articles

Cerebral mechanisms of word masking and unconscious repetition priming

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We used functional magnetic resonance imaging (fMRI) and event-related potentials (ERPs) to visualize the cerebral processing of unseen masked words. Within the areas associated with conscious reading, masked words activated left extrastriate, fusiform and precentral areas. Furthermore, masked words reduced the amount of activation evoked by a subsequent conscious presentation of the same word. In the left fusiform gyrus, this repetition suppression phenomenon was independent of whether the prime and target shared the same case, indicating that case-independent information about letter strings was extracted unconsciously. In comparison to an unmasked situation, however, the activation evoked by masked words was drastically reduced and was undetectable in prefrontal and parietal areas, correlating with participants' inability to report the masked words.

A visual word that is flashed for only a few tens of milliseconds remains readable. However, when the same word is presented in close spatial and temporal proximity with other visual stimuli, it becomes indistinct or even invisible, a perceptual phenomenon called masking. Behavioral evidence indicates that the visual, orthographic and phonological properties of masked words, and even their meaning, can be extracted under masking conditions that do not elicit consciousness of those processing steps[1–6]. This suggests that masked words can unconsciously activate part of the cerebral networks for word processing. However, this hypothetical activation has not been measured directly, not is it understood why it fails to elicit consciousness. Here we demonstrate that unseen masked words activate extrastriate, fusiform and precentral regions, and cause a significant reduction in response time and in brain activity to subsequent conscious words, yet fail to elicit the correlated and distributed pattern of activation observed when the same words are consciously perceived.

RESULTS

The goal of experiment 1 was to image, within the circuit for word processing, the areas activated by masked words. Brain activity was measured with fMRI and ERPs while participants viewed a random series of masking shapes and blank screens. This continuous visual stream was briefly interrupted by a short presentation of words that participants were asked to name in their head. In one condition, the presence of blanks immediately surrounding the words made them consciously perceptible and reportable (**Fig. 1a**, left). In the other condition, the order of the masks and blanks was reversed so that the words were surrounded by masks that rendered them invisible (**Fig. 1a**, right). Two control situations were created in which the temporal context was identical but the words were omitted. This allowed us to subtract

the brain activation due to the masking stream alone, and to isolate the activation caused solely by a masked or unmasked word.

Behavioral tests of word visibility

Several behavioral tests run immediately before and after brain imaging demonstrated that the masked words could not be detected, named or remembered (**Fig. 1b**). First, participants were shown a continuous stream with 37 visible words, 37 masked words and 37 control blank trials appearing in random order at two-second intervals. Whenever they thought that a word had appeared, participants were asked to name it aloud or, if they felt unable to name it, merely say the word '*vu*' ('seen' in French). Participants detected 90.2% of the visible words, and 88.9% of those were then correctly named. In contrast, the masked words were only detected on 0.7% of trials and only one word was ever named. Thus, although the detection rate of 0.7% for masked words slightly exceeded the false alarm rate of 0.2% observed on trials when no word was present ($t_{26} = 2.38$, $p = 0.02$), 99.3% of masked words were never detected and 99.95% could not be named.

For the recognition memory test, after imaging, participants were shown each of the 37 visible words, the 37 masked words, and 37 distractors that had never been presented before, in random order, for an unlimited time. They decided whether or not the word had been presented earlier. Participants recognized 85.9% of the visible words, but only 7.1% of the masked words. The 7.1% detection rate for masked words did not differ from the 6.0% commission errors that were made to the distractors ($t_{26} = 1.27$, n.s.). The response times to the masked words and to the distractors also did not differ (1501 and 1505 ms). Thus, the masked words were treated just like words that had never been seen.

Finally, in the forced-choice test, on each of 37 trials, a short stream comprising a single masked word was presented. Partici-
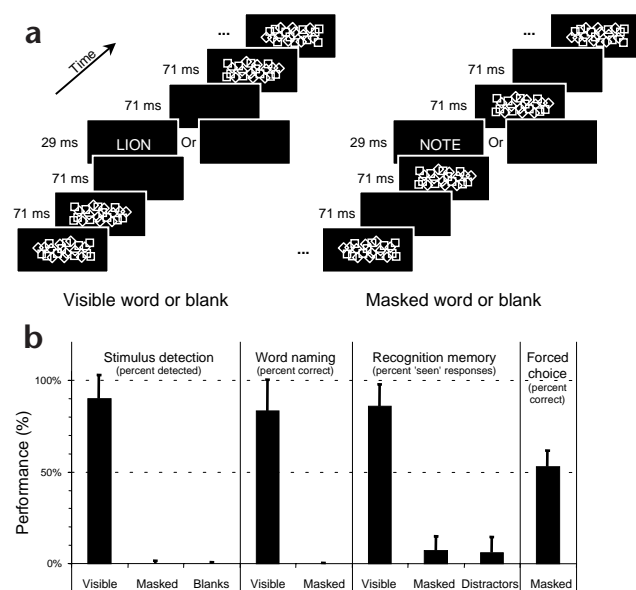
Fig. 1. Design and behavioral results of experiment 1. **(a)** Stimulus sequence. Short presentations of words or blank screens were embedded into a continuous stream of blank screens and random masks. The type of stimulus (word or blank) and its visibility (visible or masked) were manipulated independently. **(b)** Performance in various behavioral tests assessing word perceptibility. All plots indicate mean performance ± 1 s.e.m.

(48, 12, 24; $t = 4.72$), right dorsolateral prefrontal cortex (48, 28, 24; $Z = 3.83$), supplementary motor area (0, 0, 64; $Z = 4.00$), anterior cingulate (0, 8, 44; $Z = 3.37$) and left inferior frontal/anterior temporal cortices (–56, 8, –4; $Z = 3.85$). Furthermore, within the network for visible words, a significant increase in functional connectivity with the left fusiform gyrus when the words became visible was observed in the left supplementary motor area (–4, 0, 64; $Z = 2.85$), the left mesial prefrontal cortex (–4, 12, 52; $Z = 2.74$) and the left putamen (12, 4, 8; $Z = 2.64$).

Event-related potentials
The subtraction of ERPs evoked by visible words and by visible blanks revealed a standard sequence of events for word reading, with delayed peaks presumably due to stimulus degradation. This sequence included an initial occipital positivity (P1, peaking at 164 ms after onset), a left-lateralized occipitotemporal negativity (N1, 252 ms), a short-lived central negativity (N400, 340 ms) and an extended central positivity (P3, 476 ms) (**Fig. 3**).

When contrasting masked words with masked blanks, an occipital P1 was also detectable, though it was smaller and slightly delayed relative to the P1 evoked by visible words (peak at 180 ms). Mean voltages were computed from left and right occipital electrodes in the range of 116 to 148 ms (early P1) and 156 to 188 ms (late P1). For visible stimuli, there was a main effect of stimulus presence; ERPs were more positive for words than for blanks ($F_{1,11} = 5.91$, $p = 0.033$; 0.94 μV difference), with no interactions with time or hemisphere. For masked stimuli, a presence by time interaction ($F_{1,11} = 6.01$, two-tailed $p = 0.032$) indicated that ERPs were also significantly more positive in response to masked words, but only during the second time window ($t_{11} = 2.04$, $p = 0.033$; 0.22 μV). The amplitude of the P1 in response to masked words was only 23.4% of that to visible words.

The P1 was followed by a negativity that was similar in latency to the conscious N1 (peak at 252 ms), but that was strictly unilateral and restricted to left anterior temporal electrodes. Mean voltages were computed from left and right anterior and posterior occipitotemporal electrodes in the range of 212 to 300 ms (N1). For visible stimuli, ERPs were significantly more negative in response to words than to blanks ($F_{1,11} = 25.8$, $p = 0.0004$; –2.59 μV), and this effect was larger on posterior than on anterior electrodes (interaction, $F_{1,11} = 18.4$, $p = 0.0013$), though it was significant at all four sites ($p < 0.0015$). For masked stimuli, ERPs were more negative in response to words than to blanks only over left anterior temporal electrodes ($F_{1,11} = 9.79$, $p = 0.005$; –0.16 μV), though interactions with hemisphere, location or both were not significant ($p > 0.12$). On that site, the voltage evoked by masked words was 8.3% of that evoked by visible words, in agreement with the 8.6% figure observed for the left fusiform fMRI signal.

After this time point, masked and unmasked words differed radically. Neither an N400 nor a P3 was observed for masked words. Rather, the left N1 in response to masked words was prolonged, and a second negativity restricted to left precentral electrodes was observed simultaneously with a focal central positivity. Although we did not attempt to construct dipole models of this complex sequence, the observed negativities were found at scalp

pants were told about the presence of a hidden word and were asked to select it among two choice words presented left and right of fixation. The success rate of 52.9% did not differ from the 50% value expected by chance ($t_{26} = 1.63$, $p > 0.10$).

Functional magnetic resonance imaging
In fMRI, visible words activated a left-lateralized set of areas including the left fusiform gyrus, left parietal cortex, bilateral inferior prefrontal/anterior insular cortex, anterior cingulate, precentral cortex and the supplementary motor area (**Table 1**; **Fig. 2**, left). This network is similar to that found in PET studies of word reading[7], except for the absence of anterior inferior temporal areas, which undergo signal loss in fMRI. Masked words activated two significant clusters of voxels in this circuit (**Table 1**; **Fig. 2**, right). The first spanned a sizeable length of the left fusiform gyrus. Activation ranged from extrastriate visual cortex to a more anterior site that corresponded with published coordinates of the 'visual word form area,' a region of the fusiform gyrus that responds to words independently of their retinal location[8]. The second cluster was in the left precentral sulcus. No other areas were found significant when the search was extended to the whole brain.

All the areas activated by visible words showed a significant interaction of stimulus type with visibility, indicating that the activation was reduced when the words were presented in the masked condition compared to the visible condition. In the left extrastriate cortex, the activation to masked word was already reduced to 19.0% of that found to conscious words. In left fusiform cortex, this figure dropped to 8.6%, and in left precentral cortex it was only 5.2%. An analysis of variance confirmed that this posterior-to-anterior decrease in activation ratios was significant (region by visibility interaction, $F_{2,28} = 4.84$, $p = 0.016$).

Functional connectivity techniques were used to examine the pattern of correlations between the left fusiform region and other distant areas and to test the hypothesis of a better transmission of word information to distant areas when the words were visible (see Methods). Even after removing correlations imposed by the visual stimuli, the residual activity of the left fusiform region correlated with extensive bilateral occipital and ventral occipitotemporal regions, the bilateral posterior intraparietal sulci (coordinates, –28, –80, 36; $Z = 3.83$ and 28, –80, 28; $Z = 4.63$), right precentral cortex

Table 1. Coordinates of activation peaks.

Area	Number of voxels in cluster	Cluster-level *p*-value (corrected)	*Z* value at local maximum	Talairach coordinates		
				x	*y*	*z*
Activation to visible words (experiment 1)						
left fusiform gyrus	170	< 0.00001	6.88	−40	−56	−24
left extrastriate cortex			4.83	−35	−72	−4
left extrastriate cortex			4.50	−40	−84	−12
left anterior insula / inferior prefrontal	32	< 0.00001	5.75	−32	24	0
bilateral anterior cingulate	63	< 0.00001	5.53	−4	8	48
bilateral supplementary motor area			4.88	8	4	64
left intraparietal sulcus	33	< 0.00001	5.36	−32	−56	40
left intraparietal sulcus	24	< 0.00001	5.10	−28	−76	28
left precentral gryus	41	< 0.00001	5.28	−52	8	32
left central sulcus			4.54	−52	−12	40
left inferior prefrontal	13	< 0.00001	5.03	−48	8	4
right intraparietal sulcus	13	< 0.00001	4.85	32	−48	40
right fusiform gyrus	27	< 0.00001	4.89	36	−60	−24
right anterior insula / inferior prefrontal cortex	39	< 0.00001	5.53	32	20	0
right precentral gyrus	36	< 0.00001	5.51	44	0	36
Activation to masked words (experiment 1)						
left extrastriate cortex	34	< 0.00001	2.81	−32	−72	−16
left extrastriate cortex			2.76	−36	−88	−8
left fusiform gyrus			2.38	−48	−60	−12
left fusiform gyrus			2.33	−44	−52	−16
left precentral sulcus	6	0.013	2.34	−56	−4	36
left precentral sulcus			2.12	−44	0	28
Physical repetition suppression (experiment 2)						
right extrastriate cortex	15	0.044	4.15	32	−80	−16
right extrastriate cortex	17	0.027	4.06	24	−88	4
Case–independent repetition suppression (experiment 2)						
left fusiform gyrus	22	< 0.00001	3.32	−44	−52	−20
(left precentral gyrus)	2	0.17	2.52	−44	4	28
(right precentral gyrus)	3	0.078	2.24	44	4	28

For visible words, only clusters over 8 voxels are listed. Voxels were $4 \times 4 \times 4$ mm^3.

locations close to the cortical sites where unconscious activations were found with fMRI (**Fig. 3**). For statistical purposes, mean voltages were computed from left and right precentral sites and from the vertex (central electrodes surrounding electrode Cx) in the range of 400 to 500 ms. For visible stimuli, a presence by location interaction ($F_{2,22} = 43.6$, $p < 0.0001$) indicated that words evoked left and right negativities (−0.83, $p = 0.003$ and −1.71 μV, $p = 0.0003$, respectively) surrounding a large central positive P3 (2.04 μV; $p < 0.0001$). For masked stimuli, although the topography was much more focal, the effects were also significant (presence by location interaction, $F_{2,22} = 5.55$, $p = 0.011$; left negativity, −0.31 μV, $p = 0.061$; right negativity, −0.31 μV, $p = 0.032$; central positivity, 0.33 μV, $p = 0.002$). The ratios of masked-to-visible activations were relatively large on these three sites (37%, 18%
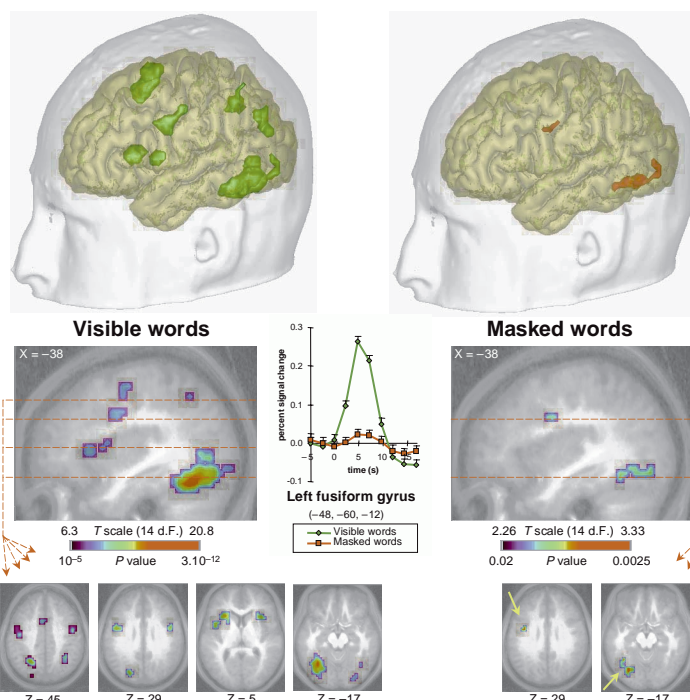
and 16%, respectively). However, those figures may not be meaningful because the broad P3 evoked by visible words presumably reflects the superimposition of activity from many sites, and it was not possible to find strict equivalents of the more focal activations evoked by masked words.

Cerebral bases of masked repetition priming

Although experiment 1 imaged activations evoked by an isolated masked word, its design did not allow us to assess their specificity. The difference between masked words and masked blanks might merely reflect the permeation of cerebral reading circuits by a small, non-specific activity independently of the particular stimulus shown and without direct relation to priming phenomena. Thus, the goal of experiment 2 was to demonstrate that the masked words

Fig. 2. fMRI activations to visible and masked words in experiment 1. Top, group activations in the left hemisphere only, as seen through translucent three-dimensional reconstruction of the skull and brain of one of the participants. In these transparent views, the deep activations in fusiform, parietal and mesial frontal cortex appear through the overlying lateral cortices. Bottom, sagittal and axial views of the group activations in Talairach space, superimposed on the mean anatomical image of the 15 participants. Middle, activation at the left fusiform peak, showing a twelvefold increase in activation on visible trials relative to masked trials. Error bars, inter-subject s.e.m.

caused measurable repetition priming. On each trial, we presented a short visual stream comprising a masked 29-ms prime word followed by a 500-ms target word (**Fig. 4**). Because an overt naming task would have caused head motion, participants performed a semantic classification task by clicking with the left or right hand to indicate whether the target was natural or man-made respectively. On different trials, the prime and target could be the same word or a different word, and could appear in either lower or upper case. On the basis of previous physiological and brain-imaging work[9–14], we expected to observe 'repetition suppression,' a reduced activation in word-processing areas when the same word was presented twice. Crucially, the design allowed us to examine in which areas this repetition suppression was independent of case, indicating that the abstract identity of the letter string had been extracted, and in which areas it occurred only when the same physical stimulus was repeated.

Behaviorally, participants again denied seeing the primes and were unable to select them in a two-alternative forced-choice test (53.6% correct, $t_9 = 2.10$, $p > 0.10$). However, case-independent repetition priming was observed in response times recorded during imaging (**Fig. 4**). Reaction times were significantly shorter when the prime and target were the same word ($F_{1,9} = 36.0$, $p = 0.0002$), independently of whether they appeared in the same

case (same-case priming, $F_{1,9} = 15.5$, $p = 0.003$; different-case priming, $F_{1,9} = 34.5$, $p = 0.0002$; interaction of repetition and case change, $F_{1,9} = 1.05$, n.s.).

Within the word-processing circuit, significant repetition suppression was observed in the left fusiform gyrus (**Table 1, Fig. 5**). At this site, priming was significant on same-case trials ($t_9 = 1.98$, one-tailed $p = 0.040$) and on different-case trials ($t_9 = 2.68$, one-tailed $p = 0.013$), and did not differ across those two conditions (interaction, $t_9 = -0.74$, NS). Case-independent priming was also found at an uncorrected significance level in the left precentral gyrus (4 mm from the peak observed in experiment 1) and in a symmetrical right precentral region. When the search was extended to the whole brain, no additional regions exhibited case-independent priming. However, physical repetition priming restricted to same-case trials was observed in two right extrastriate regions (**Table 1, Fig. 5**). In both regions, the interaction of repetition with case change was significant ($t_9 = 2.73$ and 3.25, respectively; $p < 0.05$).

DISCUSSION

Previous imaging studies of masked word processing measured how the conscious processing of a visible word was modulated by masked priming at the orthographic[15], semantic[16–18] or motor level[6]. In contrast, the design of experiment 1 allowed us to image the unconscious activity induced by isolated unseen words in the absence of any visible target and without any perceivable change in the ongoing stream. The results revealed a sequence of activations, with an early positive occipital waveform in ERPs (~170 ms) plausibly
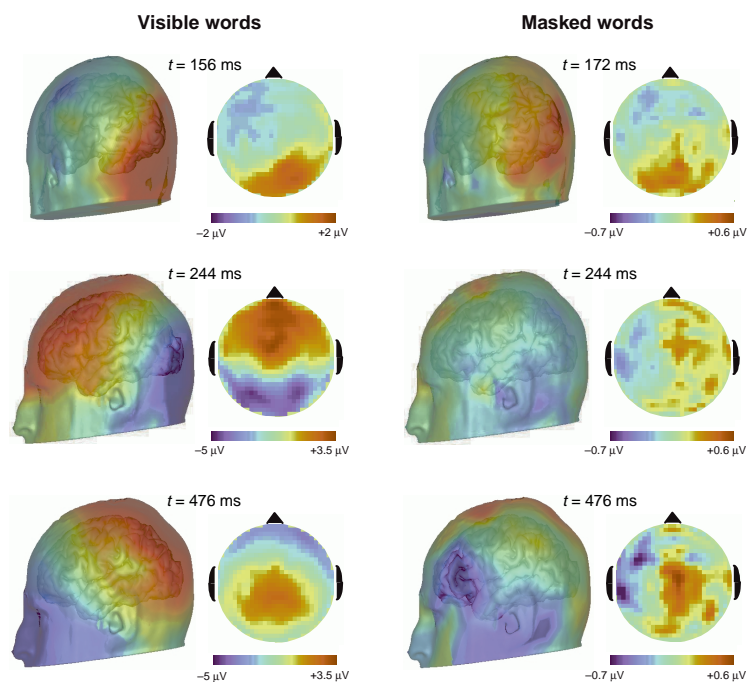

Fig. 3. Cartography of ERPs in reponse to visible words and to masked words. Spherical spline interpolations are shown at three different times following trial onset. ERPs in response to the relevant controls (visible or masked blanks) have been subtracted.
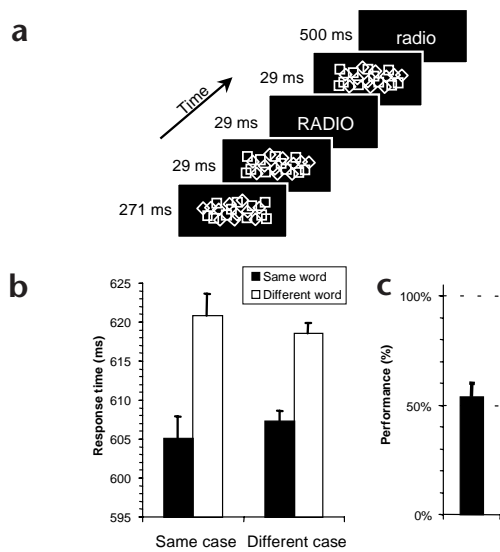
a

500 ms — radio

29 ms

Time

29 ms — RADIO

29 ms

271 ms

b

c

Fig. 4. Design and behavioral results of experiment 2. (**a**) Sample stimulus sequence. Prime case, target case and prime–target relationship (repeated or non-repeated) were manipulated independently. (**b**) Behavioral repetition priming effect in response times. (**c**) Chance-level performance in forced-choice prime identification.

corresponding to the extrastriate activation seen in fMRI, and two subsequent negative left-lateralized ERP components (~240 and 470 ms), which may correspond to the left fusiform and precentral activations seen in fMRI. Thus, a complex processing stream that included high-level visual activity occurred in the absence of consciousness.

Images of unconscious processing in experiment 1 were obtained by contrasting masked words with masked blanks. Thus, they might have reflected an undifferentiated burst of visual activity. Experiment 2 examined the specificity of the processing level achieved by masked words by using repetition priming. When visible words were preceded by a masked presentation of the same words, behavioral responses were significantly accelerated. Furthermore, brain activation was reduced in extrastriate, fusiform and precentral regions similar to those observed in experiment 1. This shows that the repetition suppression phenomenon, which was previously obtained with consciously visible stimuli[9–14], can be replicated with unseen masked primes[17]. As this phenomenon depends only on the identity of the masked prime, specific information about word identity must have been extracted and encoded unconsciously in the regions where repetition suppression was found. This information is sufficiently differentiated as to discriminate between two words of the same length. Single-unit recording in the inferotemporal cortex of the monkey indeed confirm that, although picture-masking reduces evoked activity to a short-lived burst[19], this burst still carries significant information about the masked stimulus[20].

Repetition suppression was case-specific in the right extrastriate cortex, and independent of case in the fusiform and precentral gyri. The hypothesis that the right extrastriate cortex is involved in feature-specific visual coding is supported by previous behavioral[21], PET and ERP studies[22,23]. The right lateralization, however, should be interpreted with caution given that a smaller case-specific priming effect was
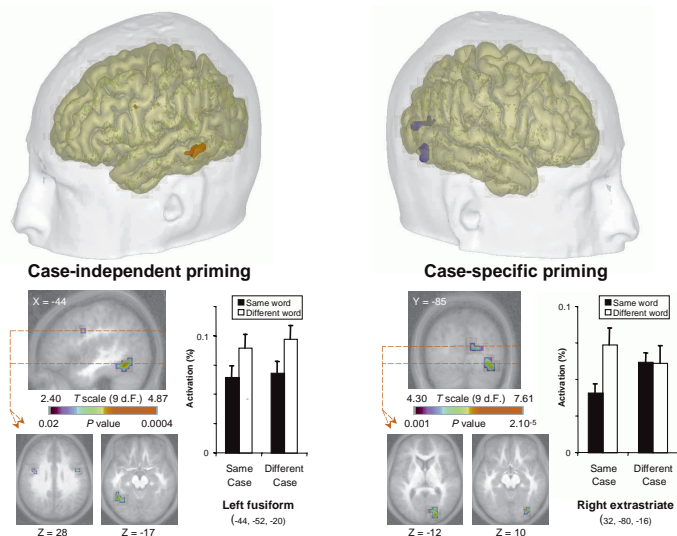
also observed below the chosen level of significance in a symmetrical left extrastriate region (−36, −76, 4; $Z = 3.82$, uncorrected $p = 0.00006$). Conversely, the case-independent priming effect indicates that the left fusiform region processes letter strings at a shape-invariant level. This adds to previous evidence that this region also normalizes for the retinal location at which words are presented[8]. It is consistent with a left-hemispheric specialization for extracting the prototypical form of variable shapes[24]. Previous studies with conscious pictures[10,12,14] or single letters[14] have also demonstrated some degree of invariance for size, image details and retinal location in ventral occipitotemporal cortex.

Our study did not separate the contributions of letter-level, graphemic, phonological and semantic codes to the observed priming. By varying the level at which repetition suppression is occurring, priming offers a general tool to study the nature of the code in a given brain region[17]. For instance, the hypothesis that the left precentral cortex is engaged in the phonological encoding of words[7,25] could be tested by using homophonic primes (such as prime 'one,' target 'won').

Previous studies found a close correlation between the activation of the ventral visual stream and the contents of visual consciousness[26–30]. Our results, however, establish that fusiform activation can also occur without conscious reportability. What activity patterns, then, differentiate reportable and non-reportable stimuli? Experiment 1 suggests that two factors might be relevant: activation intensity and correlated activation of distant areas.

First, compared to an unmasked situation, the presence of forward and backward masks caused a drastic reduction in activation, down to a statistically undetectable level in most areas. A similar reduction in visual activity has been described with masked pictures[27,30]. In fMRI, part of the reduction observed may be artifactual, due to the non-linear interactions that affect the BOLD response when stimuli are presented with short onset asynchronies[31]. However, it is unlikely that this is the sole explanation for the effect, because a comparable reduction in signal ampli-

Fig. 5. fMRI correlates of unconscious repetition priming. Graphs show the average of the BOLD response at 4.8 and 7.2 s following the target, relative to the target-absent baseline. Error bars, inter-subject s.e.m. Left, case-independent repetition suppression in the left fusiform gyrus and, at an uncorrected level of significance, in the left and right precentral gyrus. Right, case-specific physical repetition priming in the right extrastriate cortex.

Case-independent priming

X = -44

2.40 *T* scale (9 d.F.) 4.87

0.02 *P* value 0.0004

Z = 28 Z = -17

Left fusiform
(-44, -52, -20)

Case-specific priming

Y = -85

4.30 *T* scale (9 d.F.) 7.61

0.001 *P* value 2.10⁻⁵

Z = -12 Z = 10

Right extrastriate
(32, -80, -16)

tude was observed in ERP recordings, which directly reflect synaptic activity. The first detectable ERP response (P1) was reduced to about 23% of its size in response to unmasked words, a value comparable to the 19% figure observed in extrastriate cortex with fMRI. The second event (N1) was reduced to 8%, again comparable to the 9% figure for the fMRI fusiform activity.

The hypothesis that masking acts by reducing the duration and/or the intensity of the evoked neural activity concurs with an electrophysiological study in the monkey[32], where strong reductions in firing rates were seen in V1 neurons when forward and backward masks were combined. Competing theories attribute this reduction either to lateral inhibition among groups of neurons coding for incompatible features of the word and of the masks[33], or to a failure of amplification of the short-lived bottom-up activation by top-down re-entrant signals[34,35]. Although our experiment cannot discriminate between those two possibilities, the progressive decrease in unconscious activation intensity from extrastriate (~19%) to fusiform (~8%) and precentral cortex (~5%) suggests that the effects of masking start early on in the visual system and exert a gradual influence at successive processing stages, each time reducing the potential for activation at the next level.

A second difference between masked and unmasked words was the presence of increased activity at distant parietal, prefrontal and cingulate sites, only when the words were visible. Those regions were permanently intercorrelated, and part of those correlations increased when visible words appeared. Likewise, in ERPs, only the visible words evoked a large P300, a component that has been postulated to reflect the synchronous activation of multiple distant sites and the updating of consciousness[36,37]. In brief, unmasking the words enabled the propagation of activation and the ignition of a large-scale correlated cerebral assembly.

In our protocol, part of this activation probably reflected the performance of the covert naming task itself, which participants performed as a consequence of becoming aware of the words. Further research is needed to decide which of the observed correlates of masking are causally involved in stimulus perceptibility, and which merely reflect its consequences. Correlated frontal amplification has been observed in several protocols involving a transition to a conscious state[38–41]. In particular, our results parallel those from neglect patients, in whom the activation elicited by neglected stimuli is confined to the ventral occipitotemporal region, whereas non-neglected stimuli yield both an amplification of this activity and an increase in its correlation with co-activated parietal and frontal areas[42,43]. This converging evidence, although still inconclusive, is consistent with theories that relate conscious perception to the top-down amplification of sensory information through synchronous co-activation of distant regions including prefrontal cortex[35,44,45].

METHODS

Participants. Thirty-seven right-handed French students 19 to 34 years old gave written informed consent to participate in the study (average, 23.3 years; fMRI experiment 1, 3 men and 12 women; ERP experiment 1, 6 men and 6 women; fMRI experiment 2, 3 men and 7 women). The project was approved by the regional ethical committee (Hôpital Bicêtre).

Experiment 1. We generated for each participant 3 lists of 37 four-letter French nouns (frequency > 20 per million), to be used respectively as masked words, unmasked words and distractors for the recognition memory test. Masks were created by semi-random arrangements of diamond and square shapes with the same line thickness as the letter font used, covering up the central area of screen where words could appear (approximately 2.5° × 1°).

Each of the four stimulus types (visible words, visible blanks, masked words and masked blanks) comprised a precisely timed sequence (**Fig. 1a**). To increase sensitivity, stimuli were grouped into 2400-ms-long trials comprising 4 stimuli of the same type presented at a 500-ms interval, with the rest of the trial filled up by random presentations of blanks (28% probability) or masks (72% probability), each appearing for a random duration of 43, 57 or 71 ms. The seamless succession of trials gave a subjective impression of a continuous stream of masks interrupted at random times by four flashed words. Each participant was imaged while viewing a total of 5 streams, each comprising 5 leading blank trials followed by 30 trials of each type, randomly intermixed, for a total stream duration of 5 min. Each participant was also tested behaviorally while lying in the scanner, both before imaging (detection/naming test) and just after imaging (detection/naming, recognition memory and forced-choice tests).

Experiment 2. Forty 5-letter imageable French nouns with frequency higher than 10 per million were selected. Half were man-made (such as radio, train), and half were natural (such as fruit). Participants were asked to classify them as fast as possible using two hand-held response buttons, whose assignment was randomized and reversed in the middle of the experiment. Each trial consisted in the presentation of a masked prime and a visible target (**Fig. 4a**). We used a 2 × 2 design with factors of prime-target repetition (same or different word) and case change (prime and target in the same or different case). When the prime and target word differed, they always belonged to different categories (one natural, the other artificial), and they had no letter in common at the same location. A fifth type of trial, comprising the same sequence of masks and prime but no target, served as a baseline to measure event-related activation. Participants were imaged in 4 sessions, each comprising 5 initial training trials followed by 150 trials (30 trials of each type, in random order). After imaging, participants were also tested behaviorally in a forced-choice test (64 trials).

fMRI methods. We used a 3-Tesla whole-body system (Bruker, Germany) and a gradient-echo echo-planar imaging sequence sensitive to brain oxygen-level dependent (BOLD) contrast (26 contiguous axial slices, 4–5 mm thickness; TR, 2.4 s; TE, 40 ms; angle, 90°; field of view, 192 × 256 mm^2; matrix, 64 × 64). High-resolution anatomical images (3-dimensional gradient-echo inversion-recovery sequence; TI, 700 ms; TR, 1600 ms; FOV, 192 × 256 mm^2; matrix, 256 × 128 × 256; slice thickness, 1.2 mm) were also acquired. For each experiment, a random-effect group analysis was performed with SPM99 software (http://www.fil.ion.ucl.ac.uk/spm). Images were corrected for different slice acquisition times and for head motion, normalized to Talairach coordinates using a linear transform calculated on the anatomical images, and smoothed to about 15 mm. For each participant, the generalized linear model was used to fit each voxel with a linear combination of functions derived by convolving a standard hemodynamic response function and its time derivative with the known time series of the stimulus types (four categories in experiment 1, five in experiment 2). Degrees of freedom were adjusted for high-pass filtering (120-s period) and low-pass filtering by a Gaussian function with a 4-s width. Activation curves were obtained by event-related averaging[46] of the band-pass-filtered data extracted from a given voxel.

For the contrast between visible words and visible blanks, and for the interaction term for greater activation to visible words than to masked words (experiment 1), the voxelwise threshold was set to $p < 10^{-5}$, and clusters were reported only if their extent was significant at $p < 0.05$ corrected for multiple comparisons across the entire brain volume. For the contrast between masked words and masked blanks (experiment 1) and for the repetition suppression effects (experiment 2), the small volume correction of spm99 was used to search only the volume of the circuit activated by visible words in experiment 1 (527 voxels, as compared to 29137 voxels for a full-brain search). The voxelwise threshold was set to $p < 0.02$, and clusters were reported if their extent was significant at $p < 0.05$ corrected for multiple comparisons across the small volume. The same effects were also explored with a classical whole-brain search (voxelwise, $p < 0.001$; cluster-level corrected, $p = 0.05$).

Functional connectivity analysis. For each participant in experiment 1, the local maximum of left fusiform activity nearest to published coordinates[8] was identified using the fMRI model just described. The residual of

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the above-described model provided an estimate of the fast variations of activity in this region, above and beyond the activation induced by the stimulation protocol. This residual was multiplied by the previous stimulus variables, and the resulting functions were entered as additional predictors in a new model of fMRI activity. This allowed us to detect areas of which the fine temporal variations in activity, above and beyond those imposed by the stimuli, correlated with those in the left fusiform region. Two random-effect analyses were done. The first searched the whole brain for areas correlating with the left fusiform independently of the protocol (voxelwise threshold, $p < 0.001$; cluster size threshold, $p < 0.05$; corrected for multiple comparisons). The other searched only the circuit activated by visible words for areas showing a significantly greater increase in correlation to visible words than to masked words, relative to their respective blank controls (voxelwise threshold, $p < 0.02$; cluster size threshold, $p < 0.05$ after small volume correction).

ERP methods. ERPs were sampled at 125 Hz with a 128-electrode geodesic sensor net-referenced to the vertex. We rejected voltages exceeding $\pm 100\ \mu V$, transients exceeding $\pm 50\ \mu V$, or electro-oculogram activity exceeding $\pm 70\ \mu V$. The remaining trials were averaged in synchrony with stimulus onset, digitally transformed to an average reference, band-pass filtered (0.3–20 Hz) and corrected for baseline over a 100-ms window before stimulus onset. We first identified three time windows in which groups of electrodes showed a significant difference between visible words and visible blanks, as defined by sample-by-sample t-tests with a criterion of $p < 0.05$ for at least 7 consecutive samples on at least 10 electrodes. An analysis of variance on average voltage to the first stimulus of a trial tested for the main effect of visible stimulus (word or blank) and its interactions with hemisphere and time window when appropriate. We then applied the same analysis of variance to test for effects of the same sign and topography with unconscious words, using one-tailed tests and voltages averaged across the four words of a trial to increase statistical power.

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