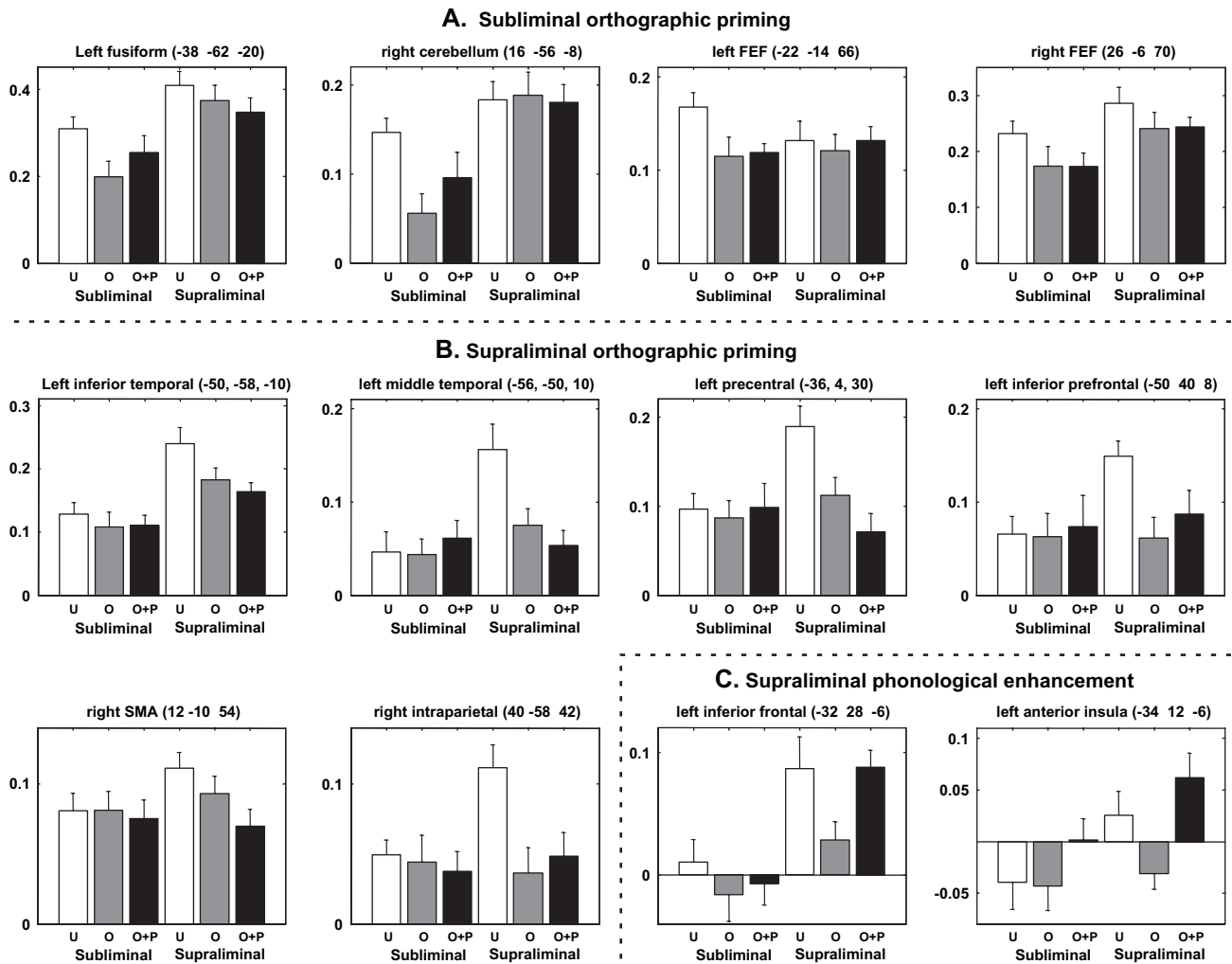


Figure 4. Histograms of percent BOLD signal change across the 6 conditions of the experimental design, for several brain regions of interest showing orthographic repetition suppression from subliminal primes (A) and/or supraliminal primes (B), or phonological repetition enhancement from supraliminal primes (C).

effect (Weekes 1997; Rastle et al. 2000, 2003, 2005; Coltheart et al. 2001). It is therefore possible that pseudowords flashed subliminally would nevertheless evoke a brief activation in eye- and attention-movement circuitry, thus creating a repetition suppression effect in those regions if the subsequent word shares most of its constituent letters with the pseudoword prime.

Subliminal repetition suppression was also observed in the right superior cerebellum. Cerebellar activations, with a consistent right lateralization, have been observed consistently in fMRI studies of reading (Fulbright et al. 1999; Turkeltaub et al. 2002). The activation we observed matches tightly with that observed by Fulbright et al. (1999) in an fMRI study using orthographic, phonological, and category judgment tasks on written words. Although these observations suggest a potential cerebellar contribution to visual word recognition processes, which remains to be characterized functionally, great caution remains needed in drawing such a conclusion because the activation might also be imputed to contamination from the neighboring lingual gyrus, due to spatial smoothing and group analysis. In future work, the issue of a specific contribution of the cerebellum to reading and to orthographic priming could be further clarified by high-resolution fMRI studies and single-subject analysis.

As concerns phonological priming, as predicted on the basis of our previous work (Kouider and Dupoux 2001), phonological effects did not show up under subliminal conditions, either at the behavioral or at the neural level. Phonological priming was only observed under supraliminal conditions. Those results are consistent with previous research indicating that suprathreshold primes are necessary to obtain phonological effects in word recognition tasks (Shen and Forster 1999; Kouider and Dupoux 2001). Relative to these previous findings, the present effect was rather small and the interaction of phonological priming with visibility did not quite reach significance, perhaps due to a small degradation of stimulus visibility related to the projector, screen and mirror used to present stimuli in the fMRI scanner. Nevertheless, the present experiment is the first to afford an examination of the cerebral mechanisms of such phonological priming. Unexpectedly, instead of being associated with repetition suppression, phonological priming was associated with a small increase in activation of the left inferior frontal cortex and anterior insula. These regions are well known to be implicated in phonological and articulatory processing (Dronkers 1996; Burton 2001; Booth et al. 2002; Poeppel and Hickok 2004). The left inferior frontal cortex has been associated with sublexical phonological processing during

speech perception (Burton et al. 2000), whereas the left anterior insula has been linked to subvocal rehearsal (Fiez et al. 1996) during both language production and language perception (Wise et al. 1999). Importantly, these regions have been associated with phonological processing not only during speech processing but also during reading, especially in grapheme-phoneme conversion tasks such as rhyme judgment (Pugh et al. 1996; Fiez and Petersen 1998; Poldrack et al. 2001; Booth et al. 2002).

Although it is unclear why phonological repetition enhancement rather than suppression was obtained in those regions, we note that past experiments have systematically observed enhancement when using unfamiliar or degraded stimuli whose perception is facilitated by priming (Henson et al. 2000; Turk-Browne et al. 2006). Our results therefore hint that the phonologically related primes may have facilitated access to a phonological representation of the target, which would not have been accessed otherwise. Another, related interpretation is that the phonological condition was the only condition in which the prime was recognizable as a misspelled version of a real word (e.g., “garaje”). It appears possible that this condition, under suprathreshold presentation, draws attention to the misspelled homophone of the target and incites subjects to mentally rehearse or check the pronunciation of the target.

Examination of the regions’ blood oxygen level-dependent (BOLD) response profiles (Fig. 4C) tentatively suggests that the phonological response enhancement effect might be additive with the classical orthographic repetition suppression effect. Such a superimposition would explain the unusual response profile of the left inferior frontal and left anterior insula regions, which were the only regions where the O condition was lower than both the U and O + P conditions.

The absence of phonological priming under subliminal conditions is compatible with the hypothesis that heavy masking interrupts the propagation of visual activity into anterior cortical areas. However, future studies will be needed to examine the generality of this observation. In the present study, subjects were engaged in a semantic categorization task, which mainly involves lexico-semantic processes and may not require phonological encoding. It remains possible that phonological priming would show up under subliminal conditions when the task emphasizes grapheme-phoneme conversion processes. Indeed, behavioral cross-task comparisons suggest that masked phonological priming occurs when participants are engaged in explicit phonological production such as in the naming task but not when they perform a word recognition tasks such as lexical decision (Shen and Forster 1999). Unfortunately, although masking was used in this study, no assessment of prime visibility was made, making it difficult to evaluate the subliminal nature of these effects. Also, it remains possible that the primes in this study were presented too shortly to allow for the emergence of phonological priming under subliminal conditions. We remain open to the possibility that phonological effects might occur under special masking conditions that allow to use longer prime durations while keeping the prime invisible (Grainger et al. 2003).

Neural Correlates of Prime Visibility

Previous brain imaging experiments contrasting the processing of visible and invisible stimuli have led to inconsistent results. Although some studies have argued that the brain mechanisms

of conscious visual perception lie in the activation of posterior occipito-temporal areas (Grill-Spector et al. 2000; Bar et al. 2001; Moutoussis and Zeki 2002; Ress and Heeger 2003), other studies have claimed that they also involve a large set of higher-level associative regions of parietal, frontal, and cingulate cortices (Beck et al. 2001; Dehaene et al. 2001; Gross et al. 2004; Haynes et al. 2005; Sergent et al. 2005). As discussed in the introduction, those previous studies do not resolve whether the latter areas play a genuine role in conscious perceptual access, or are merely associated with the various executive and attentional processes that follow it.

In order to address this issue, we studied the brain activations evoked by visible and invisible masked stimuli while subjects attended to another subsequent conscious target. Our results clarify the above inconsistencies and show how they may in fact lead to a 2-stage view of conscious access (Dehaene et al. 2006).

On the one hand, we observed that the neural correlates of prime visibility (the main difference between subliminal and supraliminal primes) corresponded primarily to the activation of a restricted set of occipito-temporal areas, without extension into higher associative regions. This aspect of our results is compatible with many converging observations from neuroimaging (Grill-Spector et al. 2000; Bar et al. 2001; Moutoussis and Zeki 2002; Haynes et al. 2005; Tse et al. 2005), transcranial magnetic stimulation (Ro et al. 2003), and monkey electrophysiology (Rolls and Tovee 1994; Kovacs et al. 1995; Macknik and Livingstone 1998; Lamme et al. 2002), which indicate that masking is due to competition between the cortical representations of the stimulus and mask within occipito-temporal regions. These regions form only a small subset of the regions observed in previous work (Dehaene et al. 2001) where we contrasted subliminal and supraliminal visual words, which the subjects attempted to report. Thus, it seems likely that the many additional regions that were observed in this previous study (inferior parietal, left precentral, left inferior frontal/insula, and mesial prefrontal cortices) were indeed linked to additional processes such as recognition, report, evaluation, or memory storage that were available only when the words were visible. Indeed, a crucial difference with the present work is that, in the present study, subjects were explicitly asked not to attend to the prime and were probably actively trying to suppress any interference that this prime might cause.

On the other hand, however, supraliminal primes affected fMRI activation in a widely distributed set of cortical areas that included the occipito-temporal and lateral inferotemporal areas but also extended broadly into the left middle temporal gyrus, precentral sulci, left inferior prefrontal cortex, SMA, right intraparietal cortex, and right thalamus. By contrast, the effects of subliminal primes remained confined to a narrow set of regions (occipito-temporal cortices, FEF, and perhaps cerebellum). Those results fit with the suggestion that subliminal activation remains confined to a few specialized processors, whereas stimuli that pass the visibility threshold become available to a much broader range of processors including more anterior cortical sites (Dehaene and Changeux 2004). Indeed, the set of regions showing supraliminal priming effects in the present study overlaps consistently with the previous set of parieto-frontal regions associated with conscious access for masked relative to unmasked words (Dehaene et al. 2001).

Examination of the fMRI activation profiles (Fig. 4) shows clearly that, in many regions, the supraliminal but not the subliminal primes caused considerable changes of fMRI activation.

Although we have described such changes as repetition suppression, based on the relative differences within the supraliminal block, this interpretation could be debated, because it appears as if activation in fact increased in the unrelated condition (Fig. 4). Yet although it is straightforward to examine the relative levels observed in the 3 priming conditions within each type of run (supra- or subliminal), it is more difficult to interpret the absolute levels of activation across blocks. Understanding whether priming effects reflect facilitation, competition, or both requires the definition of an absolute neutral condition, which is classically a very difficult problem in psychological studies of priming (Neely 1991). Here it is tempting to consider a priori that the unrelated condition constitutes such a neutral baseline common to both supraliminal and subliminal runs. Subjectively, however, these are remarkably different conditions: In one case, subjects see only 1 word (the target), in the other they see 2 unrelated words (prime and target) and therefore may suffer from a competition. Thus, a tentative interpretation of the overall profile of results might be that supraliminal but not subliminal unrelated primes create competition with the target, thus creating a transient increase in inferior frontal, SMA/preSMA, and premotor activation prior to the stable identification and categorization of the target. This large-scale competition would not occur for subliminal primes, in agreement with psychological theories that postulate a tight relation between large-scale competitive interactions and conscious processing (Posner and Snyder 1975). Note that, unlike our previous work (Dehaene, Naccache et al. 1998), this competition effect cannot be ascribed to a motor conflict because the unrelated primes were pseudowords irrelevant to the semantic categorization task. Nevertheless, competition could have occurred at any of several other processing stages including lexical, semantic, and phonological levels.

In summary, consistent with previous work, only supraliminal primes appeared to contact a parieto-frontal network. The sole difference was that, under the present conditions where the primes did not have to be actively processed, they mostly modulated the activation of these regions by a subsequent target rather than creating a major activation in and of themselves. Only in the supraliminal unrelated condition, where prime-target competition could occur, was visibility associated with increased anterior activation. The results therefore suggest that only the supraliminal, but not the subliminal, primes had enough strength to compete with the target word for access into higher associative areas, even though the task required processing only the target word.

Theoretical Implications for Models of Conscious Access

How do these results relate to current theories of conscious access? It could be argued that, by comparing the activation evoked by task-irrelevant subliminal versus supraliminal primes, the present experimental design gave access to a “pure” cerebral correlate of conscious perception uncontaminated by any subsequent change in processing. Conscious perception would then be associated solely with the amplification of occipito-temporal activation, as suggested by others (Lamme 2003; Pins and Ffytche 2003; Zeki 2003; Tse et al. 2005). In agreement with this proposal, Tse et al. (2005) recently proposed that inattention minimizes the task-specific contamination that follows conscious perception. Under conditions of distracted attention, they found correlates of stimulus visibility to be restricted to occipital areas, and therefore argued that occipital activation may suffice to maintain visual conscious perception.

However, a major difficulty with this interpretation is that, in the absence of attention, even an unmasked stimulus is not guaranteed to be consciously perceived. On the contrary, converging behavioral (e.g., Simons and Rensink 2005), brain imaging (e.g., Kanwisher 2001), and neuropsychological (e.g., Driver and Vuilleumier 2001) evidence suggest that attention may be a necessary (although not a sufficient) condition for conscious perception, inasmuch as under conditions of inattention, even a salient visual stimulus may fail to be consciously detected. For instance, Mack and Rock (1998) have shown that an unattended stimulus presented for as long as 700 ms in the fovea may still not be detected, a phenomenon which they termed “inattention blindness” (Mack and Rock 1998). The attentional blink paradigm also demonstrates that unmasking of a stimulus is not sufficient to induce its conscious perception. In this paradigm, a lightly masked stimulus, normally quite visible, becomes totally invisible when presented while participants are engaged in actively processing an earlier stimulus (Raymond et al. 1992; Sergent and Dehaene 2004; Sergent et al. 2005). Along the same lines, change blindness experiments have shown that participants fail to detect important changes in a visual scene as long as these changes occur at unattended locations (O’Regan et al. 1999; Simons and Rensink 2005).

Thus, a stimulus, which is potentially *visible*, can still fail to be *seen* when attention is drawn away from it. Dehaene et al. (2006) have recently proposed that conditions where stimuli are visible but unattended reflect preconscious rather than conscious processing. The term “preconscious” would refer to conditions in which the stimulus carries enough activation strength for conscious access, and thus is *potentially* accessible for conscious report but still fails to be accessed. According to this theory, a suprathreshold stimulus may remain temporarily buffered in a preconscious store while it temporarily waits for top-down attentional amplification (for instance due to executive engagement in another task or attention orientation to another competing stimulus). In this interpretation, the activation increases due to stimulus visibility, which were restricted to extrastriate regions in Tse et al. (2005) and to posterior occipito-temporal areas in the present study, might be attributed to a difference between subliminal and preconscious processing, rather than between subliminal and conscious perception.

An important methodological consequence of this theoretical interpretation is that even supraliminal primes are not necessarily consciously processed in the priming paradigm, where participants are usually asked not to pay attention to the primes. Indeed, during debriefing, most participants claimed that they were aware that some flashed letters preceded the target stimuli, but they also claimed that they could hardly identify the primes or its relation to the target because they were busy performing the semantic decision task on the target stimuli. It is only during the subsequent forced-choice prime identification task, which required focused attention on the prime, that they could identify the prime stimuli.

Although we propose that the term “conscious” should be reserved to a condition in which the subject has actual access to stimulus content and can report it, this issue remains controversial and contrasts with the theory put forward by the philosopher Block (1995, 2005). According to Block, stimuli that are not accessed, but fall in the proposed preconscious state, might nevertheless receive a certain form of “phenomenal” conscious processing. We acknowledge that this is a tenable

philosophical position but its empirical testability remains highly debated (Dehaene et al. 2006). It is not at all clear how one could empirically probe whether any form of consciousness is associated with the increased occipito-temporal activity seen here in the supraliminal condition, without relying on any sort of report by the subject. Given the lack of scientific criterion, at this stage at least, for defining conscious processing without reportability, the dissociation between access and phenomenal consciousness remains largely speculative and even possibly immune to scientific investigation. Nevertheless, we remain open to the possibility that further research may ultimately clarify both the objective processing steps and the putative subjective states preceding conscious access.

In summary, our results, in combination with similar previous work (Dehaene et al. 2001), suggest that conscious perception of briefly flashed words is jointly determined by 2 factors: the strength of the bottom-up stimulus activation (which can be manipulated by masking), and the amount of top-down attention (which can be manipulated by task instructions). Future research should combine both factors within the same experiment to disentangle the roles of top-down access versus bottom-up stimulus visibility in conscious perception.

Notes

Conflict of interest: None declared.

Address correspondence to Sid Kouider, Unité INSERM 562 "Cognitive Neuroimaging," IFR 49, Service Hospitalier Frédéric Joliot, CEA/DSV, 91401 Orsay cedex, France. Email: sidk@lscp.cea.fr.

References

- Bar M, Tootell RBH, Schacter DL, Greve DN, Fischl B, Mendola JD, Rosen BR, Dale AM. 2001. Cortical mechanisms specific to explicit visual object recognition. *Neuron*. 29:529-535.
- Beck DM, Rees G, Frith CD, Lavie N. 2001. Neural correlates of change detection and change blindness. *Nat Neurosci*. 4:645-650.
- Block N. 1995. On a confusion about a function of consciousness. *Behav Brain Sci*. 18:227-287.
- Block N. 2005. Two neural correlates of consciousness. *Trends Cogn Sci*. 9:46-52.
- Booth JR, Burman DD, Meyer JR, Gitelman DR, Parrish TB, Mesulam MM. 2002. Modality independence of word comprehension. *Hum Brain Mapp*. 16:251-261.
- Burton MW. 2001. The role of inferior frontal cortex in phonological processing. *Cogn Sci*. 25:695-709.
- Burton MW, Locasto PC, Krebs-Noble D, Gullapalli RP. 2005. A systematic investigation of the functional neuroanatomy of auditory and visual phonological processing. *Neuroimage*. 26:647-661.
- Burton MW, Small SL, Blumstein SE. 2000. The role of segmentation in phonological processing: an fMRI investigation. *J Cogn Neurosci*. 12:679-690.
- Cohen L, Jobert A, Le Bihan D, Dehaene S. 2004. Distinct unimodal and multimodal regions for word processing in the left temporal cortex. *Neuroimage*. 23:1256-1270.
- Coltheart M, Rastle K, Perry C, Langdon R, Ziegler J. 2001. DRC: a dual route cascaded model of visual word recognition and reading aloud. *Psychol Rev*. 108:204-256.
- Dehaene S, Changeux JP. 2004. Neural mechanisms for access to consciousness. In: Gazzaniga M, editor. *The cognitive neurosciences*. 3rd ed. New York: Norton. p. 1145-1157.
- Dehaene S, Changeux JP, Naccache L, Sackur J, Sergent C. 2006. Conscious, preconscious, and subliminal processing: a testable taxonomy. *Trends Cogn Sci*. 10:204-211.
- Dehaene S, Jobert A, Naccache L, Ciuciu P, Poline JB, Le Bihan D, Cohen L. 2004. Letter binding and invariant recognition of masked words: behavioral and neuroimaging evidence. *Psychol Sci*. 15:307-313.
- Dehaene S, Kerszberg M, Changeux JP. 1998. A neuronal model of a global workspace in effortful cognitive tasks. *Proc Natl Acad Sci USA*. 95:14529-14534.
- Dehaene S, Naccache L. 2001. Towards a cognitive neuroscience of consciousness: basic evidence and a workspace framework. *Cognition*. 79:1-37.
- Dehaene S, Naccache L, Cohen L, Bihan DL, Mangin JF, Poline JB, Riviere D. 2001. Cerebral mechanisms of word masking and unconscious repetition priming. *Nat Neurosci*. 4:752-758.
- Dehaene S, Naccache L, Le Clec'h G, Koechlin E, Mueller M, Dehaene-Lambertz G, van de Moortele PF, Le Bihan D. 1998. Imaging unconscious semantic priming. *Nature*. 395:597-600.
- Dehaene-Lambertz G, Pallier C, Serniclaes W, Sprenger-Charolles L, Jobert A, Dehaene S. 2005. Neural correlates of switching from auditory to speech perception. *Neuroimage*. 24:21-33.
- Desimone R, Duncan J. 1995. Neural mechanisms of selective visual attention. *Annu Rev Neurosci*. 18:193-222.
- Devlin JT, Jamison HL, Matthews PM, Gonnerman LM. 2004. Morphology and the internal structure of words. *Proc Natl Acad Sci USA*. 101:14984-14988.
- Driver J, Vuilleumier P. 2001. Perceptual awareness and its loss in unilateral neglect and extinction. *Cognition*. 79:39-88.
- Dronkers NF. 1996. A new brain region for coordinating speech articulation. *Nature*. 384:159-161.
- Ferrand L, Grainger J. 1992. Phonology and orthography in visual word recognition: evidence from masked non-word priming. *Q J Exp Psychol [A]*. 45:353-372.
- Ferrand L, Grainger J. 1993. The time course of orthographic and phonological code activation in the early phases of visual word recognition. *Bull Psychon Soc*. 31:119-122.
- Fiez JA, Petersen SE. 1998. Neuroimaging studies of word reading. *Proc Natl Acad Sci USA*. 95:914-921.
- Fiez JA, Raichle ME, Balota DA, Tallal P, Petersen SE. 1996. PET activation of posterior temporal regions during auditory word presentation and verb generation. *Cereb Cortex*. 6:1-10.
- Forster KI. 1998. The pros and cons of masked priming. *J Psycholinguist Res*. 27:203-233.
- Friston KJ, Holmes AP, Price CJ, Buchel C, Worsley KJ. 1999. Multi-subject fMRI studies and conjunction analyses. *Neuroimage*. 10:385-396.
- Friston KJ, Holmes AP, Worsley KJ, Polina JB, Frith CD, Frackowiak RSJ. 1995. Statistical parametric maps in functional imaging: a general approach. *Human Brain Mapping*. 2:189-210.
- Frith C, Perry R, Lumer E. 1999. The neural correlates of conscious experience: an experimental framework. *Trends Cogn Sci*. 3:105-114.
- Fulbright RK, Jenner AR, Mencl WE, Pugh KR, Shaywitz BA, Shaywitz SE, Frost SJ, Skudlarski P, Constable RT, Lacadie CM, et al. 1999. The cerebellum's role in reading: a functional MR imaging study. *AJNR Am J Neuroradiol*. 20:1925-1930.
- Grainger J, Diependaele K, Spinelli E, Ferrand L, Farioli F. 2003. Masked repetition and phonological priming within and across modalities. *J Exp Psychol Learn Mem Cogn*. 29:1256-1269.
- Grill-Spector K, Kushnir T, Hendler T, Malach R. 2000. The dynamics of object-selective activation correlate with recognition performance in humans. *Nat Neurosci*. 3:837-843.
- Grill-Spector K, Malach R. 2001. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychol (Amst)*. 107:293-321.
- Gross J, Schmitz F, Schnitzler I, Kessler K, Shapiro K, Hommel B, Schnitzler A. 2004. Modulation of long-range neural synchrony reflects temporal limitations of visual attention in humans. *Proc Natl Acad Sci USA*. 101:13050-13055.
- Haynes JD, Driver J, Rees G. 2005. Visibility reflects dynamic changes of effective connectivity between V1 and fusiform cortex. *Neuron*. 46:811-821.
- Henson R, Shallice T, Dolan R. 2000. Neuroimaging evidence for dissociable forms of repetition priming. *Science*. 287:1269-1272.

- Henson RN. 2003. Neuroimaging studies of priming. *Prog Neurobiol*. 70:53–81.
- Kanwisher N. 2001. Neural events and perceptual awareness. *Cognition*. 79:89–113.
- Koivisto M, Revonsuo A. 2003. An ERP study of change detection, change blindness, and visual awareness. *Psychophysiology*. 40:423–429.
- Kouider S, Dupoux E. 2001. A functional disconnection between spoken and visual word recognition: evidence from unconscious priming. *Cognition*. 82:B35–B49.
- Kouider S, Dupoux E. 2004. Partial awareness creates the “illusion” of subliminal semantic priming. *Psychol Sci*. 15:75–81.
- Kouider S, Dupoux E. 2005. Subliminal speech priming. *Psychol Sci*. 16:617–625.
- Kovacs G, Vogels R, Orban GA. 1995. Cortical correlate of pattern backward masking. *Proc Natl Acad Sci USA*. 92:5587–5591.
- Lamme VA. 2003. Why visual attention and awareness are different. *Trends Cogn Sci*. 7:12–18.
- Lamme VA, Zipser K, Spekreijse H. 2002. Masking interrupts figure-ground signals in V1. *J Cogn Neurosci*. 14:1044–1053.
- Mack A, Rock I. 1998. Inattention blindness. Cambridge, MA: MIT Press.
- Macknik SL, Livingstone MS. 1998. Neuronal correlates of visibility and invisibility in the primate visual system. *Nat Neurosci*. 1:144–149.
- Miller EK, Cohen JD. 2001. An integrative theory of prefrontal cortex function. *Annu Rev Neurosci*. 24:167–202.
- Moutoussis K, Zeki S. 2002. The relationship between cortical activation and perception investigated with invisible stimuli. *Proc Natl Acad Sci USA*. 99:9527–9532.
- Naccache L, Dehaene S. 2001. The priming method: imaging unconscious repetition priming reveals an abstract representation of number in the parietal lobes. *Cereb Cortex*. 11:966–974.
- Nakamura K, Dehaene S, Jobert A, Le Bihan D, Kouider S. 2005. Subliminal convergence of Kanji and Kana words: further evidence for functional parcellation of the posterior temporal cortex in visual word perception. *J Cogn Neurosci*. 17:954–968.
- Neely JH. 1991. Semantic priming effects in visual word recognition: a selective review of current findings and theories. In: Besner D, Humphreys GW, editors. *Basic processes in reading. Visual word recognition*. Hillsdale, NJ: Erlbaum. p. 264–336.
- O’Regan JK, Rensink RA, Clark JJ. 1999. Change-blindness as a result of ‘mudsplashes’. *Nature*. 398:34.
- Perea M, Rosa E. 2000. Repetition and form priming interact with neighborhood density at a brief stimulus onset asynchrony. *Psychon Bull Rev*. 7:668–677.
- Pessoa L, Ungerleider LG. 2004. Neural correlates of change detection and change blindness in a working memory task. *Cereb Cortex*. 14:511–520.
- Pins D, Ffytche D. 2003. The neural correlates of conscious vision. *Cereb Cortex*. 13:461–474.
- Poeppl D, Hickok G. 2004. Towards a new functional anatomy of language. *Cognition*. 92:1–12.
- Poldrack RA, Temple E, Protopapas A, Nagarajan S, Tallal P, Merzenich M, Gabrieli JD. 2001. Relations between the neural bases of dynamic auditory processing and phonological processing: evidence from fMRI. *J Cogn Neurosci*. 13:687–697.
- Posner MI. 1994. Attention: the mechanisms of consciousness. *Proc Natl Acad Sci USA*. 91:7398–7403.
- Posner NI, Snyder CRR. 1975. Attention and cognitive control. In: Solso RL, editor. *Information processing and cognition: the Loyola symposium*. Hillsdale, NJ: L. Erlbaum. p. 55–85.
- Pugh KR, Shaywitz BA, Shaywitz SE, Constable RT, Skudlarski P, Fulbright RK, Bronen RA, Shankweiler DP, Katz L, Fletcher JM, et al. 1996. Cerebral organization of component processes in reading. *Brain*. 119:1221–1238.
- Rastle K, Croot KP, Harrington JM, Coltheart M. 2005. Characterizing the motor execution stage of speech production: consonantal effects on delayed naming latency and onset duration. *J Exp Psychol Hum Percept Perform*. 31:1083–1095.
- Rastle K, Harrington J, Coltheart M, Palethorpe S. 2000. Reading aloud begins when the computation of phonology is complete. *J Exp Psychol Hum Percept Perform*. 26:1178–1191.
- Rastle K, Kinoshita S, Lupker SJ, Coltheart M. 2003. Cross-task strategic effects. *Mem Cognit*. 31:867–876.
- Raymond JE, Shapiro KL, Arnell KM. 1992. Temporary suppression of visual processing in an RSVP task: an attentional blink? *J Exp Psychol Hum Percept Perform*. 18:849–860.
- Rees G. 2001. Seeing is not perceiving. *Nat Neurosci*. 4:678–680.
- Rees G, Kreiman G, Koch C. 2002. Neural correlates of consciousness in humans. *Nat Rev Neurosci*. 3:261–270.
- Rees G, Wojciulik E, Clarke K, Husain M, Frith C, Driver J. 2002. Neural correlates of conscious and unconscious vision in parietal extinction. *Neurocase*. 8:387–393.
- Ress D, Heeger DJ. 2003. Neuronal correlates of perception in early visual cortex. *Nat Neurosci*. 6:414–420.
- Ro T, Breitmeyer B, Burton P, Singhal NS, Lane D. 2003. Feedback contributions to visual awareness in human occipital cortex. *Curr Biol*. 13:1038–1041.
- Rolls E, Tovee M. 1994. Processing speed in the cerebral cortex and the neurophysiology of visual masking. *Proc R Soc Lond B Biol Sci*. 257:9–15.
- Schall JD. 2004. On the role of frontal eye field in guiding attention and saccades. *Vision Res*. 44:1453–1467.
- Schmolesky MT, Wang Y, Hanes DP, Thompson KG, Leutgeb S, Schall JD, Leventhal ArG. 1998. Signal timing across the macaque visual system. *J Neurophysiol*. 79:3272–3278.
- Sergent C, Baillet S, Dehaene S. 2005. Timing of the brain events underlying access to consciousness during the attentional blink. *Nat Neurosci*. 8:1391–1400.
- Sergent C, Dehaene S. 2004. Is consciousness a gradual phenomenon? Evidence for an all-or-none bifurcation during the attentional blink. *Psychol Sci*. 15:720–728.
- Shallice T. 1988. *From neuropsychology to mental structure*. New York: Cambridge University Press.
- Shen D, Forster KI. 1999. Masked phonological priming in reading Chinese words depends on the task. *Lang Cogn Process*. 14:429–459.
- Simons DJ, Rensink RA. 2005. Change blindness: past, present, and future. *Trends Cogn Sci*. 9:16–20.
- Thompson KG, Schall JD. 1999. The detection of visual signals by macaque frontal eye field during masking. *Nat Neurosci*. 2:283–288.
- Tse PU, Martinez-Conde S, Schlegel AA, Macknik SL. 2005. Visibility, visual awareness, and visual masking of simple unattended targets are confined to areas in the occipital cortex beyond human V1/V2. *Proc Natl Acad Sci USA*. 102:17178–17183.
- Turk-Browne NB, Yi DJ, Leber AB, Chun MM. 2006. Visual quality determines the direction of neural repetition effects. *Cereb Cortex*. 10.1093/cercor/bhj159.
- Turkeltaub PE, Eden GF, Jones KM, Zeffiro TA. 2002. Meta-analysis of the functional neuroanatomy of single-word reading: method and validation. *Neuroimage*. 16:765–780.
- Weekes BS. 1997. Differential effects of number of letters on word and nonword naming latency. *Q J Exp Psychol*. 50A:439–456.
- Wise RJ, Greene J, Buchel C, Scott SK. 1999. Brain regions involved in articulation. *Lancet*. 353:1057–1061.
- Zeki S. 2003. The disunity of consciousness. *Trends Cogn Sci*. 7:214–218.