Task-specific change of unconscious neural priming in the cerebral language network

Kimihiro Nakamura*,†, Stanislas Dehaene‡, Antoinette Jobert§, Denis Le Bihan¶, and Sid Kouider**

*Laboratoire des Sciences Cognitives et Psycholinguistique, L’Ecole des Hautes Etudes en Sciences Sociales/Centre National de la Recherche Scientifique/Ecole Normale Supérieure, 75005 Paris, France; ‡Institut National de la Santé et de la Recherche Médicale US562 and §Unité de Neuroimagerie Anatomique et Fonctionnelle, Service Hospitalier Frédéric Joliot, Commissariat à l’Énergie Atomique/Directeur des Sciences du Vivant, 91401 Orsay, France; and ¶Unité de Neuroimagerie Anatomique et Fonctionnelle, Service Hospitalier Frédéric Joliot, Commissariat à l’Énergie Atomique/Directeur des Sciences du Vivant, 91401 Orsay, France; and

†Department of Speech Physiology, Graduate School of Medicine, University of Tokyo, 3-7-1, Hongo, Tokyo 113-0033, Japan

Edited by Edward E. Smith, Columbia University, New York, NY, and approved October 15, 2007 (received for review May 15, 2007)

We explored the impact of task context on subliminal neural priming using functional magnetic resonance imaging. The repetition of words during semantic categorization produced activation reduction in the left middle temporal gyrus previously associated with semantic-level representation and dorsal premotor cortex. By contrast, reading aloud produced repetition enhancement in the left inferior parietal lobe associated with print-to-sound conversion and ventral premotor cortex. Analyses of effective connectivity revealed that the task set for reading generated reciprocal excitatory connections between the left inferior parietal and superior temporal regions, reflecting the audiovisual integration required for vocalization, whereas categorization did not produce such backward projection to posterior regions. Thus, masked repetition priming involves two distinct components in the task-specific neural streams, one in the parietotemporal cortex for task-specific word processing and the other in the premotor cortex for behavioral response preparation. The top-down influence of task sets further changes the directions of the unconscious priming in the entire cerebral circuitry for reading.


The authors declare no conflict of interest.

*To whom correspondence should be addressed. E-mail: kimihiro@m.u-tokyo.ac.jp.

This article contains supporting information online at www.pnas.org/cgi/content/full/0704487104/DC1.

© 2007 by The National Academy of Sciences of the USA.
greater for categorization relative to reading \( P(1, 15) = 1.45, P > 0.2 \). No other interactions reached significance.

Planned comparisons confirmed that the repetition of words accelerated the participants' response systematically in each of the four priming conditions, both for reading \( F(1, 15) = 38.36, P < 0.001; F(1, 15) = 6.58, P < 0.05; F(1, 15) = 26.67, P < 0.001; F(1, 15) = 5.74, P < 0.05 \), for the Kanji–Kanji, Kanji–Kana, Kana–Kanji, Kana–Kana trials, respectively and for categorization \( F(1, 15) = 24.54, P < 0.001; F(1, 15) = 37.33, P < 0.001; F(1, 15) = 7.78, P < 0.05; F(1, 15) = 14.54, P < 0.005 \), each respectively.

Between-task comparison revealed that participants responded 85 ms faster in reading than in categorization \( F(1, 30) = 15.05, P < 0.001 \). The magnitude of priming was 11 ms greater for categorization relative to reading \( F(1, 30) = 8.67, P < 0.01 \), suggesting that the task context affects the subliminal priming during word recognition. This task-by-priming interaction changed with target script [triple-interaction; \( F(1, 30) = 9.71, P < 0.01 \)] but not with prime script \( F(1, 30) = 2.63, P > 0.1 \), suggesting greater saving effects for Kana targets during categorization and for Kanji targets during reading. No other interactions with task were significant.

**Imaging Results**

**Repetition Priming Effects.** Both reading aloud and semantic categorization produced widespread activation of the bilateral frontoparietotemporal regions. We searched for the brain regions showing script-specific activation irrespective of the task requirements. In the cerebral network for reading, Kanji targets activated a medial part of the bilateral FG (\( x = -30, y = -51, z = -18, Z = 3.68 \), and \( x = 42, y = -67, z = -12, Z = 3.80 \)) relative to Kana targets [supporting information (SI) Fig. 6]. Conversely, Kana targets activated the bilateral occipital pole (\( x = -14, y = -97, z = -10, Z = 5.12 \), and \( x = 20, y = -97, z = -4, Z = 3.71 \)) relative to Kanji targets. No other region exhibited significant script-specific activation across the two tasks.

We then examined two forms of neural priming, i.e., repetition suppression and enhancement (13), by searching for the cerebral regions showing the repetition-induced decrease and increase of activation. For reading aloud, the global priming effect was detected as repetition enhancement in the left ventral premotor cortex (PMv), inferior parietal lobe (IPL), and posterior FG (Figs. 2 and 3). Note that the script-dependent, asymmetric pattern of priming at this fusiform cluster came mainly from primes in Kana. Only the left lateral prefrontal cortex and posterior MTG exhibited response enhancement in cross-script trials (i.e., when primes and targets were presented in different scripts). However, no significant repetition suppression was found throughout the entire brain volume.

For semantic categorization, the main effect of repetition suppression was significant only in the left anterior MTG (see Fig. 2). This region exhibited reduced response in cross-script conditions.

**Fig. 1.** Experimental paradigm and behavioral results. (A) Sequence of events used for the behavioral tasks. Participants either read aloud visible targets or categorized them as representing natural or artificial objects. (B) Mean reaction times (±SEM) during reading and categorization.

**Fig. 2.** Neural priming in the left parietotemporal cortex. Global priming effects (green blobs) were significant in the left IPL and posterior FG for reading and in the left MTG for categorization (shadowed in dark gray). The left posterior MTG (blue blob) exhibited cross-script repetition enhancement during reading (in light gray). Bars represent the mean percent signal change (±SEM) for each condition relative to the baseline.

**Fig. 3.** Neural priming in the premotor cortex. The left PMv (green) exhibited repetition enhancement during reading, whereas the PMd (blue) showed repetition suppression during categorization across the four priming conditions.
trials but not in within-script trials. When the search was extended to the brain regions involved in hand response (masked at $P < 0.05$ for categorization vs. baseline), the main effect of repetition suppression was detected in the bilateral dorsal pre-motor cortex (PMd: $x = -22, y = -13, z = 43$, $t = 3.03$, and $x = 16, y = 5, z = 53, Z = 2.88$). Note that the left PMv, which showed repetition enhancement during reading aloud, now exhibited repetition suppression under categorization for both the within- and across-task contrast (8 voxels, $x = -24, y = -12, z = 41, Z = 2.96$) and cross-script conditions. For each task, other regions showing priming effects are presented in SI Table 1.

The task-dependent change of priming directions was also found in the left IFG, which showed repetition enhancement during reading but exhibited a nonsignificant trend of repetition suppression during categorization ($Z = 2.70$). The categorization task produced no significant repetition enhancement in the entire search volume, neither at the global nor at the within-script levels. Only the cross-script repetition produced response enhancement in the left precentral area ($x = -61, y = -14, z = 34, Z = 3.90$), bilateral basal ganglia ($x = 24, y = 15, z = 10, Z = 3.89$), and cerebellum ($x = -8, y = -67, z = -13, Z = 3.36$).

In the joint analysis of reading and categorization, the global repetition enhancement across the two tasks was significant at the left frontoparietal junction and bilateral posterior parietal area and cerebellum. In this neural circuit, the repetition effect interacted with task at the left IPL ($x = -38, y = -57, z = 32, Z = 3.48$) and precuneus ($x = -8, y = -78, z = 43, Z = 3.47$). A weaker trend of between-task difference was found for the left PMv ($x = -34, y = -2, z = 31, Z = 2.94$). In contrast, the global repetition suppression across the two tasks was detected only as a nonsignificant trend in the bilateral medial frontal and posterior temporal cortical areas and deep grey. However, the priming-by-task interaction (corrected at $P < 0.05$ across the search volume) was significant in the left medial superior temporal gyrus (STG: $x = -36, y = -30, z = 25$), caudate ($x = -26, y = 27, z = 8$), MTG ($x = -46, y = -35, z = -7$), and PMD ($x = -20, y = -13, z = 43$).

Effective Connectivity Analysis. We examined the interregional connectivity between the left prefrontal and parietal cortical regions showing global priming effects during each task. We focused on the influence of cognitive set over the two task-dependent cerebral networks for reading, each of which was assumed to receive the visual input commonly at the FG during the execution of tasks. Specifically, we constructed a dynamic causal model (DCM), which comprises the IPL and PMv for the “dorsal” stream involved in reading aloud (Fig. 4). For the “ventral” stream involved in categorization, we created another DCM comprising the MTG and PMv. Based on the known role of the left temporal lobe in word comprehension, we additionally included the left STG in both DCMs (see Methods). The stimulus-free contextual effects were then estimated as the latent or intrinsic interregional coupling under a given task (14).

Mean intrinsic connection parameters for each task are presented in SI Table 2. For the dorsal network, there were significant excitatory inputs from STG to PMv and IPL during reading aloud, whereas these connections were not significant under categorization (Fig. 4A). No other within-task connections exceeded zero, neither for reading nor for categorization (all $t < 1.1$). Between-task comparisons confirmed that the task set for reading increased the reciprocal intrinsic coupling between STG and IPL relative to the task set for categorization ($t = 2.98, P = 0.006$ for STG-IPL; $t = 3.02, P = 0.005$ for IPL-STG). The between-task difference was marginally significant for the PMv-STG projection ($t = 1.95, P = 0.06$). No other intrinsic connections differed between the two tasks (all $t < 1.3$).

For the ventral stream, there were significant excitatory projections from STG to PMd and MTG during categorization (Fig. 4B). However, these connections were also significant during reading aloud and did not differ between the two tasks (both $t < 1$). The categorization task produced reciprocal excitatory inputs from FG to MTG and PMd, but neither of these connections differed from those under reading aloud (all $t < 1.2$). The intrinsic coupling from PMd to MTG was marginally significant during categorization, but did not survive the between-task comparison ($t < 0.1$). No other intrinsic connections differed between the two tasks (all $t < 1$).

For each task, we further estimated the modulatory effects of repetition (across the four priming conditions) on the task-relevant regions. The repetition of words induced an increase of connectivity from PMv to IPL for reading aloud [mean connection strength: $+0.021/0.007$ for repeated/unrepeated trials, respectively; $F(1, 15) = 4.45, P = 0.05$] but not for categorization [$+0.0006/0.0007; F(1, 15) < 0.1$]. In between-task comparisons, this modulatory influence interacted with task set at a trend level [$F(1, 30) = 2.80, P = 0.10$]. For categorization, the repetition of words produced a marginally significant change of connectivity in two forward projections, i.e., increase at the FG-PMd [$+0.0040/0.0015; F(1, 15) = 3.73, P = 0.07$] and decrease at the FG-STG [$-0.0004/0.0002; F(1, 15) = 3.71, P = 0.07$] connections, but it was not the case for reading aloud, neither for FG-PMd [$+0.0038/0.0018; F(1, 15) = 3.08, P = 0.1$] nor for FG-STG [$+0.0002/0.0007; F(1, 15) = 0.36$]. The modulatory effect at the FG-PMd projection was significant across two tasks [$F(1, 30) = 6.73, P < 0.02$] but did not differ between the two tasks [$F(1, 30) < 1$]. No other projections exhibited significant modulatory effects, neither for within-task nor for across-task analyses.

Discussion
We performed the two subliminal priming experiments to investigate the influence of task instructions over the neural network involved in unconscious word processing. Behavior-
Neurocognitive components of unconscious repetition priming. The left FG receiving the visual input is associated with abstract, shape-invariant representations of pronounceable letter-strings (3). The ventral stream from the FG, comprising the IPL for print-to-sound translation and PMd for speech planning (dark gray), operates in the generation of subliminal priming during reading aloud. In contrast, the dorsal stream from the left FG, comprising the MTG for semantic representations and PMd for manual response preparation (light gray), is involved in repetition priming during categorization.

For categorization, the observed activation reduction in the PMd is in accord with a recent fMRI study showing that stimulus–response congruency induces response attenuation in the same area (18). This region is involved in the learning of arbitrary associations between visual cues and hand response, in both primates (19) and humans (20). Hence, the observed priming in PMd can be attributed to the accumulated response bias for generating the manual response required for the categorization task.

For categorization, the observed activation reduction in the PMd is in accord with a recent fMRI study showing that stimulus–response congruency induces response attenuation in the same area (18). This region is involved in the learning of arbitrary associations between visual cues and hand response, in both primates (19) and humans (20). Hence, the observed priming in PMd can be attributed to the accumulated response bias for generating the manual response required for the categorization task.

For categorization, the observed activation reduction in the PMd is in accord with a recent fMRI study showing that stimulus–response congruency induces response attenuation in the same area (18). This region is involved in the learning of arbitrary associations between visual cues and hand response, in both primates (19) and humans (20). Hence, the observed priming in PMd can be attributed to the accumulated response bias for generating the manual response required for the categorization task.

For categorization, the observed activation reduction in the PMd is in accord with a recent fMRI study showing that stimulus–response congruency induces response attenuation in the same area (18). This region is involved in the learning of arbitrary associations between visual cues and hand response, in both primates (19) and humans (20). Hence, the observed priming in PMd can be attributed to the accumulated response bias for generating the manual response required for the categorization task.
response during concrete-abstract judgment about consciously perceived words. This observation may also reflect the strategic allocation of attention, because the task demand could interact with the semantic relatedness of stimuli [see Neely (35) for a review].

It is interesting to note that such temporal shifting of fMRI priming after the backward or top-down modification may correspond to the reversal of priming directions observed in magnetoencephalography studies (36, 37). Namely, the left occipitotemporal cortex exhibits increased response to the repeated presentation of words at ~230 ms after the stimulus onset. By contrast, a distributed left hemisphere network, extending from the parietotemporal to lateral prefrontal regions, exhibits attenuated response in a later period (~400 ms), whereas this late neural priming is more pronounced in the frontal and anterior temporal regions.

Conclusion
Our results suggest that unconscious word perception primes the entire task-relevant neural circuit for processing visible targets, setting up more efficient functional coupling between the left parietotemporal regions associated with word processing and premotor regions associated with behavioral response. The voluntary task control guides even invisible words to the task-relevant processing streams in the left hemisphere, whereas the top-down influence of task sets affects the neural priming direction within the task-relevant language network.

Methods
Participants. Two groups of sixteen right-handed, native Japanese speakers (age range 25–38 years) were recruited separately for the reading aloud and semantic categorization experiments. The behavioral and brain imaging results for categorization were reported previously (6). All participants gave written informed consent before the imaging experiment. The protocol of this study was approved by the regional ethical committee.

Materials and Procedures. The visual stimuli consisted of 40 Japanese nouns written commonly both in Kanji and Kana. These words were composed of 1–2 characters when written in Kanji and 2–3 characters when written in Kana. Half of them represented natural objects and the other half artifacts. Each trial consisted of a precisely timed sequence of a masked prime and a visible target (Fig. 1A). In the reading-aloud task, participants named the visible targets as quickly as possible, whereas in the categorization task, they responded by key-press to classify the targets as natural or artificial as quickly and as accurately as possible.

Each fMRI experiment was arranged in a 2 × 2 factorial design in which the main effects of interest were repetition (identity or control), prime script (Kanji or Kana) and target script (Kanji or Kana). A ninth type of trials comprising the same sequence of masks without prime and target words served as a baseline to measure the event-related activation by words. In each experiment, participants received four scanning sessions, each comprising five initial training trials followed by 200 trials (20 trials for each event type except for the “word-absent” baseline with 40 trials, all in random order).

Immediately after the imaging sessions, participants performed a forced-choice test for prime visibility (64 trials). Each trial comprised the same sequence of masks and words as in the activation task, followed by a pair of choices (a same word as the prime and a distractor) presented left and right of the fixation. Participants determined which of the two items corresponded to the prime word in the preceding event sequence.

fMRI Procedures. Both experiments were conducted by using a 3-Tesla whole-body system (Bruker) with a standard head coil optimized for a gradient echo-echo planar imaging sequence (26 contiguous axial slices, thickness 4.5 mm with 0.5 mm gap, echo time = 40 ms, flip angle = 90°, field-of-view = 192 × 256 mm², 64 × 64 pixels). The repetition time was 2,400 ms for both tasks but included a 1,000-ms silence period for reading aloud (thus acquisition time was 2,400 ms for categorization and 1,400 ms for reading). Participants received four scanning sessions each of which lasted ~8 min, giving 207 volumes for reading and 205 volumes for categorization.

Data Analysis. After image reconstruction, the functional images were processed by using the SPM2 software (Wellcome Department of Cognitive Neurology, London, U.K.). Five initial images were discarded to eliminate nonequilibrium effects of magnetization. Images were corrected for head motion, resampled every 2 mm by using trilinear interpolation and normalized to the standard brain space, and spatially smoothed with an isotropic Gaussian filter (5 mm full-width at half-maximum). These images were 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 nine event types convolved with a canonical hemodynamic response function with time and dispersion derivatives. Group-based statistical inference was made by using random-effect analysis. We first identified the brain regions active during reading aloud by pooling the eight word-present conditions relative to the baseline (voxel-level P < 0.05). The resulting SPM served as a masking image for searching the priming effects in the cerebral network involved in reading. For each task, mean percent signal change was calculated for the eight word-present conditions by using the most significant voxel for each participant.

The effects of repetition suppression and enhancement each were calculated as the decrease and increase of activation in repeated trials relative to nonrepeated trials (13). We examined the neural priming effects associated with the “within-script priming” (including prime–Kanji/target–Kanji and prime–Kana/target–Kana trials) and those associated with “cross-script priming” (including Kanji–Kana and Kana–Kanji trials) corresponding to more abstract, script-independent representations beyond orthographic processing. For each task, global priming effects were computed by collapsing the four priming conditions.

The neural priming effects were compared between reading and categorization by entering the two sets of 16 individual contrast images into one-way ANOVA, treating the task as a between-group factor. We examined the priming-by-task interaction by selecting the voxels showing either global repetition suppression or enhancement across the two tasks (inclusive masking at P < 0.05). Unless stated otherwise, all effects were tested at voxel-level P < 0.005 (spatial extent > 15 contiguous voxels).

We used dynamic causal modeling to estimate the effective connectivity between the brain regions involved in task-specific priming effects. In brief, DCM treats the brain as a nonlinear dynamic system that is subject to inputs and produces outputs. By using a bilinear approximation to the dynamics of interactions among states, the parameters of the implicit causal model reduces to three sets, i.e., (i) parameters of the extrinsic input to the system, (ii) parameters representing the intrinsic or latent connections that couple responses in one area to the state of others, and (iii) the bilinear parameters representing the changes in the intrinsic coupling induced by inputs (14). The connectivity parameters are estimated in the Bayesian framework whereby inferences about particular connections are made by using the posterior or conditional density. Based on the group results from random-effect analyses, we constructed two different DCMs with four interconnected regions, each of which was seeded with the left FG receiving the visual input. One is the cerebral network including the left PMv and IPL that exhibited neural priming during reading aloud.
neural circuits for reading, the intrinsic-connection parameters from four sessions were collapsed per participant and submitted to a second-level analysis by using the classical t-statistics. For each of the interregional coupling, we performed a one-sample t test to examine whether the across-participant mean differed from zero for each task. A lenient statistical threshold (P < 0.05, two-tailed) was used to determine the significant neural connections during each task. We selected the connections that reached the significance in either of reading and categorization and then compared the coupling strength between the two tasks using unpaired t test. All across-task comparisons of connection parameters were made for each DCM, and not between different models. The modulatory effects of repetition were further examined within and across tasks by submitting the bilinear coupling parameters to repeated-measures ANOVA treating the main effect of repetition as a within-participant factor and the task set as an additional between-group factor (the latter only for between-task comparisons).

This work was supported by Institut National de la Santé et de la Recherche Médicale, Commissariat à l’Energie Atomique, a centennial fellowship of the McDonnell foundation (to S.D.), a postdoctoral fellowship from the Fondation de la Recherche Médicale, and Grants-in-Aid from the Japan Ministry of Education, Culture, Sports, Science and Technology (15700252) and the Japan Society for the Promotion of Science (19500264) (to K.N.).