



Global perception depends on coherent work of bilateral visual cortices: Transcranial magnetic stimulation (TMS) studies

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Previous research suggests that the right and left hemispheres dominate global and local perception of hierarchical patterns, respectively. The current work examined whether global perception of hierarchical stimuli requires coherent work of bilateral visual cortices using transcranial magnetic stimulation (TMS). Subjects discriminated global or local properties of compound letters in Experiment 1. Reaction times were recorded when single-pulse real TMS or sham TMS was delivered over the left or right visual cortex. While a global precedence effect (i.e., faster responses to global than local targets and stronger global-to-local interference than the reverse) was observed, TMS decreased global-to-local interference whereas increased local-to-global interference. Experiment 2 ruled out the possibility that the effects observed in Experiment 1 resulted from perceptual learning. Experiment 3 used compound shapes and observed TMS effect similar to that in Experiment 1. Moreover, TMS also slowed global RTs whereas speeded up local RTs in Experiment 3. Finally, the TMS effects observed in Experiments 1 and 3 did not differ between the conditions when TMS was applied over the left and right hemispheres. The results support a coherence hypothesis that global perception of compound stimuli depends upon the coherent work of bilateral visual cortices.

Global perception of complex visual scenes is one of the central topics of the research of visual perception. A classic approach to the relationship between global and local perception was to measure behavioral responses to global or local levels of hierarchically organized patterns. Navon^[1] had subjects responding to compound stimuli, i.e., global letters made up of local ones as illustrated in Figure 1(a), and found that reaction times (RTs) were faster to global than local targets (global RT advantage) and local RTs were slowed by incongruent global letters (global-to-local interference) but not . Navon's findings support a global precedence hypothesis proposing that global information is coded first whereas local information is analyzed at a later stage of visual perception.

Brain lesion studies found that the left temporal-

parietal damage impairs memory of local shapes or delays responses to local shapes whereas the right hemisphere lesions in the corresponding areas result in deficits in memory of global shapes or delay of global response



Figure 1 Illustration of compound stimuli and TMS sites. (a) Compound letters used in Experiments 1 and 2. Global and local letters are consistent (top row) or inconsistent (bottom row). (b) Compound shapes used in Experiment 3. Global and local arrows are consistent (top row) or inconsistent (bottom row). (c) Locations of occipital single-pulse TMS. The horizontal cross section at the bottom shows left and right (O1 and O2) stimulation sites. The sagittal section in the top shows the location of the right hemisphere O2. Magnetic stimulation sites are indicated by white arrows.

inferior occipital cortex^[7,8]. While these studies emphasized the role of the right hemisphere in global perception, a fact about global processing has been ignored, i.e., half of a compound stimulus presented at the fixation is projected to the left hemisphere while the other half to the right hemisphere. The global perception requires integration of information in both the left and right visual cortices. In contrast, this may not be necessary for local perception because each hemisphere receives at least one local letter and thus obtains enough information about the local level. This coherence hypothesis, which emphasizes the coherent work of the two hemispheres in global perception, is different from the lateralization hypothesis that stresses the dominance of the right hemisphere in global perception. Previous neuroimaging studies show only stronger activation in the right occipital cortex when attending to global than local shapes^[7,8], but tell little about the integration of processing in the two hemispheres.

The current work tested the coherence hypotheses using transcranial magnetic stimulation (TMS). The magnetic field produced by TMS pulses induces random neural activity and interferes with cortical information processing temporarily^[9]. We stimulated the right visual cortex that showed activations in association with global processing in neuroimaging studies^[8,10] and the corresponding area in the left hemisphere. According to the

lateralization hypothesis, TMS over the right hemisphere should disrupt global processing whereas TMS over the left hemisphere should not, or at least right hemisphere TMS should produce larger effect on global processing than left hemisphere TMS. We then would expect either the global RT advantage was reduced or the global-to-local interference was weakened by TMS over the right visual cortex. Moreover, TMS over the left hemisphere should disrupt local processing. Nevertheless, according to the coherence hypothesis, stimulation of the visual cortex in each of the two hemispheres should impair global perception because it disrupts the coherence of the processing in bilateral striate and extrastriate cortices. In addition, as TMS over the left or right hemisphere would disrupt the coherent work of bilateral visual cortices, we would expect that the TMS effect on global perception should not differ between left and right TMS. Finally, stimulation of the visual cortex in one hemisphere should not disrupt local processing since local perception does not require coherent processing of the two hemispheres.

We recorded behavioral responses to the global or local levels of compound stimuli (Figure 1(a)) in Experiment 1, while single-pulse real TMS or sham TMS was applied over the left and right occipital areas. Previous event related potential (ERP) studies have shown that a positive wave (P1), which has larger amplitudes over the

lateral occipital cortex and peaks at about 100 ms after sensory stimulation, is modulated by selective attention to the global or local aspects of compound stimuli^[11–14], suggesting that global and local processing begins to differentiate at about 100 ms. Therefore, in the current study, we delivered TMS over the left and right visual cortices (Figure 1(c)) 90 ms after a compound stimulus was presented in order to produce disruptions of the processing in the visual cortex that differentiate global/local perception. Because real TMS was always applied after the sham TMS in Experiment 1, it was possible that the difference in behavioral performance between the real and sham TMS conditions might result from the effect of perceptual learning. Experiment 2 was designed to rule out this possibility. All aspects of Experiment 2 were the same as those in Experiment 1 except that no real or sham TMS was applied. Data in the early and late sessions, which corresponded to the sham and real TMS sessions in Experiment 1, were compared to examine the effect of perceptual learning.

Experiment 3 further validated the coherence hypothesis using compound shapes (Figure 1(b))^[15,16]. Subjects were asked to identify the orientations of global or local arrows. If the coherence hypothesis is correct, TMS effects on global processing should occur regardless of whether compound letters or shapes are used. In addition, as previous studies shows responses of cells in the striate and extrastriate cortex are sensitive to orientations^[17], TMS pulses delivered over these areas may produce strong effects on discrimination of orientations of large or small arrows.

1 Methods

1.1 Subjects

Three independent groups of subjects participated in this study as paid volunteers. Ten normal healthy adults (6 men, 4 women; aged between 19 and 23 years) participated in Experiment 1. Ten normal healthy adults (8 men, 2 women; aged between 19 and 22 years) participated in Experiment 2. Eleven normal healthy adults (7 men, 4 women; aged between 19 and 26 years) participated in Experiment 3. All were right-handed, had normal or corrected-to-normal vision and no history of neurological disorders. All the subjects gave informed consent. The experimental procedures were approved by the local ethical committee.

1.2 Stimuli and procedures

1.2.1 Experiment 1

(1) Stimuli. The stimuli, which were black on a grey background, were presented on a monitor placed 57 cm from subject eyes. Each stimulus consisted of a global letter made up of local letters in 7×7 matrix (Figure 1(a)). In half of the trials the global and local letters were congruent (the top row in Figure 1(a)) whereas in the other half the global and local letters were incongruent (the bottom row in Figure 1(a)). The global and local letters subtended an angle of $6.1^\circ \times 4.2^\circ$ and $0.67^\circ \times 0.44^\circ$ (high and wide), respectively. Each trial began with the presentation of a fixation cross subtending $0.3^\circ \times 0.2^\circ$ of visual angle. The stimulus displays were presented at the location of fixation for a duration of 100 ms. The intervals between the onset of compound stimuli in two successive trials were randomized between 4000 and 4200 ms. Subjects were asked to identify the global and local letters in separate blocks of trials by pressing one of the two keys on a standard keyboard.

(2) TMS protocol. A standard rapid stimulator (MagStim, Whitland, UK) with a 70-mm figure-eight coil was used. The computer used to present visual stimuli was connected with the stimulator to trigger single-pulse TMS that was time-locked to stimulus onset. A 90-ms interval between stimulus onset and TMS was used. The output strength of the TMS was the same as the motor threshold (between 53% and 74% of the maximum output), defined as the minimum intensity of stimulation capable of inducing visible twitch of the left thumb. TMS was performed on two different sites on the scalp over the right and left occipital areas at O1 and O2 locations (according to 10/20 EEG system). Previous studies showed MRI evidence that these positions are situated in a region overlying the striate and extrastriate cortex (BA 17 and 18)^[18]. The TMS sites were further localized in three subjects by MRI using vitamin E capsules as markers of stimulated skull positions (Figure 1(c)). The mean coordinates of the TMS sites in Talairach space^[19] were $x = 16, y = -92, z = 4$.

Each of the subjects was tested in two sessions, each on a different day: 1) TMS over the left hemisphere; 2) TMS over the right hemisphere. To obtain a baseline to contrast the real TMS effect and control for the characteristic sound of real TMS, in each session we first recorded subject's responses in the global and local tasks when sham TMS was applied to the scalp positions by

positioning the coil perpendicularly to the scalp. Subsequently, real TMS was delivered while responses were recorded. Subjects were seated comfortably on a chair with their heads fixed using a chinrest. In each session, after 32 practice trials, there were two blocks of 24 trials with sham TMS for the identification of the global or local letters, respectively. Then subjects were given two blocks of 24 trials with real TMS for the identification of the global or local letters, respectively. Subjects were encouraged to respond as quickly and accurately as possible. The order of left/right TMS sessions and global/local tasks was counterbalanced across subjects.

(3) Data analysis. RTs and error rates were subjected to a repeated measure analysis of variance (ANOVA) with TMS (sham or real TMS), Globality (discriminating the global or local letters), Consistency (global and local letters are congruent or incongruent), and Hemisphere (TMS over the left or the right visual cortex) as independent variables.

1.2.2 Experiment 2

Stimuli, TMS protocol, and data analysis. All aspects of Experiment 2 were the same as those in Experiment 1 except the following. No real or sham TMS was applied in Experiment 2. RTs and error rates were subjected to ANOVAs with Practice (early or late sessions (corresponding to the sham or real TMS condition in Experiment 1)), Globality (discriminating the global or local letters), and Consistency (global and local letters are congruent or incongruent) as independent variables.

1.2.3 Experiment 3

Stimuli, TMS protocol, and data analysis. These were the same as those in Experiment 1 except that compound shapes were used in Experiment 3, as shown in Figure 1(b). Each stimulus consisted of a global arrow made up of local arrows pointing down left or down right. The directions of local arrows were either congruent or incongruent with that of the global one. The local arrows or triangles were arranged in an 8×8 matrix. The global and local figures subtended a visual angle of $6.4^\circ \times 6.4^\circ$ and $0.69^\circ \times 0.69^\circ$, respectively. Subjects were asked to identify orientations of the large or small arrows in separate blocks of trials while sham or real TMS was applied.

2 Results

2.1 Experiment 1

The mean percentage of errors was 3.7% and 5.4% for

global and local tasks, respectively. ANOVAs revealed only a significant main effect of Consistency ($F(1,9) = 10.3, p < 0.01$), error rates were lower when global and local letters were congruent than incongruent (3.0% vs. 6.1%). Comparisons between the error rates and the mean RTs indicated that there was no speed-accuracy trade-off, therefore the error data will not be discussed further.

Figure 2 shows average RTs for correct responses in the sham and real TMS conditions. There were significant differences between the sham and real TMS conditions ($F(1,9) = 10.24, p < 0.01$).

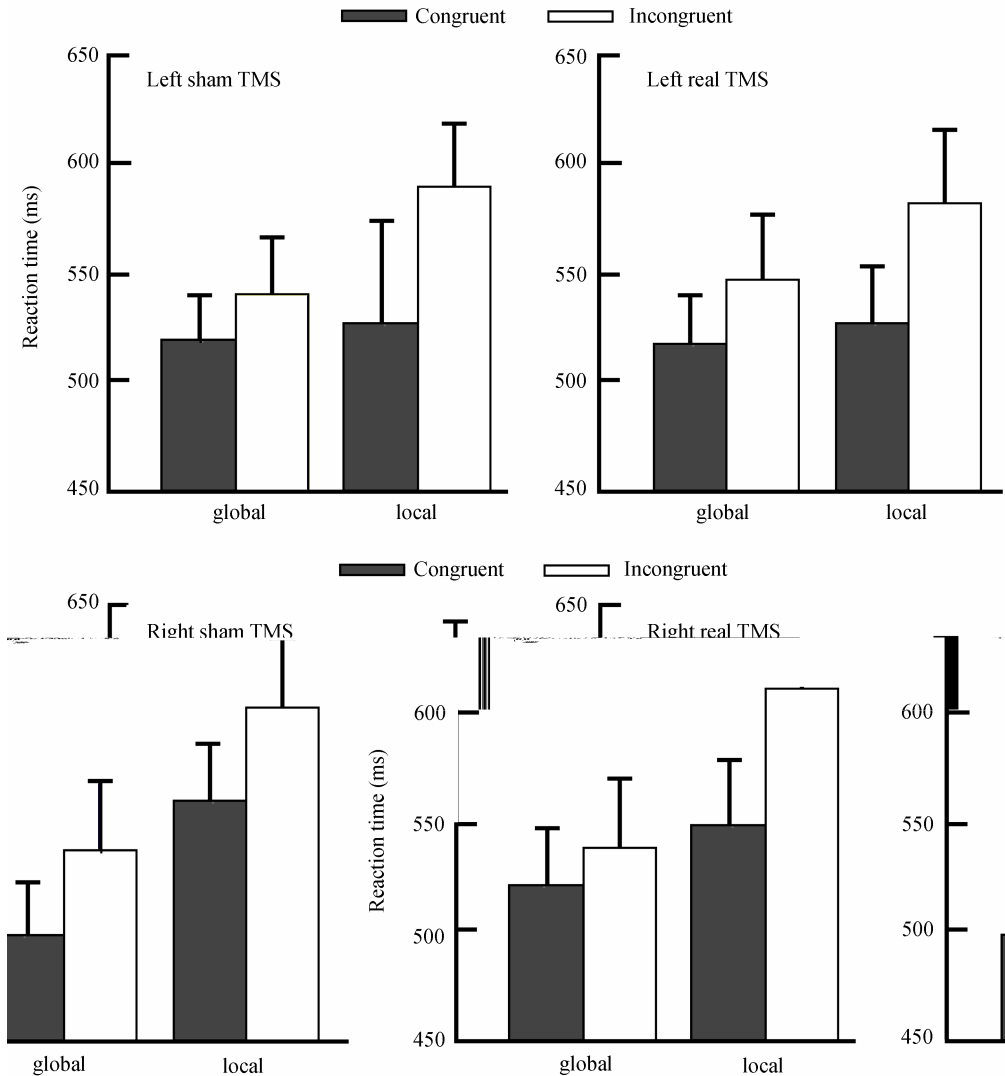


Figure 2 Mean RTs in the sham and real TMS conditions in Experiment 1. Data in the left and right hemisphere TMS conditions were averaged together since ANOVAs did not show difference between the two conditions. Error bars represent standard errors.

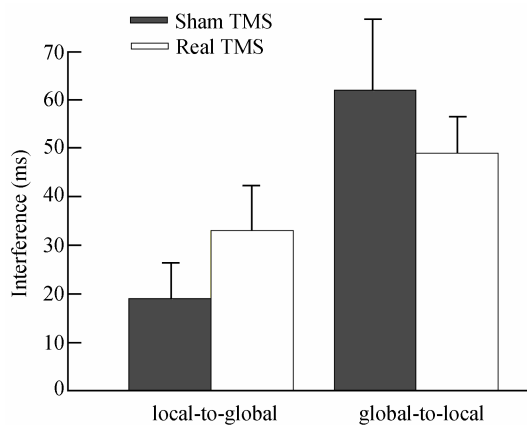


Figure 3 Interference effect (RTs in the incongruent condition minus RTs in the congruent condition) in the sham and real TMS conditions in Experiment 1.

in the congruent condition were faster than those in the incongruent condition. There was only a significant interaction of Practice \times Consistency ($(1,9) = 6.37, < 0.03$), suggesting that the interference effect was slightly smaller in the late than early sessions. However, the practice effect did not differ between global and local responses (> 0.1).

2.3 Experiment 3

The mean percentage of errors was 2.4% and 2.7% for global and local tasks, respectively. ANOVAs revealed only a significant main effect of Consistency ($(1,10) = 5.32, < 0.04$), error rates were lower when global and

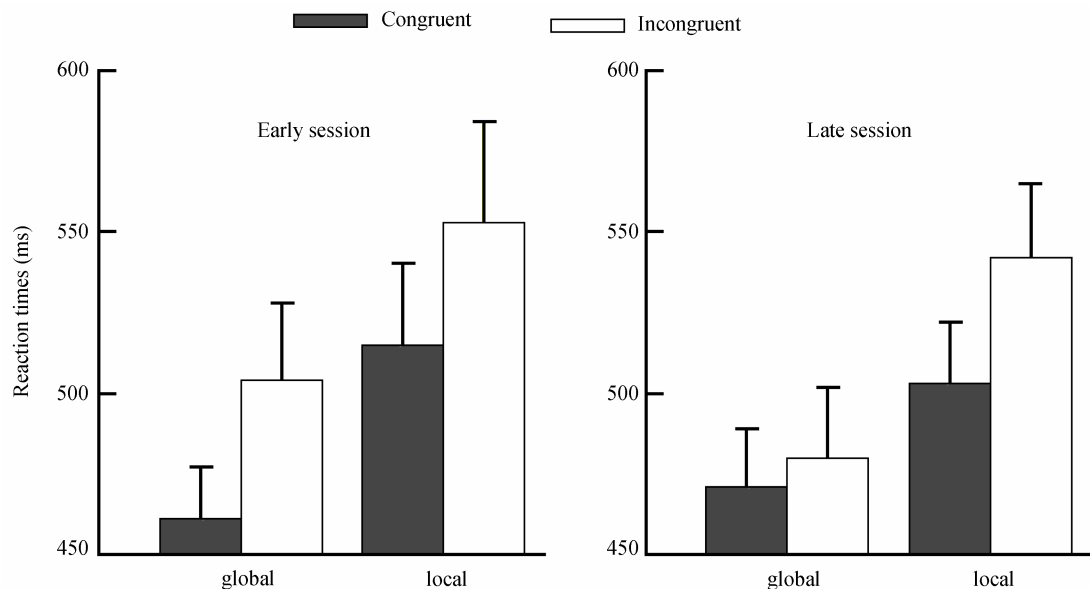


Figure 4 Mean RTs in the early and late sessions in Experiment 2. Error bars represent standard errors.

Figure 5 shows average RTs for correct responses in the sham and real TMS conditions. There were significant main effects of Globality ($F(1,10)=45.0, <0.001$) and Consistency ($F(1,9)=93.6, <0.001$). Subjects responded faster to the global than local shapes. RTs in the congruent condition were faster than those in the incongruent condition. There was also a significant interaction of Globality \times Consistency ($F(1,10)=14.9, <0.01$), due to the larger interference effect on local than on global responses. Interestingly, TMS slowed global responses but speeded up local responses, resulting in the two-way interaction of TMS \times Globality ($F(1,10)=6.32, <0.03$). In addition, there was a reliable triple interaction of TMS \times Globality \times Consistency ($F(1,10)=6.74, <0.03$), reflecting the fact that, relative to the sham condition, real TMS reduced global-to-local interference but increased local-to-global interference. Figure 6 illustrates the differential TMS effect on global and local processing by showing the interference in each stimulus conditions. Finally, neither the main effect of Hemisphere nor its interaction with other factors was significant (>0.2). Particularly, neither the interaction of TMS \times Globality \times Hemisphere (>0.09) nor the interaction of TMS \times Globality \times Consistency \times Hemisphere was significant (<1), suggesting that the effect of TMS on the global RT advantage and the interference between global and local processing did not differ between the left and right TMS conditions.

3 Discussion

The current work used TMS to study the effect of temporal disruption of neural activities in the visual cortex on responses to the global or local aspects of compound stimuli. In Experiment 1 subjects identified global or local levels of compound letters. RTs showed both global RT advantage and larger global-to-local interference than the reverse. Thus we observed a global precedence effect, similar to the previous work^[1,20]. Interestingly, we found that, relative to the sham TMS condition, single-pulse TMS delivered over the striate and extrastriate cortex decreased global-to-local interference whereas increased local-to-global interference. Experiment 2 showed further that the order of the tasks (i.e., early or late sessions) did not influence global-to-local and local-to-global interference differentially. These results ruled out the possibility that the TMS effect on global and local processing observed in Experiment 1 simply originated from perceptual learning. Experiment 3 further confirmed the TMS effect on global and local processing using compound shapes. TMS decreased global-to-local interference and increased local-to-global interference. In addition, TMS delayed global RTs but speeded up local RTs. More importantly, both Experiments 1 and 3 showed that the TMS effect did not differ when the left and right hemispheres were stimulated.

The fact that functional disruption of the neural activities in the striate and extrastriate cortex produced by

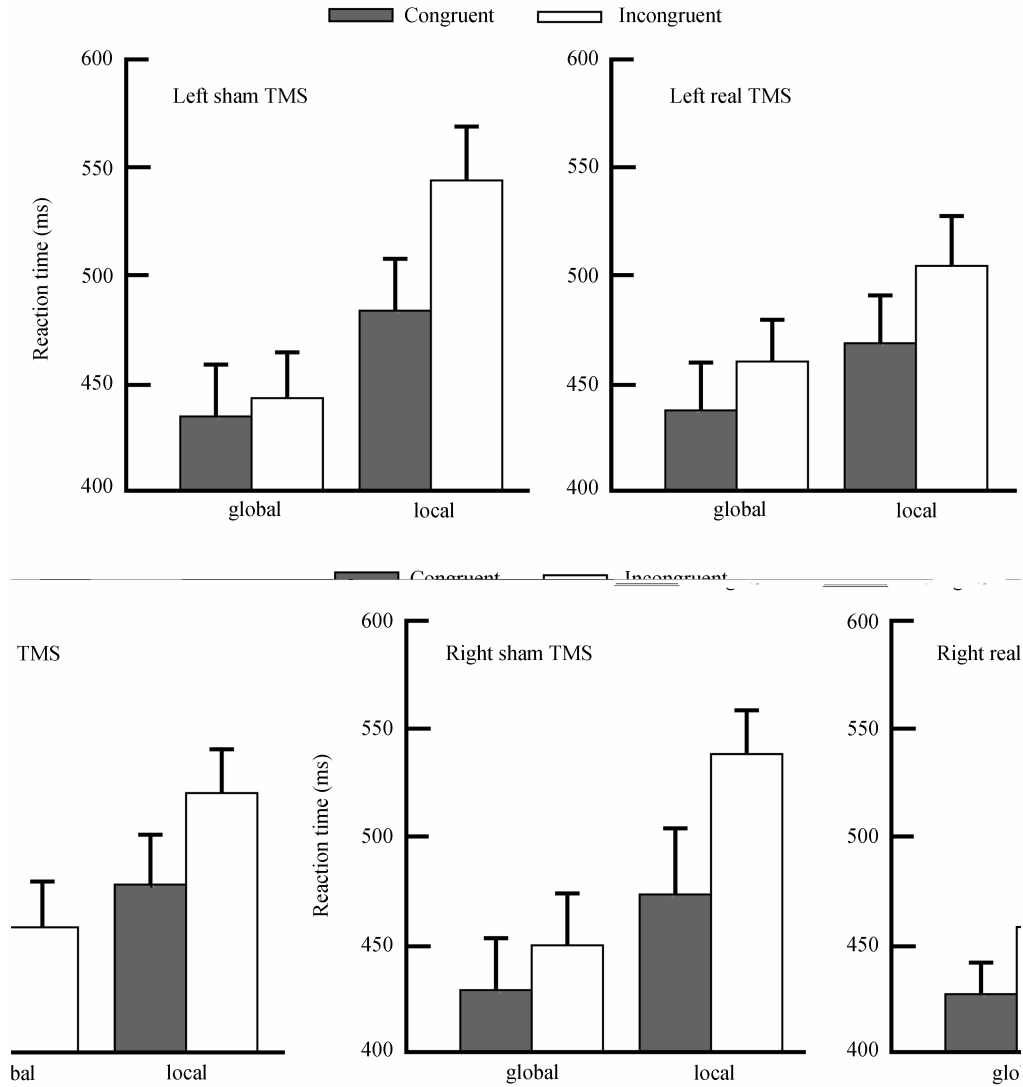


Figure 5 Mean RTs in the sham and real TMS conditions in Experiment 3. Data in the left and right hemisphere TMS conditions were averaged together since ANOVAs did not show difference between the two conditions. Error bars represent standard errors.

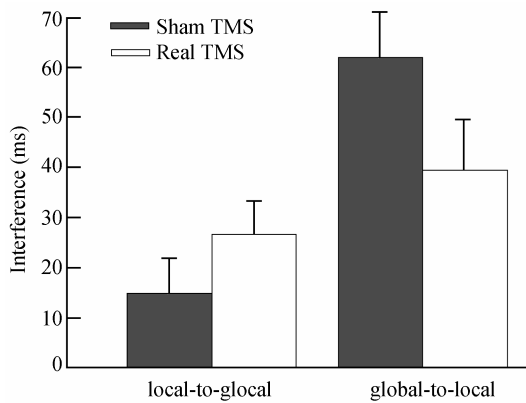


Figure 6 Interference effect (RTs in the incongruent condition minus RTs in the congruent condition) in the sham and real TMS conditions in Experiment 3.

single-pulse TMS weakened global perception (i.e., reducing global-to-local interference and slowing global RTs) first demonstrates that the visual cortex plays an important role in the perception of global structures of compound stimuli, consistent with neuroimaging studies^[7,8,10]. In addition, TMS facilitated local processing (i.e., increasing local-to-global interference and speeding up local responses) rather than disrupted it. If the TMS effects reflect general impairment of low-level sensory processing (such as changes in threshold sensitivity) or high-level cognition (such as identification and recognition) resulting from disruption of activities in the visual cortex, one would expect negative TMS effect on both global and local processing because both have to

undergo such low-level sensory and high-level cognitive processes before behavioral responses are made. The contrast between the TMS effects on global and local processing suggests that perceptual processes that are specific for global perception are impaired (e.g., perceptual grouping, see discussion below).

Most importantly, our finding that the TMS effect on global perception did not differ between left and right hemisphere stimulations is not in agreement with the lateralization hypothesis, which assumes that global perception is mainly mediated by the right hemisphere^[6]. Even considering possible transcallosal homotopic connections, which may lead to occipital activations contralateral to the TMS stimulation sites with about 30 ms delay^[21], one would still expect larger TMS effect on global perception when stimulating the right than left occipital areas according to the lateralization hypothesis. However, our results showed that this is not true. Our results fit well with a coherence hypothesis that postulates that global perception of a compound stimulus presented at fixation depends upon that the left and right visual cortices work simultaneously and coherently to integrate information processed in each hemisphere. Functional disruption of each hemisphere impairs the coherence of bilateral visual cortices and thus generates negative effect on global perception.

A few previous studies concerned the role of interactions between the two hemispheres in the interference effect. For example, patient studies found that unilateral damage to the temporal-parietal junction in either hemisphere eliminates global-to-local interference regardless of locations where compound stimuli are presented^[3,4]. In addition, responses to compound stimuli from split-brain patients whose cortical commissures were severed showed global RT advantage but not interference between global and local processing^[22], suggesting that normal interference between global and local processing requires communication over callosal connections between globally and locally biased mechanisms associated with right or left temporal-parietal areas, respectively.

However, studies of normal subjects suggest that interhemispheric interactions reduce interstimulus interference^[23]. The researchers have subjects decided at a prespecified level if a lateralized compound shape presented below fixation is identical to either of two lateralized probe compound stimuli presented above fixation. RTs are slower when the shapes at the irrelevant level of

probe stimuli are incongruent than congruent with the shapes at the relevant level. This interference is smaller when items matched at the relevant level are projected to different hemifields than to the same hemifield, suggesting that the role of interhemispheric communication is not increasing but decreasing the interference between global and local processing.

Regardless of the contradiction between these studies, none of them can account for the results of the current work. The analyses based on patient studies^[3,4,22] or normal subjects^[23] predict that disruption of the interhemispheric interaction either increases or decreases the interference between global and local processing. We showed here, however, that functional disruption of the left or right visual cortex produced opposite effect on global-to-local and local-to-global interference.

The contrast between the TMS effects on global and local processing can be interpreted in a framework proposed in our previous studies^[15,16,24]. According to this framework, two important aspects of hierarchical analysis are perceptual grouping of local elements and selection of individual local elements. The former is critical for global perception whereas the latter for local perception. The bias towards grouping local elements into a unitary whole parallels and competes with a bias for the selection of individual local elements in determining which, the global or the local level of compound stimuli, dominates hierarchical processing. It is likely that the TMS applied to the left or right visual cortex in the present study disrupted local element grouping by weakening the coherence of bilateral visual cortices. This may in turn weaken global processing in its competition with local element segmentation and selection. Consequently, local processing is facilitated under the circumstance of weak global processing. Decreased global-to-local interference and increased local-to-global interference reflect the parallel and competitive processes in hierarchical analysis.

How can the results of previous neuroimaging studies be reconciled with the current work? Stronger activation in the right extrastriate cortex in the global than local conditions observed in previous research^[7,8] does not necessarily mean that the global perception is fully accomplished in the right hemisphere. It only implies dominance of the right and left hemispheres in global than local processing, respectively. Our results did not indicate the absence of hemispheric asymmetry in global/local processing. Instead, the results recommend

the importance of coherent work of bilateral visual cortices in global perception. Besides the right hemispheric dominance in global perception, the coherent work of the left and right hemispheres may also contribute to global processing.

The coherence hypothesis also provides an alternative account for the findings of lesion studies^[3,4,22]. It is possible that the mechanisms in the left and right temporal-parietal areas contribute to high-level cognitive processes such as identification and recognition that is specialized for local and global perception, respectively. However, damages in each hemisphere or commissurotomy disrupt the communication between corresponding areas in the two hemispheres and thus engender failure of integration of information from the two hemispheres, which, according to the coherence hypothesis, is important for global perception. Therefore the results of pa-

tient studies may at least partially reflect the effect of disruption of the coherent work between the two hemispheres.

In conclusion, we found that functional disruption of the left or right visual cortex induced by TMS impaired global perception (i.e., decreasing global-to-local interference and slowed global responses) but facilitated local perception (i.e., increased local-to-global interference and speeded up local responses). The results support a coherence hypothesis emphasizing that the coherent work of bilateral visual cortices is critical for the processing of the global structure of compound stimuli. The opposite TMS effects on global and local processing are consistent with a parallel and competitive model of hierarchical analysis, which proposes that perceptual grouping and local selection interact with each other and contribute to global and local perception, respectively^[15,16,24].

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