Selective Priming of Syntactic Processing by Event-Related Transcranial Magnetic Stimulation of Broca's Area

Kuniyoshi L. Sakai,[1,2,4] Yasuki Noguchi,[1]
Tatsuya Takeuchi,[1] and Eiju Watanabe[2,3]
[1]Department of Cognitive and Behavioral Science
Graduate School of Arts and Sciences
The University of Tokyo, Komaba
3-8-1 Komaba, Meguro-ku
Tokyo 153-8902
[2]CREST
Japan Science and Technology Corporation
Kawaguchi-shi 332-0012
[3]Department of Neurosurgery
Tokyo Metropolitan Police Hospital
Tokyo 102-8161
Japan

Summary

It remains controversial whether Broca's aphasia is an articulatory deficit, a lexical-access problem, or agrammatism. In spite of recent neuroimaging studies, the causal link between cortical activity and linguistic subcomponents has not been elucidated. Here we report an experiment with event-related transcranial magnetic stimulation (TMS) to clarify the role of Broca's area, more specifically, the left inferior frontal gyrus (F3op/F3t), in syntactic processing. An experimental paradigm contrasted sentences requiring syntactic decisions with those requiring semantic decisions. We found selective priming effects on syntactic decisions when TMS was administered to the left F3op/F3t at a specific timing, but not to the left middle frontal gyrus (F2). Our results provide direct evidence of the involvement of the left F3op/F3t in syntactic processing.

Introduction

The specialization of syntactic processing in human cognitive systems is one of the central issues in neuroscience, and it has been highly debated from a number of perspectives based on lesion studies of Broca's aphasia and functional imaging studies of the prefrontal cortex (Caplan and Waters, 1999; Sakai et al., 2001). The narrowest definition of Broca's area is the left pars opercularis (F3op, Brodmann's area [BA] 44) and the left pars triangularis (F3t, BA 45), a part of the third frontal convolution (F3) or the left inferior frontal gyrus (IFG). However, the syndrome referred to as permanent Broca's aphasia arises from a considerably larger brain lesion that includes the insula and subjacent white matter as well as the F3op/F3t (Mohr, 1976). The left precentral gyrus of the insula has been implicated in the motor planning of speech (Dronkers, 1996). Nevertheless, the functional role of the left F3op/F3t still remains unknown. Transcranial magnetic stimulation (TMS), which is used to produce physiological effects on neuronal activity, has been recently applied to the study of various brain

functions (Pascual-Leone et al., 2000; Hallett, 2000). To clarify the essential role of Broca's area in syntactic processing, here we used event-related TMS, administering magnetic pulses time-locked to every stimulus (an "event"). We targeted the left F3op/F3t (Figure 1), whose activation has been recently reported both in an implicit syntactic task (Dapretto and Bookheimer, 1999) and in an explicit syntactic task (Embick et al., 2000).

We tested two language tasks that require specific linguistic decisions: a syntactic decision (Syn) task and a semantic decision (Sem) task (Figure 2), which were developed in our recent optical topography (OT) study (Noguchi et al., 2002). In the Syn task, subjects judged whether sentences were either syntactically normal (N) or anomalous (A), while word combinations in each sentence were semantically related. We focused on a universal aspect of syntactic operations that are common to both English and Japanese: a distinction between transitive verbs (vt) and intransitive verbs (vi). This distinction is critical in sentence comprehension, because the choice of a transitive or intransitive verb determines the syntactic structure of a sentence (Smith and Wilson, 1979). Subjects were explicitly instructed to detect a syntactic anomaly, but they were not instructed to pay attention to the distinction between vt and vi. In the Sem task, subjects judged whether sentences were either semantically normal or anomalous while presented sentences were syntactically correct as to the usage of vt and vi. Here we focused on the lexico-semantic relationship (selectional restrictions) between a noun and a verb. In both tasks, the same set of nouns and verbs were used. Because normal sentences were identical among these tasks, we tested each task in separate sessions so that the TMS effect on judging whether a normal sentence is syntactically correct can be dissociated from that on judging whether the same sentence is semantically correct. In contrast, anomalous sentences had only one type of linguistic error in each task. Therefore, these stimuli formed minimal pairs for both intra-task pairs (N and A sentences) and intertask pairs (anomalous sentences for Syn and Sem). We named this experimental design a minimal-pair paradigm.

Results

Event-related TMS was delivered over the left F3op/F3t at a specific timing ("Real" condition). As a control condition to the Real condition, the recorded discharge click without concomitant TMS was presented at the same volume and timing as each Real condition ("Sham" condition, the "click" control). Therefore, whether the magnetic stimulus was present or not was the only difference between these two conditions. TMS was delivered at one of three time points in separate sessions (Figure 2): at the onset of a verb stimulus (T = 0), at 150 ms after the onset (T = 150), and at 350 ms after the onset (T = 350).

The subjects performed the tasks at the accuracy of 92 $\pm$ 4.8% (mean $\pm$ SD), ranging from 75% to 100%

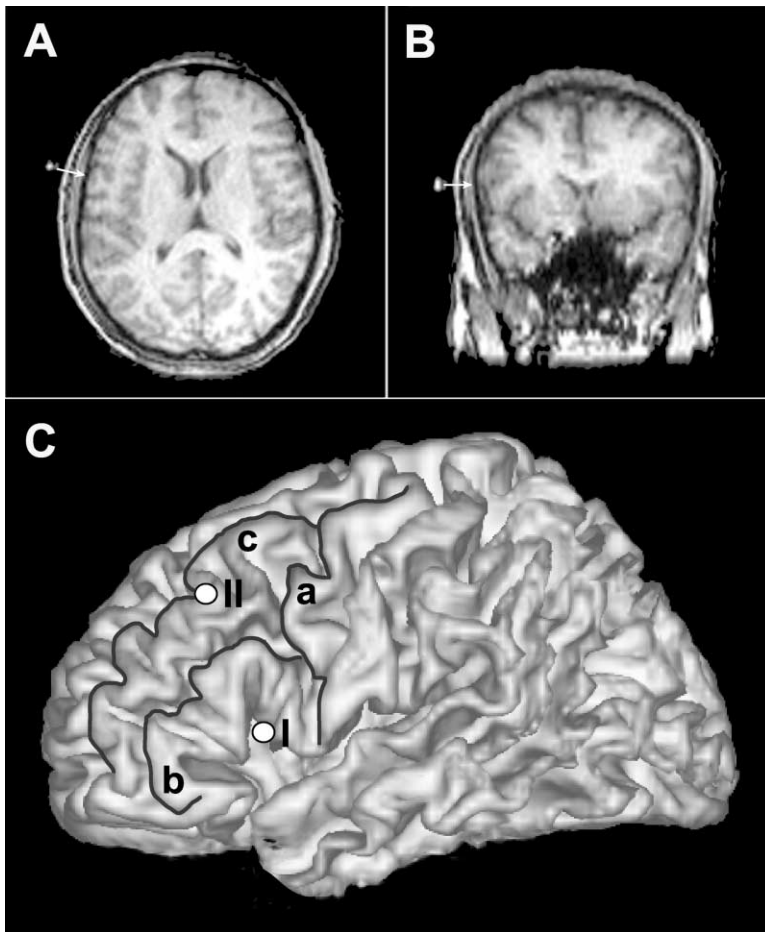[4]Correspondence: sakai@mind.c.u-tokyo.ac.jp

Figure 1. The Targeted Regions in the Left Prefrontal Cortex

Horizontal (A) and coronal (B) MR images indicating the position of the TMS coil for a representative subject. In each panel, the nearest MR marker to the center of the coil, which locates over the center of the left F3op/F3t, is shown (arrow for the stimulated site). The stimulation sites in the left F3op/F3t and in the left F2 are labeled as sites I and II, respectively, on the lateral surface image of the MNI standard brain (C). a, the precentral sulcus; b, the inferior frontal sulcus; c, the superior frontal sulcus.

across all individuals and conditions. We analyzed the correct and incorrect trials separately according to subjects' responses. Reaction times (RTs, measured from the presentation of a verb stimulus) in the correct trials of all conditions for TMS over the left F3op/F3t are shown in Table 1. According to an analysis of variance (ANOVA) with two variables (sentence type × task; subject as a random factor) on the Sham data for each time point, there was no main effect or interaction in any of three time points (p > 0.1 for all). Therefore, the two tasks without TMS were equated in terms of difficulty. To examine the TMS effects on each task, we pooled individual correct trials for each TMS condition and calculated ΔRTs (RT changes: Real − Sham) for each subject.

When TMS was delivered at T = 0, ΔRTs were not significantly different from ΔRT = 0 for either N or A sentences in the Syn task (p > 0.1, one group t test) and in the Sem task (p > 0.5) (Figure 3A). Therefore, TMS at T = 0 had no effect on either task. When TMS was delivered at T = 150, ΔRTs were significantly negative for both sentence types in the Syn task (N: t(5) = −3.4, p < 0.05; A: t(5) = −4.5, p < 0.01), whereas ΔRTs in the Sem task were not different from ΔRT = 0 (p > 0.1) (Figure 3B). Moreover, ΔRTs in Syn N and Syn A were negative (range: −45 to −2 ms) for all subjects, whereas those in Sem N and Sem A were distributed evenly around ΔRT = 0 (range: −42 to 32 ms). It should be noted that TMS induced differential effects on physically identical

"normal" sentences between the two tasks, which parallel those on anomalous sentences. These results clearly demonstrated that TMS at T = 150 over the left F3op/F3t selectively enhanced syntactic processing. In contrast, when TMS was delivered at T = 350, ΔRTs were not significantly different from ΔRT = 0 for either N or A sentences in the Syn task (p > 0.1) and in the Sem task (p > 0.5) (Figure 3C). We also confirmed that TMS at T = 450 did not result in significant changes of ΔRTs under any conditions (p > 0.1).

To establish the specificity of the effect in the left F3op/F3t, we obtained data on responses to TMS at another location in the left prefrontal cortex. We targeted a part of the left middle frontal gyrus (F2, MFG) as a control site, whose mean position was 39 mm away (see Experimental Procedures) from the region of the left F3op/F3t on the cortical surface (Figure 1C). When TMS was delivered at T = 150 over the left F2, which was a critical timing for syntactic processing in the left F3op/ F3t, ΔRTs were not significantly different from ΔRT = 0 for either N or A sentences in the Syn task (p > 0.1) and in the Sem task (p > 0.1) (Figure 4). RTs in the correct trials of all tested conditions for TMS over the left F2 are shown in Table 2. These results clarified that the left F3op/F3t, but not the left F2, is specialized in syntactic processing, demonstrating functional parcellation within the left prefrontal cortex. We further applied the same analyses to RTs for incorrect trials (excluding time-out
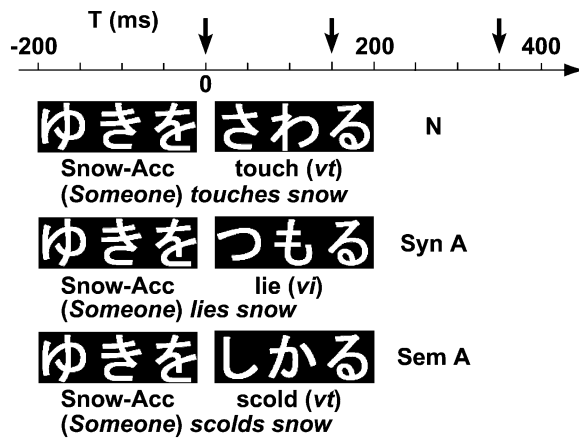
Figure 2. Language Tasks with a Minimal Pair Paradigm

Normal (N) sentences used in the two tasks were physically identical. In a syntactic decision (Syn) task, syntactically anomalous (Syn A) sentences were intermixed with normal sentences. In a semantic decision (Sem) task, semantically anomalous (Sem A) sentences were intermixed with normal sentences. Arrows on the time scale indicate three time points of TMS: T = 0, 150, and 350 ms from the presentation of a verb. Acc, accusative case particle; vt, transitive verb; vi, intransitive verb.

trials) and accuracy data, and we observed no significant ΔRT or Δaccuracy (accuracy changes: Real − Sham) under any conditions (p > 0.05).

Discussion

The results are striking in three ways: (1) event-related TMS pulses selectively reduced RTs in explicit syntactic decisions but not in explicit semantic decisions, which is an unexpected phenomenon for known TMS effects on cognitive processes, (2) this effect was observed during syntactic decisions regarding both normal and anomalous sentences, and (3) it was observed when magnetic stimulation was administered to the left F3op/F3t at a specific timing (150 ms from a verb stimulus), but not to the left F2. The present TMS study thus demonstrates the causal link between syntactic processing and activation of the left F3op/F3t, indicating how syntactic processing is specialized and instantiated in the brain.

Our results are consistent with previous functional imaging studies, which have implicated selective activation of the left F3op/F3t during syntactic processing in comparison with semantic processing (Dapretto and Bookheimer, 1999; Ni et al., 2000). Recent neuroimaging
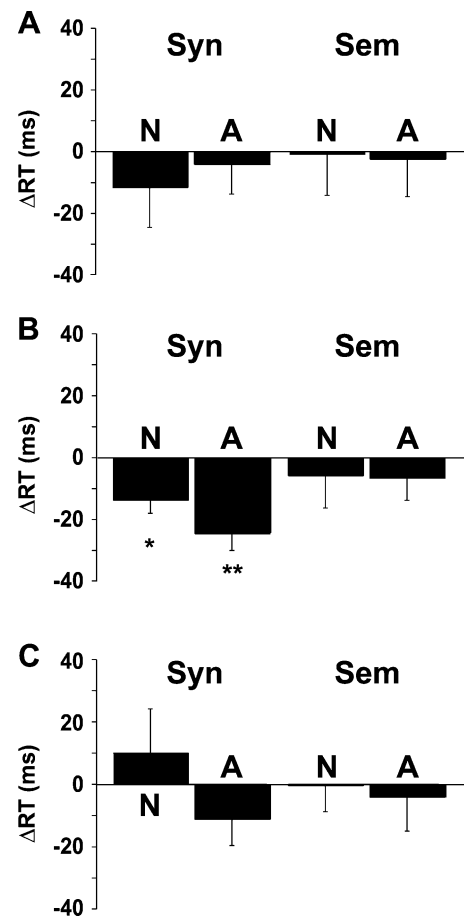

Figure 3. Selective Priming Effects of TMS on Syntactic Processing at the Left F3op/F3t

ΔRT (mean and standard error across subjects) indicates the change of RTs (Real − Sham) elicited by the TMS. Each bar denotes ΔRT for either normal (N) or anomalous (A) sentences. TMS was delivered at one of three time points: 0 ms (A), 150 ms (B), and 350 ms (C) from the presentation of a verb. *p < 0.05, **p < 0.01 (t test, n = 6).

studies have accumulated consistent evidence of the involvement of the left F3op/F3t in various cognitive tasks including syntactic processing (Stromswold et al., 1996; Just et al., 1996; Embick et al., 2000; Moro et al., 2001; Indefrey et al., 2001). In these studies, the knowledge of English, German, or Italian languages was tested in native speakers. The consistency among these studies and the present study using Japanese, a non-Indo-European language, suggests that syntactic specialization of the left F3op/F3t is universal among natural

Table 1. TMS Effects on RTs for Two Language Tasks at the Left F3op/F3t

Stimulus Type	Task	T = 0		T = 150		T = 350	
		Real	Sham	Real	Sham	Real	Sham
Normal (N)	Syn	600 ± 41	612 ± 32	601 ± 30	615 ± 29	626 ± 32	616 ± 25
	Sem	618 ± 38	619 ± 27	645 ± 33	651 ± 27	646 ± 27	647 ± 33
Anomalous (A)	Syn	639 ± 40	643 ± 32	640 ± 31	665 ± 31	664 ± 32	675 ± 39
	Sem	645 ± 45	647 ± 33	669 ± 37	676 ± 33	670 ± 30	674 ± 35

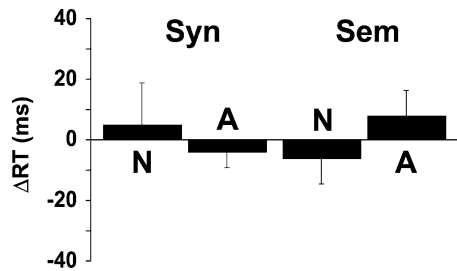Values are in ms, mean ± standard error across subjects (n = 6).

Figure 4. The Absence of TMS Effects on the Language Tasks at the Left F2

Each bar denotes ΔRT for either N or A sentences. TMS was delivered at 150 ms from the presentation of a verb.

languages. The present TMS results clearly established that activation of the left F3op/F3t underlies syntactic processing.

We found that the TMS effects on normal and anomalous sentences were similar in each task (Figure 3), which was in agreement with the left F3op/F3t activation observed in our event-related OT study (Noguchi et al., 2002). These results consistently indicate that common processes were involved both in judging a sentence to be normal and in judging it to be anomalous for each task. Therefore, explicit syntactic processing subsists not only in detecting syntactic anomalies per se, which has been tested in previous functional MRI studies, but in analyzing syntactic consistency in a sentence. This finding was achieved by utilizing event-related TMS, thereby differentiating trials with normal and anomalous sentences. Even if "normal" sentences are physically identical between the contrasting tasks, we demonstrated that TMS on normal sentences resulted in differential effects that paralleled the effects for anomalous sentences, depending on the types of explicit linguistic decisions.

The temporally restricted and syntax-selective reduction of RTs reported here suggests physiological effects of facilitation or priming, such that the stimulation of the left F3op/F3t at a specific timing enhances its normal function. Indeed, the mean reduction of RTs at T = 150 (N: 14 ms, A: 25 ms) was comparable to that of a previous behavioral study in which RTs for lexical decision were reduced when primed by a syntactically appropriate word (Goodman et al., 1981). In contrast, it has been reported that TMS applied to V5 enhanced performance at a wide time range (~250 ms), when its normal function of motion processing was *not* required in a detection task (Walsh et al., 1998). Thus the underlying mechanisms of this paradoxical facilitation may not be directly relevant to the present study. On the other hand, cortico-

cortical inhibition has been reported in the primary motor cortex when TMS is applied in pairs of a subthreshold conditioning pulse and a suprathreshold pulse with an interstimulus interval (ISI) of less than 5 ms (Kujirai et al., 1993). However, such an inhibitatory effect disappeared when the first pulse was set to the motor threshold (Trompetto et al., 1999), and the effect of subthreshold paired pulses has not been previously reported. It is possible that a focal TMS temporarily raises the overall excitability of neurons, which leads to more effective activation when specific responses of those cells are required for syntactic decisions.

While it has been reported that repetitive TMS (rTMS) (4–25 Hz, 1–10 s) over Broca's area induced speech arrest (Pascual-Leone et al., 1991; Epstein et al., 1996; Stewart et al., 2001), rTMS (20 Hz, 2 s) over Wernicke's area resulted in reduction of RTs in a picture-naming task (Mottaghy et al., 1999). A recent study reported that rTMS (1 Hz, 300 s) over the left F2, just anterior and superior to Broca's area, increased RTs for verb production in contrast to noun production (Shapiro et al., 2001). Because rTMS causes the spread of cortical excitation (Pascual-Leone et al., 1993), spatial resolution becomes lower than the maximum resolution of single-pulse or paired-pulse TMS (a few millimeters) (Walsh and Cowey, 2000). Moreover, because rTMS requires a longer time for stimulation than neural events, temporal resolution also becomes lower than the maximum resolution of single-pulse or paired-pulse TMS (~20 ms) (Pascual-Leone et al., 2000). The present study with event-related TMS, in which paired pulses were time-locked to every stimulus, took the full advantage of its spatio-temporal resolution, thereby narrowing the time window for the priming effects within ±150 ms. Because we observed no inhibitatory effects on any conditions, possible interferences of TMS with reading processes are excluded in the present study, in spite of the fact that rTMS causes speech arrest. Furthermore, it opens a new possibility for the use of TMS in neuroscience, not only for a blockade of sensory processes, but for a selective enhancement of higher cognitive processes with a restricted spatio-temporal window.

Experimental Procedures

Subjects
Six male native Japanese speakers (age: 22–49) participated in all the TMS experiments. All subjects showed right-handedness (laterality quotient: 81–100) by the Edinburgh inventory (Oldfield, 1971). During the experiments, their heads were held in place with a TMS coil and a chin rest. Informed consent was obtained from each subject after the nature and possible consequences of the studies were explained. All experiments strictly followed the safety guidelines of TMS experiments (Wassermann, 1998) and those adapted by Japan Neuroscience Society. Approval for these experiments was obtained from the institutional review boards of the University of Tokyo, Komaba.

Visual Stimuli
Sentence stimuli were visually presented to native Japanese speakers. For each trial, a noun phrase stimulus (a noun and a case particle) was presented against a dark background, which was followed by a verb stimulus (Figure 2). Each stimulus (visual angle: 3° × 9°) was presented for 200 ms and was always three letters (three syllables or moras) in hiragana to ensure constant reading time. All presented words were frequently used and commonly writ-

Table 2. TMS Effects on RTs at the Left F2 (T = 150)			
Stimulus Type	Task	Real	Sham
Normal (N)	Syn	639 ± 32	634 ± 21
	Sem	667 ± 37	673 ± 34
Anomalous (A)	Syn	668 ± 26	672 ± 23
	Sem	713 ± 44	704 ± 37

Values are in ms, mean ± standard error across subjects (n = 6).

ten in hiragana alone. The intertrial interval was 6 s, and subjects were asked to fixate on a central cross and to respond by pressing one of two buttons as quickly as possible while ensuring correct responses.

Tasks
Before the experiments, we explicitly explained the nature of the two tasks to the subjects, providing examples of Syn A, Sem A, and Syn N/Sem N with the following instruction (Figure 2): "The sentence 'yuki-wo tsumoru' (snow-Acc lie; Acc, the accusative case particle) is anomalous because of the syntactic violation between a verb and a noun phrase. Because 'yuki' (snow) and 'tsumoru' (lie) are semantically associated, as 'yuki-ga tsumoru' (Snow lies [on the ground]) is acceptable, it is not a semantic but a syntactic error. In contrast, the sentence 'yuki-wo shikaru' (snow-Acc scold) is anomalous because of the semantic mismatch between 'yuki' (snow) and 'shikaru' (scold). Because this sentence is syntactically correct as to the relationship between a verb and a noun phrase, this is not a syntactic but a semantic error. Finally, the sentence 'yuki-wo sawaru' (snow-Acc touch) is normal because it is both syntactically and semantically correct."

The Syn and Sem tasks were performed in separate sessions, each of which contained 60 consecutive trials with randomized N or A sentences. Before each session, the subjects were explicitly informed about which task they should have performed. In the Syn task, we instructed: "Press the green button if the presented sentence is syntactically correct; press the red button if it is syntactically incorrect." In the Sem task, we instructed: "Press the green button if the presented sentence is semantically correct; press the red button if it is semantically incorrect." Other details of the tasks were described in our previous paper (Noguchi et al., 2002). For each session, TMS was delivered at one of three time points: $T = 0$, 150, and 350 ms from the presentation of a verb (Figure 2). Six sessions were tested in a 1 day experiment, and they were repeated ten times for each subject. The order of the session sequences was completely counterbalanced within and across subjects.

Magnetic Stimulation
Before the experiments, a 3D magnetic resonance (MR) image of the brain was taken of each subject, who wore a cap with multiple MR markers (alfacalcidol beads; diameter: 3 mm) on its surface. Using the MR image, the vertically projected position of the center of the left F3op/F3t (close to the vertical ramus of the sylvian fissure) on the scalp surface (site I) was estimated relative to these markers (Figures 1A and 1B). This position was then transferred to the distances from the lateral canthus and from the acoustic meatus, and it was marked on a headband around the subject's head. TMS was delivered through a focal 8-shaped coil (dual 70 mm coil), which was placed tangentially on the scalp with the coil's center fixated on the marked position. The control site (site II) of the left F2 was 40 mm anterior (parallel to the canthus-meatus line) and 40 mm dorsal (perpendicular to the canthus-meatus line) to site I on the scalp surface. The distance (mean $\pm$ SD across subjects) between the two sites (I and II) was 39 ± 4.9 mm on the cortical surface. With SPM99 software (Wellcome Department of Cognitive Neurology, London, UK), each individual brain was spatially normalized to the standard brain space as defined by the Montreal Neurological Institute (MNI) (Figure 1C). Stereotactic coordinates (x, y, z; mean $\pm$ SD across subjects) of the sites I and II were (-63 ± 1.1, 11 ± 5.7, 15 ± 4.4) and (-42 ± 4.0, 25 ± 4.5, 48 ± 3.5), which corresponded to BA 44 and BA 8/9, respectively. These SDs reflected the overall spatial errors of the current method.

In order to increase the power of TMS, we used paired pulses (equal intensity; ISI, 2 ms) by combining two Magstim 200 stimulators with a bistimulation module (Magstim, Carmarthenshire, UK). TMS intensity of paired pulses was set at 33%–50% (mean: 42% across subjects) of the maximum output of each stimulator. This intensity corresponded to 55%–98% (mean: 75%) of the tonically active motor threshold (10% maximal voluntary contraction) for paired pulses, which was measured from electromyographic responses in the contralateral first dorsal interosseous muscle (Terao et al., 1998). The same TMS intensity was used at both sites I and II for each subject. Under the Sham condition, the recorded discharge

click without concomitant TMS was presented at the same volume and timing as each Real condition, while maintaining tangential coil placement. Sixty consecutive trials in each session were divided into four epochs, each of which contained either Real or Sham trials, and their order was either R-S-S-R or S-R-R-S (R: Real, S: Sham). Both RTs and accuracy were recorded online, while the visual stimulus presentation and TMS application (or discharge click) with a particular delay were controlled using LabVIEW software and interface (National Instruments, Austin, TX).

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