

Task-Guided Selection of the Dual Neural Pathways for Reading

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Summary

The visual perception of words is known to activate the auditory representation of their spoken forms automatically. We examined the neural mechanism for this phonological activation using transcranial magnetic stimulation (TMS) with a masked priming paradigm. The stimulation sites (left superior temporal gyrus [L-STG] and inferior parietal lobe [L-IPL]), modality of targets (visual and auditory), and task (pronunciation and lexical decision) were manipulated independently. For both within- and cross-modal conditions, the repetition priming during pronunciation was eliminated when TMS was applied to the L-IPL, but not when applied to the L-STG, whereas the priming during lexical decision was eliminated when the L-STG, but not the L-IPL, was stimulated. The observed double dissociation suggests that the conscious task instruction modulates the stimulus-driven activation of the lateral temporal cortex for lexico-phonological activation and the inferior parietal cortex for spoken word production, and thereby engages a different neural network for generating the appropriate behavioral response.

Introduction

Behavioral studies have shown that printed words rapidly activate the representation of their spoken forms, even when the stimuli are perceived unconsciously (Frost, 2003). This phonological activation constitutes a mandatory and crucial component of visual word recognition, the dysfunction of which is known to correlate with difficulties in literacy acquisition (Paulesu et al., 2000; Shaywitz et al., 1998). The automatic nature of such print-to-sound translation during reading is mirrored by brain imaging data showing that the mere exposure to visual words induces widespread activation

of the left perisylvian area, associated with phonology, beyond the functional demands of the task (Price et al., 1996).

Typically, the stimulus-driven response to pronounceable letter-strings extends beyond the left occipitotemporal cortex (associated with visual word perception), which responds approximately 150–200 ms after the stimulus onset (Cohen et al., 2000; Nobre et al., 1994; Tarkiainen et al., 1999), down to a middle part of the left superior temporal gyrus/sulcus (L-STG/STS) that is associated with the auditory representation of spoken words (Demonet et al., 1992; Howard et al., 1992; Price, 1998). More recent work, however, has shown that the distributed activation during reading is drastically reduced and localized to the left occipitotemporal region under the visual masking procedure where participants are unable to perceive written words consciously (Dehaene et al., 2001). This observation indicates that it is an open question what neural mechanisms mediate the connection between the occipitotemporal region and the auditory association cortex to achieve the feed-forward activation of phonological code from letter-strings, because such automatic phonological computation is in itself an obligatory component of reading, which operates even under the subliminal perception of words.

Several other recent studies have further suggested that the interregional connectivity changes in the left-hemisphere language network as a function of task requirements (Bokde et al., 2001; Horwitz et al., 1998; Mechelli et al., 2005). Thus, the neural connections mediating the cross-modal translation from print to sound may be modulated by task instructions, presumably under the executive control of the prefrontal cortex (Fuster, 1997; Miller and Cohen, 2001). Critically, such top-down, strategic control may further exert a modulatory influence over the stimulus-driven neural activation triggered by unconsciously perceived words. In fact, past behavioral studies have shown that the voluntary allocation of attentional resources produces a measurable impact on the unconscious or autonomous processing of visual stimuli (Naccache et al., 2002; Ramachandran and Cobb, 1995).

Specifically, there are at least two candidate large-scale neural networks involved in automatic phonological computation during reading. First, brain imaging and neuropsychological studies both point to a central role of the left inferior parietal lobe (L-IPL) in orthography-to-phonology conversion during reading (Price, 1998). Here, the spreading activation from the occipitotemporal cortex is assumed to reach the L-IPL before activating the phonological representation associated with the L-STG region. Indeed, behavioral studies have suggested that the serial computation of phonology occurs in an earlier stage of reading prior to the lexical activation (Frost, 2003). Second, recent brain imaging studies have suggested the existence of polysensory neurons in a posterior part of the STS which respond to both visual and auditory stimuli (Beauchamp et al., 2004; Wright et al., 2003). As an anatomical substrate for multisensory

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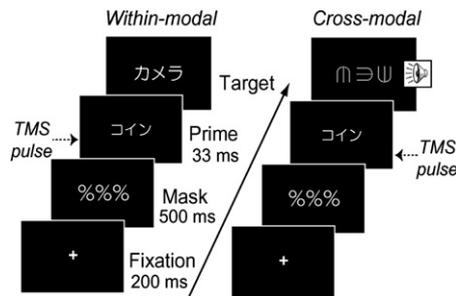


Figure 1. Sequence of Events Used for the Behavioral Paradigm

Each trial consisted of a masked prime followed either by a visual target (“within-modal trials”) or by an auditory target synchronized with a string of three or four letter-like symbols (€,fl,≡,∪) as a backward mask (“cross-modal trials”). The two types of trials were randomly intermixed in each TMS session, which lasted 480 s. For the LD task, participants determined whether or not the target stimuli represented a real Japanese word irrespective of their modality, while for the PRN task, they simply read aloud the visual targets or repeated the auditory targets. Experiment 1 was a behavioral experiment using the same event sequence without TMS. A post-hoc prime-visibility test confirmed that participants were unable to see the primes consciously (see [Experimental Procedures](#)). In Experiment 2, a single-pulse TMS synchronized to the fixation cross was applied to the target brain site in each trial.

integration ([Beauchamp, 2005](#)), this posterior lateral temporal sector might constitute an alternative neural pathway that can relay an input signal from the occipito-temporal area for cross-modal word processing.

Using event-related transcranial magnetic stimulation (TMS) with a masked repetition priming paradigm ([Figure 1](#)), we explored the degree of relative contribution of the L-IPL and L-STG/STS in unconscious phonological activation during reading under two different task instructions, lexical decision (LD) and pronunciation (PRN). The behavioral response to a written word is known to be facilitated after the brief, subliminal presentation of the same word, both for LD ([Forster et al., 2003](#)) and PRN ([Kinoshita, 2003](#)). We examined the TMS-induced interference in the two types of repetition priming while manipulating the stimulation site (L-IPL and L-STG), target modality (visual and auditory), and lexicality (word and nonword). The cross-modal manipulation of the priming condition has previously been used as a behavioral index of phonological activation during reading ([Grainger et al., 2003](#); [Kouider and Dupoux, 2001](#)). Crucially, our experimental paradigm with visual masking enables minimization of potential strategic or attentional effects induced by the conscious perception of words and thereby targets bottom-up activations of the neural code. Combined with a real-time 3D navigation system, the present TMS experiment thus allowed inferences about the neural processes operating during the later stage of reading (>200 ms after the stimulus onset) at the cerebral loci targeted with high-resolution structural MRI.

Results

Experiment 1

We first conducted a behavioral experiment without TMS to confirm a reliable masked repetition priming effect under within- and cross-modal conditions under

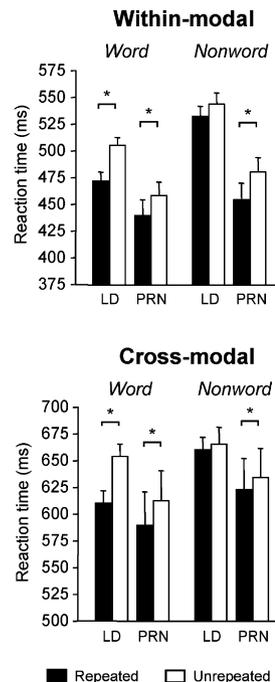


Figure 2. Mean Reaction Times, \pm SEM, During the LD and PRN Tasks in Experiment 1

For the within-modality condition, the priming effect in LD was significant only for words, whereas the onset priming effect in PRN was significant both for words and nonwords (upper panel). This same pattern of priming was also obtained for the cross-modal condition (lower panel). (*) indicates a priming effect significant in the planned pairwise comparison (see [Results](#)).

the two task instructions (see [Figure 1](#)). Participants made few errors during the two tasks (mean error rate = 3.48% for LD and 0.89% for PRN). Mean reaction times (RT) for each of the four priming conditions are presented in [Figure 2](#). Planned pairwise comparison was made separately for words and nonwords using analysis of variance (ANOVA). For words, a significant priming effect was obtained under the LD task in the within-modal ($F[1,13] = 20.56, p < 0.001$) and cross-modal ($F[1,13] = 18.98, p < 0.001$) conditions. There was also a significant priming effect under the PRN task in the within-modal ($F[1,13] = 15.76, p < 0.005$) and cross-modal ($F[1,13] = 34.51, p < 0.001$) conditions. For nonwords, the priming effect in LD did not reach significance for the within-modal condition ($F[1,13] = 3.78, p = 0.07$) or for the cross-modal condition ($F[1,13] < 1$). For PRN, there was a robust “onset priming” effect ([Kinoshita, 2003](#)) for the within-modal condition ($F[1,13] = 31.13, p < 0.001$), while the same effect did not reach significance in the cross-modal condition ($F[1,13] = 3.01, p = 0.11$).

The same participants also performed a forced-choice test designed to evaluate the visibility of primes (80 trials). Each trial comprised the same sequence of masks and words as in the main experiment described above, except that the prime stimuli appeared as a left-right inverted mirror image of the original words with a probability of 50%. Participants were asked to determine whether or not prime words were flipped as accurately as possible without time pressure. The mean

accuracy of this forced-choice test was 50.59% for the within- and 48.27% for the cross-modal conditions, respectively. This accuracy level did not depart significantly from the chance-level trials, neither for the within-modal ($t = 0.33$, $p > 0.5$) nor for the cross-modal ($t = -0.72$, $p = 0.48$) ones, suggesting that participants were unable to perceive the masked primes consciously in both conditions.

Experiment 2

In this experiment, we examined the impact of TMS on the repetition priming effects observed in Experiment 1. Guided by the real-time MRI-based monitoring, we delivered a precisely targeted single-pulse TMS either to the L-IPL or L-STG during the execution of the LD and PRN tasks (Figures 3A and 3B). The overall spatial displacement of the stimulation points during the TMS session was ~ 8 mm for the L-IPL and ~ 11 mm for the L-STG across participants, respectively. The potential effect of coil motion on the stimulation intensity would be negligible for this range of displacement given the estimated spatial extent of the electric field generated by the TMS (see *Experimental Procedures*) and the approximate volume of the anatomical target sites ($>10 \times 10 \times 10$ mm³ for both the IPL and STG, according to the stereotaxic atlas of Talairach and Tournoux [1988]).

Participants achieved a high level of accuracy for both tasks during the TMS session (mean error rate = 7.04% for LD and 3.39% for PRN). Mean RTs with respect to the lexicality and modality are presented in Figures 3C and 3D. An omnibus ANOVA for the RTs revealed significant main effects of lexicality and modality ($p < 0.001$ for both), suggesting that participants responded more quickly to (1) words than nonwords and to (2) visual targets over auditory targets, respectively. In the following analysis, the effects of repetition priming, task type, and stimulation site were examined separately for words and nonwords with respect to their modality.

For words, there was a significant priming effect under the within-modal condition ($F[1,15] = 18.14$, $p < 0.005$), whereas the effects of task and site did not reach significance (both F s < 1). Crucially, there was a significant three-way interaction between these factors ($F[1,15] = 9.82$, $p < 0.01$). None of the other interactions were significant ($p > 0.1$). Under the cross-modal condition, there was also a significant priming effect ($F[1,15] = 8.64$, $p < 0.05$), while the effects of task and site were both nonsignificant ($p > 0.1$). The three-way interaction between these factors was marginally significant ($F[1,15] = 4.31$, $p = 0.06$). No other interactions reached significance ($p > 0.1$).

For nonwords, there was a significant effect of the within-modal priming ($F[1,15] = 12.61$, $p < 0.005$). The effect of task type was marginally significant ($F[1,15] = 4.42$, $p = 0.05$), suggesting that the response latency was longer for LD than for PRN when targets were presented in the visual modality. All of the other main effects and interactions were nonsignificant ($p > 0.1$). For the cross-modal condition, none of the main effects and interactions reached significance (all F s < 1).

Planned Comparisons for the Priming Effect

Planned comparisons for words revealed a significant priming effect in the LD task when the stimulation was applied to the L-IPL, both for the within-modal

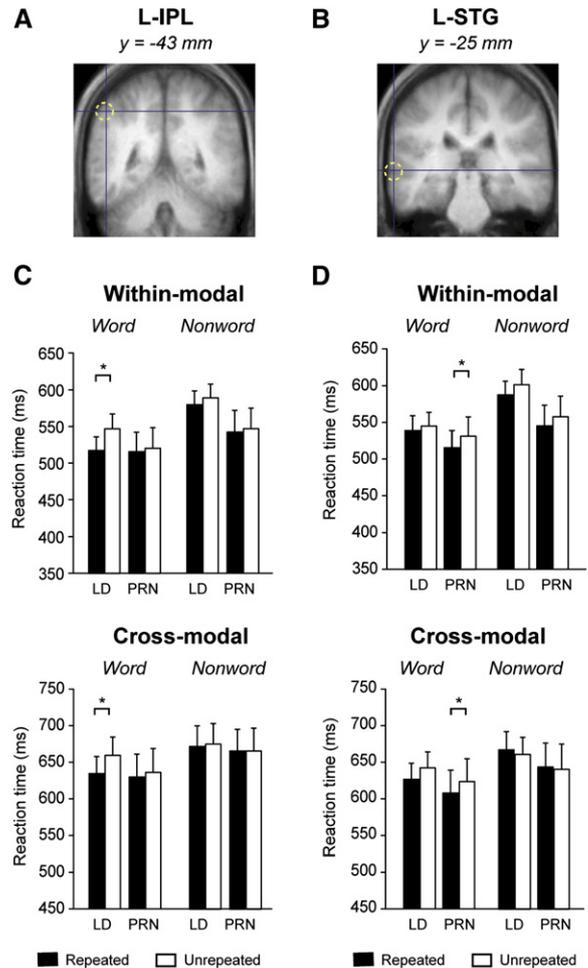


Figure 3. Locations of the Anatomical Targets and Behavioral Effects of the TMS

Each target site is rendered on a structural MRI averaged across participants. The dotted circles represent the approximate spatial extent of the induced electric field around the maximum stimulation point. (A) The L-IPL target. The mean coordinates (\pm SD) of the stimulation points were $x = -48 \pm 6$ mm, $y = -43 \pm 7$ mm, $z = 48 \pm 9$ mm according to the stereotaxic atlas of Talairach and Tournoux (1988). (B) The L-STG target. The mean coordinates (\pm SD) of the stimulation points were $x = -62 \pm 4$ mm, $y = -25 \pm 7$ mm, $z = 2 \pm 8$ mm. (C) Mean reaction times (\pm SEM) for the LD and PRN tasks during the stimulation of L-IPL. For words, the priming effect in PRN was eliminated irrespective of the target modality when the L-IPL was stimulated. In contrast, the priming for LD remained significant for both the within- and cross-modal conditions. For nonwords, the onset priming effect in PRN was also disrupted by the TMS. (D) Mean reaction times (\pm SEM) for the LD and PRN tasks during the stimulation of L-STG. For words, the priming effect in LD was eliminated regardless of the target modality when the L-STG was stimulated. In contrast, the onset priming for PRN remained significant across the within- and cross-modal conditions. For nonwords, the priming effect in PRN was also affected by the TMS.

($F[1,15] = 33.98$, $p < 0.001$) and cross-modal ($F[1,15] = 4.49$, $p = 0.05$) conditions. However, the priming effect in the PRN task did not reach significance when the same region was stimulated; this was also the case for the within-modal ($F[1,15] < 1$) and cross-modal conditions ($F[1,15] < 1$). In contrast, the priming for LD was eliminated when the L-STG was stimulated, both for the within-modal ($F[1,15] = 1.01$, $p = 0.33$) and

cross-modal ($F[1,15] = 2.74, p = 0.12$) conditions. The priming effect in PRN remained significant when the same region was stimulated in the within-modal condition ($F[1,15] = 10.47, p < 0.01$) and in the cross-modal condition ($F[1,15] = 9.14, p < 0.01$).

On the other hand, nonwords produced no significant priming effect when the L-STG was stimulated during the LD task in either within- ($F[1,15] = 1.99, p = 0.18$) or cross-modal ($F[1,15] < 1$) conditions. There was a significant effect of priming for PRN in the within-modal condition ($F[1,15] = 8.13, p < 0.05$). No significant priming was obtained for the PRN task in the cross-modal condition ($F[1,15] < 1$). When the L-IPL was stimulated, no priming effect was found for either of the two tasks irrespective of the modality ($p > 0.08$ for all Fs).

Combined Analysis of the Behavioral and TMS Experiments

For each of the planned comparisons reported above, we further examined the effect of TMS on the magnitude of the priming effect in a joint analysis of the two datasets, one from Experiment 1 without TMS and the other from Experiment 2. For each stimulation site, the mean RTs were analyzed as a 2×2 factorial arrangement with the repetition priming as a within-participant factor (identical versus unrelated) and the stimulation as a between-group factor (with TMS versus without TMS).

For words, the stimulation of the STG interfered with the priming in LD for both the within-modal and cross-modal conditions (interaction, $F[1,28] = 9.42, p < 0.01$ and $F[1,28] = 4.92, p < 0.05$, respectively). The stimulation of the same site did not produce a significant impact on the magnitude of priming in PRN ($F < 1$ for both within- and cross-modal trials). For IPL, the priming \times stimulation interaction was significant for PRN in the cross-modal condition ($F[1,28] = 4.22, p < 0.05$) and marginally significant in the within-modal condition ($F[1,28] = 3.28, p = 0.08$). However, stimulation of the same site produced no significant effect on the priming for LD ($F[1,28] < 1$ and $F[1,28] = 2.32, p = 0.14$ for within- and cross-modal conditions, respectively). For nonwords, stimulation of the IPL interacted with the priming in PRN only for the within-modal condition ($F[1,28] = 10.55, p < 0.005$). This same priming effect was also reduced by the stimulation of the STG ($F[1,28] = 4.44, p < 0.05$). None of the other interactions reached statistical significance.

Discussion

By the combined use of masked priming and TMS, the present study focused on the neural substrate of the bottom-up phonological activation during reading, while eliminating the influence of postperceptual processes, i.e., the distant global broadcasting that may occur when words cross the threshold of consciousness (Dehaene et al., 2004; Lamme, 2003; Lamme et al., 2002). Behavioral results from Experiment 1 show a significant masked priming effect across the two tasks, not only when primes and targets were presented in the same modality, but also when they were presented in differing modalities. It is important to note that each of these priming effects has a distinct cognitive locus involved in visual word processing. For the LD task, the within-modal priming is thought to reflect mainly a lexical-level

activation, while the earlier, orthographic contribution is relatively smaller and no greater than 10 ms (Forster et al., 2003). For PRN, the within-modal priming has been known to occur both for words and nonwords and has been attributed to either the orthography-to-phonology computation (Forster and Davis, 1991) or further downstream toward the speech planning process (Kinoshita, 2003). This latter process could be also involved in the cross-modal priming in PRN as a final common pathway for spoken output. On the other hand, the cross-modal priming in LD has been attributed to the activation of phonological codes through visual input (Kouider and Dupoux, 2001).

Previous behavioral studies with alphabetic readers have reported conflicting results about whether or not subliminal primes indeed facilitate the participants' responses during LD. For instance, Grainger et al. (2003) demonstrated significant masked cross-modal priming with the prime duration of 57 ms, while another study failed to obtain a significant priming effect at the same or even longer prime duration (Kouider and Dupoux, 2001). The inconsistency across studies has been attributed to several different factors in the experimental setting, such as the differences in prime duration, interstimulus interval between primes and targets, and backward masking (Grainger et al., 2003). Although the present design does not allow us to determine the relative contribution of these factors in the mechanics of masked cross-modal priming, our results provide additional evidence showing that the response facilitation across different modalities does occur even at a very brief prime duration (33 ms). The robust effect obtained here could be partially attributed to a possible advantage of the syllabic script in phonological conversion, i.e., a higher degree of transparency between orthography and phonology which would allow a more rapid computation of phonology from print.

Our TMS results revealed that the within- and cross-modal priming conditions for words both produced a significant triple interaction between repetition, task type, and stimulation site. Coupled with the joint analysis of the two datasets, this finding suggests a net component of regional-specific interference by TMS which cannot be attributed to a nonspecific, global cortical inhibition associated with the stimulation. That is, the stimulation of the L-STG and the L-IPL each produced a differential impact on the within- and cross-modal priming according to the task instruction and lexical property of the stimuli.

Specifically, the stimulation of the L-IPL eliminated the masked onset priming effect for words and nonwords, whereas these same effects were not affected by the stimulation of the L-STG. This finding is consistent with past neuropsychological and brain imaging studies suggesting that the L-IPL plays a leading role in phonological computation from orthography (Friedmann et al., 1993; Price, 1998). Importantly, however, our results suggest that when top-down effects by attentional or strategic control are eliminated by visual masking, this neural pathway for letter-to-sound mapping opens only when participants are engaged in the cognitive set for word production. Moreover, the serial phonological conversion procedure subserved by the IPL runs nonspecifically to the pronounceable word-like stimuli

irrespective of whether they represent a real word or not, since the effect size for the onset priming in PRN did not differ between words (≈ 20 ms) and nonwords (≈ 24 ms) in the within-modal condition (Experiment 1). In fact, several past studies have consistently suggested that it is the left inferior prefrontal cortex, rather than the L-IPL, that is sensitive to the lexicality and regularity of orthography of written words (Fiebach et al., 2002; Fiez et al., 1999; Herbster et al., 1997; Rumsey et al., 1997).

On the other hand, we also found that the stimulation of the L-STG, but not that of the L-IPL, reduced the masked priming effect of words in the LD task, for both the within- and cross-modal conditions. This finding suggests that the lexical activation and phonological processing subsequent to it are mediated by the ventral neural pathway extending from higher-order visual cortex to the L-STG, of which the L-IPL does not constitute a pivotal component. Since participants were unaware of the identity of primes as confirmed by the prime visibility test, this interpretation in turn implies that the unconscious perception of visual words leads to the activation of their spoken forms without the implicit mobilization of the neural mechanism for speech production.

Functional brain imaging studies converge to suggest that the ventro-lateral temporal cortex comprises distinct subregions distributed between the occipitotemporal cortex for visual object recognition and the middle part of the L-STG associated with the phonological processing of spoken words. That is, a posterior sector of the STS responding to both visual and auditory stimuli is currently thought to represent a human homolog of the polysensory neurons in the macaque STS (Beauchamp et al., 2004; Wright et al., 2003). A functional MRI study by Cohen et al. (2004) has also shown that a middle portion of the left middle temporal gyrus adjacent to the polysensory STS is associated with the abstract, lexical-level representation of words and termed it a “lateral inferotemporal multimodal area.”

More generally, a current neural model of reading proposes an anterior-to-posterior processing stream of the left occipitotemporal cortex for a progressive abstraction process in visual word recognition (Dehaene et al., 2004), which conforms to a global framework of the cortical object recognition mechanism whereby raw visual features of stimuli are transformed increasingly from perceptual to conceptual (Henson et al., 2000; Lerner et al., 2001; van Turennout et al., 2000). Indeed, a recent study using diffusion tensor tractography revealed white matter fiber bundles connecting the extrastriate cortex and lateral temporal cortex (Catani et al., 2003). Taken together with the present finding, this suggests that the ventral pathway linking the occipitotemporal cortex and L-STG via the intermediate polysensory area is “turned on” and receptive of unconsciously perceived words only when observers are in the cognitive set for word recognition. This latter neural mechanism is sensitive to the lexicality of stimuli and works for the lexical- and subsequent phonological-level activation independently of the L-IPL, which operates in the phonological computation of both words and nonwords.

Importantly, our results provide direct evidence for the proposal that even the unconscious processing of incoming stimuli operates under the strong influence

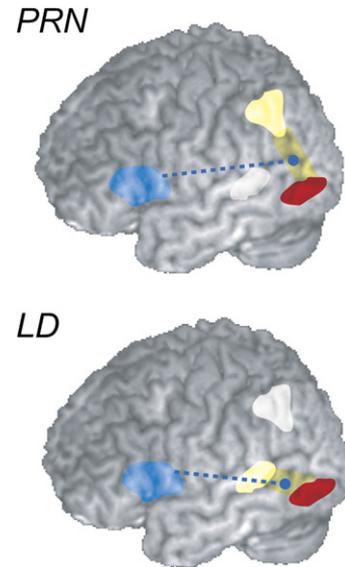


Figure 4. A Possible Schematic of the Neural Connections for Processing Subliminal Words in the Two Different Task Contexts

(Top) The lateral prefrontal cortex (blue) sends a biasing influence over the neural pathway from the left fusiform cortex (red) via the IPL (yellow) to prepare the spoken response when participants are in the cognitive set for pronunciation. This unconscious word processing proceeds without the contribution of the L-STG (gray). (Bottom) In lexical decision, the lateral prefrontal cortex (blue) selects the ventral processing stream to produce lexical- and phonological-level activation by directing the neural signal from the fusiform area to the L-STG (yellow). The L-IPL (gray) is not involved in the unconscious word processing during this task operation.

of the conscious task instructions (Dehaene et al., 1998). The finding that TMS produced a differentiated impact on the subliminal priming effect as a function of the stimulation site and task requirement is likely to reflect the task-dependent dynamic change of connection strength within the brain network involved in reading. Indeed, a recent fMRI study has shown that the effective connectivity between the left inferior frontal gyrus and task-specific temporo-parietal regions is modulated by the nature of behavioral tasks during conscious language operations (Bitan et al., 2005). The selection of these task-relevant neural pathways in posterior brain regions is thought to be achieved by the biasing influence exerted by the prefrontal cortex (Miller and Cohen, 2001). As illustrated in Figure 4, our results further suggest that such top-down, strategic control modulates the bottom-up neural activation produced by unconsciously perceived words to set up a different neural circuit for generating the intended behavioral response.

In addition, it is noteworthy that the well-known dual-route model of reading posits at least two different processing components, i.e., the lexical or whole-word system available for real words and the phonological assembly which plays an important role during reading of nonwords and low-frequency words (Coltheart et al., 2001). Under this framework, it might be said that these two components each are subserved by the ventral temporal pathway linking the occipitotemporal cortex and the L-STG and the more dorsal, parieto-temporal circuitry involving the L-IPL. This proposal seems partially

at odds with past brain imaging studies showing that nonwords relative to words produced greater activation in the left prefrontal area, whereas the opposite contrast produced either no activation difference at all (Rumsey et al., 1997) or activation difference in several distinct areas of the left hemisphere, including the fusiform (Herbster et al., 1997) and middle temporal gyri (Fiebach et al., 2002) and inferior frontal area (Fiez et al., 1999).

However, another line of evidence supporting the hypothesized dual neural systems for reading is available from the neuropsychological literature on the two polarized forms of acquired reading disorder, surface and phonological dyslexia. The former is thought to reflect a selective impairment of the whole-word reading system and is most frequently associated with damage to the left superior temporal area, whereas the latter arises from a selective impairment of the orthography-to-phonology conversion procedure and is associated with the angular and supramarginal gyri in the left hemisphere (Friedmann et al., 1993; Greenwald, 2001). In fact, it is possible that some past neuroimaging studies have failed to detect the effect of lexicality because brain activation triggered by the conscious perception of word-like stimuli should be subject to the top-down attentional amplification by the prefrontal cortex. This in turn produces a distributed activation of the fronto-temporo-parietal network, thereby causing an underestimation of the potential activation difference between words and nonwords. The combined use of visual masking and TMS may have allowed dissection of the cerebral correlates of the conventional dual-route model for reading by eliminating such top-down modification of the activation of these task-specific posterior brain areas.

Experimental Procedures

Participants

Fourteen native Japanese speakers (age range 22–37 years) volunteered to participate in Experiment 1. A separate group of 16 right-handed, native Japanese speakers (age range 20–41 years) were recruited for Experiment 2. None of them had a previous history of neurological or psychiatric disease. All participants gave written informed consent prior to the TMS experiment. The protocol of this study was approved by the ethical committee of the University of Tokyo Graduate School of Medicine.

Stimuli and Task

The stimulus materials consisted of 20 trisyllabic words spelled with three characters in kana script (Japanese syllabary) and 20 trisyllabic nonwords created by rearranging the character-string of the real word items. A set of 160 prime-target pairs was constructed such that each item appeared twice as a visual target preceded either by itself or a different item in the same modality in “within-modal” trials, and twice as an auditory target preceded either by the same or a different item in the visual modality in “cross-modal” trials. The lexical status of primes was always congruent with that of targets both for the within- and cross-modal conditions.

The sequence of events used for the present experiment is illustrated in Figure 1. In cross-modal trials, the auditory targets were presented synchronously with a backward mask which consisted of a random combination of four pseudo-characters (Ξ, Π, Ξ, Ψ). The within- and cross-modal trials were randomly intermixed in the same experimental session such that the modality of a given target was unpredictable prior to its appearance (Kouider and Dupoux, 2001). For the LD task, participants determined whether or not the target words irrespective of their modality represented a real Japanese word as quickly and as accurately as possible, whereas for the PRN task they read aloud the visual targets or repeated the auditory

targets as quickly as possible. After a brief training session, participants received four TMS sessions, each lasting 480 s for each task for each stimulation site. The effects of task order and stimulation sites were counterbalanced across participants. The experiment was arranged in a 2×2 by 2×2 factorial design in which the main factors of interest were prime-target relation (identical versus unrelated), modality (within- versus cross-), lexicality (words versus nonwords), and stimulation site (L-STG versus L-IPL).

TMS Procedures

A high-resolution anatomical MRI scan was obtained for each participant prior to the main experiment. The target sites for TMS were localized for each participant using a computerized stereotaxic system (Eximia Navigated Brain Stimulation [NBS] System, Nexstim, Finland). For the L-STG stimulation, we targeted a middle part of the left lateral temporal cortex ~15 mm posterior to the lateral edge of the primary auditory cortex or transverse temporal gyrus, keeping a spatial separation of ~20 mm from the left occipitotemporal area associated with visual word form recognition (Cohen et al., 2000). The L-IPL was located at the left inferior parietal lobule on the lower bank of the left intraparietal sulcus corresponding to Brodmann's area 40 (Price, 1998). The mean coordinates of the two anatomical targets across participants were mapped onto the standardized brain space by the Montreal Neurological Institute using affine transformation of the individual brain (Figure 3A and Figure 4A).

A single-pulse TMS was delivered in each trial using two MagStim 200 magnetic stimulators connected to a 70 mm figure-of-eight coil through a BiStim module (Magstim, UK). The magnetic pulse has a rise time of 100 ms and a duration of 1 ms, whereas the effects in the underlying cortical region are estimated to last approximately 10 ms (Ilmoniemi et al., 1997). The coil was kept tangential to the skull for stimulating the IPL and STS with the handle pointing backward parallel to the midline. In each trial, a single pulse synchronized to the onset of the fixation point (see Figure 1) was applied to the target anatomical structure at an intensity of 70% of the generator's total power output, which corresponds to approximately 90%–130% of the motor threshold for the resting hand muscles. The spatial extent of the induced electric field was estimated as a cone-shaped distribution within a diameter of 10 mm at a depth of 10 mm from the coil center.

The real-time NBS system tracked the position and orientation of the coil and the head at a rate of ~20 Hz, allowing us to minimize their mutual displacement during the TMS session. For each TMS pulse, this 3D monitoring system also computed and recorded the estimated distribution and strength of the intracranial electric field induced by the stimulation using a conventional multilayer spherical approximation (e.g., Roth et al., 1991; Sarvas, 1987). For each participant, the spatial displacement of stimulation points was then calculated for each anatomical target by computing average root mean square distance of the trial-by-trial estimated maximum electric field relative to the initial stimulation point.

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