Magnetic Stimulation of the Left Visual Cortex Impairs Expert Word Recognition

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Abstract

■ One of the hallmarks of expert reading is the ability to identify arrays of several letters quickly and in parallel. Such length-independent reading has only been found for word stimuli appearing in the right visual hemifield (RVF). With left hemifield presentation (LVF), response times increase as a function of word length. Here we investigated the comparative efficiency with which the two hemispheres are able to recognize visually presented words, as measured by word length effects. Repetitive transcranial magnetic stimulation (rTMS) of the left occipital cortex disrupted expert processing of the RVF such that a length effect was created (Experiment 1). Right occipital rTMS, on the other hand, had no such effect on RVF words and nor did it modulate the length effect already present in the LVF. Experiment 2 explored the time course of these TMS-induced effects by applying single pulses of TMS at various stimulus-onset asynchronies for the same task. We replicated the TMS-induced length effect for RVF words, but only when a single pulse was applied to the left visual cortex 80 msec after target presentation. This is the first demonstration of TMS-induced impairment producing a word length effect, and as such confirms the specialization of the left hemisphere in word recognition. It is likely that anatomical differences in the pathway linking retinal input to higher level cortical processing drive this effect. ■

INTRODUCTION

The left cerebral hemisphere (LH) appears to be critically involved in visual word recognition. The question of LH dominance for language is central to understanding why linguistic ability appears to be unique to humans. Until now, however, the degree to which the LH and right hemisphere (RH) contribute to visual word recognition has never been systematically compared. We therefore sought to examine the extent of the LH advantage by assessing the efficiency of visual word recognition when the visual functioning of the LH and RH was suppressed by transcranial magnetic stimulation (TMS) of the occipital regions.

Word Length and Visual Field Interaction

One of the hallmarks of expert reading is the ability to identify arrays of several letters quickly and in parallel (Cohen et al., 2004; Dehaene et al., 2001; Nazir, 2000). This is demonstrated experimentally by similarly quick response times (RTs) to identify words ranging from three to seven letters (Lavidor, Ellis, Shillcock, & Bland, 2001) and is known as *length-independent reading*. Interestingly, length-independent reading has only been found for word stimuli appearing in the right visual hemifield (RVF; Bub & Lewine, 1988; Ellis, Young, & Anderson, 1988; Young & Ellis, 1985). With left hemifield presentation (LVF), RTs increase as a function of length. One explanation of the RVF advantage is that the LH is highly specialized in processing language-related information (Gazzaniga, 2000). Thus, because the human visual system is contralateral in nature, word stimuli in the RVF may profit from direct projection to the language-dominant hemisphere. By contrast, stimuli in the LVF must follow a longer and therefore noisier pathway before reaching the specialist areas via callosal transfer (Ellis, 2004; Brysbaert, 1994; Young & Ellis, 1985). Alternatively, cultural factors such as attentional biasing to the right side of space during reading (Kinsbourne, 1970), reading habits, and linguistic factors might also contribute to visual field differences (Nazir, Ben-Boutayab, Decoppet, Deutsch, & Frost, 2004; Deutsch & Rayner, 1999).

Although there is a wealth of behavioral data showing the RVF advantage in lexical processing (Gazzaniga, 2000), the neural correlates of these processes have largely been ignored. In one of the few current studies examining this issue, Cohen et al. (2002) identified a left extrastriate region which was only responsive to stimulation occurring in the contralateral hemifield. Moreover, this site was activated considerably more by words than by checkerboard stimuli, which contrasted with RH extrastriate areas, for which no such difference was observed. The researchers suggested that perhaps the extrastriate region of the LH has developed greater sensitivity to written words than its right hemispheric counterpart due to the

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bias normal readers have in fixating words to the left of their geometrical center (O'Regan, 1981). A different study based on positron emission tomography (PET) scans highlighted the involvement of the primary visual cortex in the word length effect. Whiting et al. (2003) showed that word length effects (as measured in RTs) were associated only with posterior activation (BA 17), but not with brain areas more traditionally associated with language processing. As far as we are aware, this is the only study which has directly explored the neural correlates of the word length effect.

The current study aims to test whether the RVF advantage in reading words is due to structural or other factors, using repetitive transcranial magnetic stimulation (rTMS) of the occipital areas of each hemisphere.

TMS and Visual Word Recognition

The LH appears to be critically involved in visual word recognition. Until now, however, the degree to which the LH and RH contribute to visual word recognition has never been systematically compared. We therefore sought to examine the extent of the LH advantage by assessing the efficiency of the two hemispheres in recognizing words when visual functioning was suppressed with TMS of the left and right occipital areas. The basis for this study has its precedence in previous work that has used TMS to suppress visual processing. Performance on several different types of visual recognition tasks has been shown to be impaired with magnetic stimulation of the occipital cortex (e.g., Cowey & Walsh, 2000; Corthout, Uttl, Walsh, Hallett, & Cowey, 1999; Corthout, Uttl, Ziemann, Cowey, & Hallett, 1999; Kammer, 1999; Kastner, Demmer, & Ziemann, 1998; Amassian, Cracco, et al., 1993; Amassian, Maccabee, et al., 1993; Amassian, et al., 1989, 1998). Furthermore, we recently showed that processing of LVF targets was significantly impaired with rTMS to the right occipital cortex, whereas no significant impairment was observed for RVF target processing. The complementary pattern of rTMS effects was obtained with LH stimulation, which significantly impaired lexical decision performance to RVF but not LVF targets (Lavidor, Ellison, & Walsh, 2003).

The use of TMS therefore allowed us to investigate lexical processing in the right and left hemifields under conditions of TMS-induced impairment of the left and right occipital areas. We assessed the ability of subjects to recognize visually presented words in two experiments. In Experiment 1, rTMS was applied to the LH and RH occipital areas as subjects made lexical decision responses to words and pseudowords appearing mainly in the LVF or RVF. Words and pseudowords were composed of five or eight letters so that hemispheric differences in the processing of length could be observed. Experiment 2 used single pulses of TMS to index the time course of lexical processing in the LH and RH. Using this method, we expected to identify the critical moment in time when visual lexical processing is carried out in the left and right occipital areas.

EXPERIMENT 1: rTMS INVESTIGATION OF THE WORD LENGTH EFFECT

To assess the relative contribution the two hemispheres make to visual lexical processing, we applied rTMS over the left and right occipital cortex as subjects made lexical decision responses to word and pseudoword items. These items differed in their number of letters, and appeared mainly in the LVF or RVF. We expected to observe length-independent recognition of words in the RVF only, and length effects in the LVF. This prediction is based on the assumption that the RVF advantage in processing words reflects, at least partially, the LH expertise in reading (Ellis, 2004). However, we also expected rTMS of the left occipital region to cause one of two effects. One possibility was that LH rTMS might initiate an absolute suppression of RVF processing so that responses to five- and eight-letter items would be slowed uniformly. Alternatively, the expertise of the LH in word recognition might be such that LH rTMS would only affect processing of longer items, leaving processing of shorter items relatively unimpaired. If the latter occurred, then one would expect a length effect in the RVF to be observed. As length effects are normally a feature of LVF processing, we predicted that right occipital rTMS would either accentuate the size of this effect or slow RTs to LVF words uniformly.

Methods

Design

A $4 \times 2 \times 2 \times 2$ fully related design was used, with TMS (no stimulation, RH stimulation, LH stimulation, or sham), visual field of item presentation (LVF, RVF), item length (five, eight letters), and lexicality (word, pseudoword) as the four factors. rTMS was administered in alternating blocks of single-hemisphere stimulation. All other variables were randomly applied. Sham rTMS trials were included to assess the potential effects that the auditory and tactile stimulation from the coil might have on performance. During these trials, the lateral edge of the coil was held perpendicular to the scalp, using the same left and right occipital sites used for actual rTMS. This form of sham stimulation does not produce measurable evoked potentials or regional cerebral blood flow (rCBF) changes when applied over the motor cortex (Loo et al., 2000; George et al., 1997).

Participants

Twelve right-handed volunteers took part in the experiment (9 women; mean age 23.1 years, *SD* =

5.9; mean Edinburgh Handedness Inventory score [EHI; Oldfield, 1971] = 89.6; *SD* = 9.2). All reported normal or corrected-to-normal vision and were naïve to the purposes of the experiment. The experiment was reviewed and approved in advance by the local departmental committees and the Ethics of Human Research. Informed consent was obtained from each subject in accordance with the human subjects research protocol approved by the departmental committee.

Stimuli and Apparatus

Visual stimuli were presented on a Pentium PC linked to a 100-Hz colored monitor. Stimuli were 256 English words and 256 pseudowords, which were presented at fixation with a left- or right-field bias, such that the number of letters differed to the left of fixation (LVF) or to the right (RVF). This allowed us to present all stimuli within the fovea for greater acuity, while maintaining sufficient left- or right-field bias to reproduce established visual field asymmetries in processing (Brysbaert, 2004; see also Lavidor et al., 2001). Words comprised 128 strings of five letters and 128 of eight letters. In order to maximize visual similarity between the two different stimuli lengths, stimuli were selected such that half of the five-letter words had the same two initial letters as half of the eight-letter words (e.g., *Ex*cel–*Ex*orcise), and all remaining words had the same final two letters (e.g., yea*rn*–lovelo*rn*). The fixation cross appeared between the second and third letters of the initial-matched stimuli, or before the final two letters of the end-matched stimuli. In that way, five- and eight-letter words were presented so that one field contained the same visual information and the other visual field reflected the length manipulation by presenting either three or six letters from the five- or eight-letter items, respectively. Words were matched for orthographic neighborhood size (mean = 0.9 neighbors; *SD* = 1.7) and word frequency (mean = 4.4 per million words; *SD* = 1.6). Pseudowords were generated from a separate word pool by changing one letter, and were legal and pronounceable. Pseudowords were also composed of five or eight letters with the same-initial or same-final letters in equal proportion and were closely matched to the words in terms of orthographic neighborhood size (mean = 1.29 neighbors; *SD* = 0.61). Word and pseudoword stimuli were presented with Fixed System lower case font, size 12 points. The width of stimuli did not exceed 0.8° of visual angle when viewed from a distance of 90 cm. The letters appeared white on a blue background to minimize flicker.

TMS Equipment

A MagStim Super Rapid stimulator with two external boosters was used (maximum output approx. 2 Tesla). Magnetic stimulation was applied using a 70-mm figure-of-eight coil. The double wire windings, which make up the figure-of-eight coil, carry two alternating electrical currents which converge at the point where the two coils meet (at the center of the figure-of-eight). A focal electrical current can then be induced in the cortex via magnetic conduction from this central point, which undergoes minimal attenuation by the intervening soft tissue and bone. Previous studies have demonstrated that magnetic stimulation using this type of coil can produce functionally dissociable effects when moving the coil by 5–10 mm across the scalp (Brasil-Neto, McShane, Fuhr, Hallett, & Cohen, 1992). The center of the coil was positioned over the site to be stimulated such that the windings were to the left and to the right of it and the handle of the coil pointed vertically.

Procedure

Pre-experiment: Induction of stationary phosphenes. Before attempting to disrupt word processing with rTMS, the occipital stimulation sites were established by eliciting phosphenes to ensure that hemispheric stimulation selectively affected contralateral visual field processing. Participants wore a latex swimming cap and were seated with their head supported by a chin-rest and a head-strap to secure head position and stabilize fixation. The upper edge of the inion was marked on the cap, and another point (the reference point) was marked 2 cm above it. The occipital sites that were marked on the cap were 2 cm to the left (the LH site) of the reference point and 2 cm to the right (the RH site). The coordinates were selected initially on the basis of previously successful studies with TMS, in which stationary phosphenes and the suppression of visual perception tasks with TMS were reported at similar sites (Lavidor et al., 2003; Pascual-Leone & Walsh, 2001; Stewart, Ellison, Walsh, & Cowey, 2001; Cowey & Walsh, 2000; Kammer, 1999; Stewart, Battelli, Walsh, & Cowey, 1999; Kastner et al., 1998; Amassian et al., 1989).

During this pre-experiment phase, we located the stimulation sites with single pulses of TMS delivered between 60% and 90% of stimulator output. In a darkened room, participants closed their eyes while TMS was delivered to the LH and RH points. TMS was applied at increasing intensities until participants reliably reported seeing phosphenes and could describe their position in space. For some participants, the magnetic stimulation sites were changed using the "hunting procedure" described by Ashbridge, Walsh, and Cowey (1997). Once a site yielded reliable phosphene reports, an additional pre-experimental phase was carried out to further verify the site. This involved using TMS to induce artificial scotomas (as reported by Kamitani & Shimojo, 1999). We found that participants who reported phosphenes also reported this type of scotoma.

Main experiment. One rTMS train was delivered per trial at the onset of the visual stimulus and was triggered remotely by the same PC which generated visual stimuli. For the main experiment, we used the effective phosphene sites for each participant with the stimulator output fixed at 65% of maximum, at 10 Hz for 500 msec. This intensity was selected on the basis of previous experiments and has been found to sufficiently disrupt perception without masking stimuli with overt phosphenes (Lavidor et al., 2003; Lavidor & Walsh, 2003).

Trials were blocked as a function of TMS condition to allow for subject rest periods and coil heating. There were 16 blocks in total, each comprising 32 trials. Each trial began with a fixation cross at the center of the display for 3000 msec. One of the words or pseudowords then appeared for 120 msec, and rTMS (or sham rTMS) was administered at the point of visual stimulus onset. Participants gave 2-AFC lexical decision responses by pressing one of two available keys on a standard keyboard and were instructed to respond as quickly and as accurately as possible. Response keys were reversed for half of the subjects. The importance of fixating on the central cross was strongly emphasized. Participants were given a single block of 20 practice trials before the start of the experiment.

Results and Discussion

RTs that were less than 300 msec or longer than 1300 msec were discarded either as anticipatory or excessively lengthy, respectively. This resulted in the removal of approximately 1.8% of all responses in Experiment 1. The data from one subject were not included in the analysis due to technical problems in data recording. Mean RTs and error rates are summarized in Table 1.

Target Lexicality

Target lexicality had a significant effect on RTs [$F(1,10) = 5.24, p < .05$] and accuracy [$F(1,10) = 6.3, p < .05$], with faster and more accurate responses to words (667 msec, 86% correct) than to pseudowords (692 msec, 81% correct). The lexicality effect was expected and is in accordance with previous behavioral findings (Chiarello, 1988; Ellis et al., 1988). As consistent length-independent reading effects have been found for words but not for pseudowords (Ellis, 2004), the main analysis was performed only for word targets. Nevertheless, for validity reasons, we analyzed the pseudowords. None of the effects was significant, apart from length effect [$F(1,10) = 9.75, p < .05$], where five-letter pseudowords were responded to faster (mean = 674 msec) than eight-letter

Table 1. Mean Reaction Times (and Standard Deviations) to Words (msec) and Error Scores as a Function of Target Length, Visual Field, and Site of rTMS (Experiment 1)

	LVF Five-letter Words	*LVF Eight-letter Words*	*RVF Five-letter Words*	*RVF Eight-letter Words*
No TMS				
Mean RT	640	696	652	648
SD	81	110	93	95
% error	16	21	17	19
TMS—Left Occipital				
Mean RT	675	728	636	689
SD	92	116	95	113
% error	16	22	15	23
TMS—Right Occipital				
Mean RT	663	712	654	641
SD	109	134	111	108
% error	16	27	15	16
Sham TMS				
Mean RT	644	701	657	645
SD	102	113	99	101
% error	15	23	12	13

pseudowords (mean = 720 msec). As opposed to words, length effect was found in all conditions; also, the RVF advantage was absent for pseudowords, in line with previous studies (Ellis, 2004).

RT Data

There was a significant effect of visual field of word presentation [$F(1,10) = 14.2, p < .01$], with faster RTs to RVF words (mean = 652 msec) than to LVF words (mean = 682 msec). There was also a significant effect of word length [$F(1,10) = 10.0, p < .01$], with faster RTs to five-letter words (mean = 653 msec) than to eight-letter words (mean = 681 msec). The Visual field × Length interaction was significant [$F(1,10) = 12.5, p < .01$]. Analysis of this interaction revealed a significant length effect for LVF words [$F(1,10) = 7.2, p < .05$], with a mean RT to five-letter words of 656 msec compared with 709 msec for eight-letter words. RTs to five- and eight-letter words appearing in the RVF did not differ ($F < 1$) (mean RT for five-letter words = 650; mean RT for eight-letter words = 656).

Importantly, the interaction between rTMS site (LH, RH, no TMS, or sham TMS), word length, and visual field was also significant [$F(3,30) = 4.2, p < .05$]. Separate simple effects analyses were carried out to test the length and visual field effects across the four rTMS conditions. These revealed significant length and field interactions for all rTMS conditions [no TMS: $F(1,10) = 5.9, p < .05$; TMS over RH: $F(1,10) = 7.63, p < .05$; sham TMS: $F(1,10) = 6.35, p < .05$], except for when rTMS was applied over the left visual cortex ($F < 1$). These results clearly show that length effects were consistently evident in the LVF but not the RVF, but that rTMS over the left visual cortex created a length effect in the RVF. In order to illustrate the three-way interaction, we plotted the size of the length effect (i.e., the mean RT difference between five- and eight-letter words) as a function of visual field and TMS condition (see Figure 1). As can be seen in this figure, no TMS, sham TMS, and ipsilateral magnetic stimulation produced no length effect for RVF words. However, rTMS over the LH created a significant length effect for RVF words. Repeated measures analysis with visual field and TMS condition as the within-subjects factors and length effect as the dependent variable confirmed that the rTMS treatment significantly interacted with the visual field [$F(3,30) = 4.199, p < .05$].

Error Rates

There was a significant main effect of word length [$F(1,10) = 10.9, p < .01$], with fewer errors to five-letter words (mean = 15.2%) than to eight-letter words (mean = 20.4%). This was the only significant effect as the main effects of rTMS and visual field, as well as the interaction effects, all failed to reach significance.

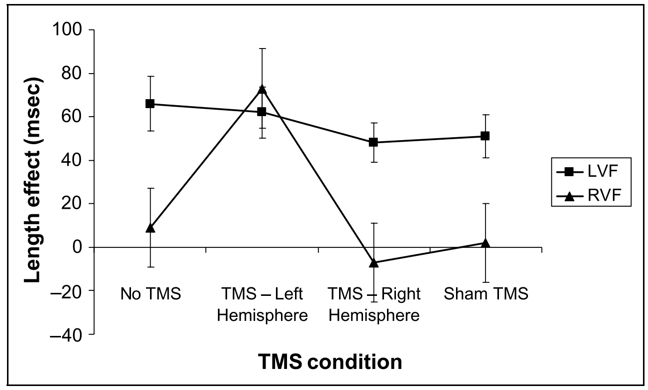

Figure 1. Word length effect size (and standard deviation) for response times for words as a function of visual field and rTMS stimulation site (Experiment 1). The bars represent the difference in milliseconds between eight-letter and five-letter word RTs. Positive bars therefore represent a length effect. Under normal reading conditions (i.e., no TMS, sham TMS, and ipsilateral magnetic stimulation), there was no length effect for RVF words. rTMS over the LH, however, created a significant length effect for RVF words.

The primary aim of Experiment 1 was to investigate the comparative efficiency with which the cerebral hemispheres can recognize visually presented words. In the baseline (no rTMS) condition of Experiment 1, we replicated the usual length-dependent and length-independent effects observed in the left and right visual hemifields, respectively (Ellis et al., 1988). The application of TMS to the left and right occipital cortex allowed us to further investigate these differences in lexical processing efficiency. We found that left occipital rTMS created a length effect that is not normally present in the RVF. Inspection of Table 1 reveals that this was primarily achieved by a slowing of responses to eight-letter stimuli, whereas processing of five-letter stimuli remained unimpaired. By contrast, right occipital rTMS slowed RTs to five- and eight-letter stimuli uniformly relative to baseline, indicating that TMS impairment of the right occipital cortex is absolute rather than selective. This dissociation between how the left and right visual cortices function under TMS clearly suggests differences in their efficiency in processing visual lexical information.

EXPERIMENT 2: SINGLE-PULSE TMS INVESTIGATION OF THE WORD LENGTH EFFECT

The results of Experiment 1 indicate that the visual cortex of the left and right cerebral hemispheres differ in their ability to process lexical information. Specifically, rTMS delivered at the point of visual stimulus onset impairs processing selectively in the LH, but uniformly in the RH. The aim of Experiment 2 was to explore the time course of these effects with single pulses of TMS using the same occipital stimulation sites as in Experiment 1. The same task used in Experiment 1 was also used here, but with a single TMS pulse delivered after an interval of 20, 80, 140, or 200 msec post visual stimulus onset (i.e., a *stimulus onset asynchrony* [SOA]).

Methods

Design

A 2 × 2 × 2 × 2 × 4 within-subjects design was employed, with TMS location (left or right occipital), visual field of target presentation (LVF, RVF), item length (five and eight letters), item lexicality (word, pseudoword), and visual-magnetic SOA (20, 80, 140, 200 msec) as the five factors.

Participants

Eight right-handed subjects took part in Experiment 2 (4 women; mean age = 24.5, *SD* = 7.6; mean EHI score = 94.4; *SD* = 6.8). All reported normal or corrected-to-normal vision and were naïve to the purpose of the experiment. The experiment was reviewed and approved in advance by the local departmental committees and the Ethics of Human Research. All participants gave informed consent before taking part.

Stimuli and Apparatus

The word and pseudoword stimuli were identical to those used in Experiment 1. The magnetic stimuli comprised single pulses of TMS delivered at 90% of each subject's phosphene threshold. The left and right occipital sites for TMS were localized as in Experiment 1.

Procedure

The number of words and pseudowords was divided equally between the experimental conditions. However, in order to accommodate the large number of experimental conditions in this experiment, each word and pseudoword was presented twice. Thus, the experiment consisted of 1024 trials in total, divided equally and randomly between the experimental conditions. Trials were blocked as a function of TMS location. There were 16 blocks in total (8 left TMS, 8 right TMS), each comprising 64 trials. This was done to counter subject fatigue and coil heating. The trial sequence was identical to that in Experiment 1, except that the fixation display remained on for 5000 msec. The interpulse interval was increased in this way to prevent single pulses occurring in close proximity behaving like rTMS.

Results and Discussion

Outliers were discarded as in Experiment 1 (in total 1.6% all responses were removed). Mean RTs and error rates to words are summarized in Table 2.

Target Lexicality

Target lexicality had a significant effect on RTs [$F(1,10) = 4.79, p < .05$], with faster responses to words (595 msec) than to pseudowords (616 msec). Accuracy was also slightly greater for words than pseudowords (82% compared to 78% correct), although this difference was not significant. This lexicality effect is consistent with the results of Experiment 1. In accordance with Experiment 1, the main analysis was performed on word responses only, however, we analyzed the pseudowords for validity reasons. As expected, none of the effects was significant, apart from length effect [$F(1,7) = 8.13$, $p < .05$], where five-letter pseudowords were responded to faster (mean = 601 msec) than eight-letter pseudowords (mean = 636 msec). As opposed to words, length effect was found in all conditions; also, the RVF advantage was absent for pseudowords, in line with previous studies (Ellis, 2004). There was a trend towards contralateral TMS effects (that is between TMS location and visual field), however, it seems that the (nonsignificant) TMS effects occurred only in the 80- and 140-msec SOA. The TMS caused nonsignificant uniform increase in RTs for both long and short pseudowords.

As we were expecting TMS to modulate the size of the length effect observed in the two visual hemifields across SOA, we decided to omit the length variable from the analysis. This allowed us to increase statistical power and avoid a four-way analysis. Thus, a three-way ANOVA was carried out incorporating TMS location (left, right occipital), visual field of word stimuli (LVF, RVF), and visual-magnetic SOA (20, 80, 140, 200 msec) as the factors. The size of the word length effect (i.e., the mean RT difference between five- and eight-letter words) was the dependent measure.

Reaction Times

The main effect of visual field was significant [$F(1,7) = 10.3$, $p < .05$], in which larger length effects were obtained in the LVF (35 msec) than in the RVF (6 msec). Most important, however, was the significant three-way interaction [$F(3,21) = 4.7, p < .05$]. Simple effects analyses revealed that TMS over the LH created a significant length effect for RVF words only when applied 80 msec after the target [for 80 msec: $F(3,21) = 7.2, p < .05$]. At other SOAs, no length effects were observed in the RVF (*F* ratios for 20, 140, and 200 msec were smaller than 1). This contrasts with LVF performance (with TMS over the LH), in which length effects were present at all SOAs [20 msec: $F(3,21) = 4.4$, $p < .05$; 80 msec: $F(3,21) =$

Table 2. Mean Reaction Times to Words (msec) and Error Scores as a Function of Target Length, Visual Field, and Site and Timing of a Single TMS Pulse (Experiment 2)

	LVF Five-letter Words	*LVF Eight-letter Words*	*RVF Five-letter Words*	*RVF Eight-letter Words*
Response Times (msec)				
Left occipital TMS				
SOA 20	616	641	588	588
SOA 80	609	631	591	650
SOA 140	602	636	584	567
SOA 200	544	583	525	532
Right occipital TMS				
SOA 20	598	635	587	595
SOA 80	626	672	581	588
SOA 140	613	669	596	591
SOA 200	558	584	538	529
% Errors				
Left occipital TMS				
SOA 20	18.2	36	15.1	17.3
SOA 80	19.9	30.1	9.6	22.2
SOA 140	15.9	31.7	10.4	13.6
SOA 200	19.1	26.2	7.9	14.2
Right occipital TMS				
SOA 20	20.1	32.3	13.1	16.1
SOA 80	15.1	32.3	10	9.3
SOA 140	16.9	20.7	6.2	14
SOA 200	17	30	6.2	13

4.3, $p < .05$; 140 msec: $F(3,21) = 4.8$, $p < .05$; 200 msec: $F(3,21) = 4.5$, $p < .05$]. When the magnetic stimulation was applied over the RH, significant F values ($p < .05$) were found for all SOAs for LVF targets, whereas no length effects were observed for RVF targets (F ratios for 20, 80, 140, and 200 msec were smaller than 1) (Figure 2).

Error Rates

The application of single pulses of TMS had an overall effect on error rates, which resemble the pattern found for latencies (see Table 2). However, none of the main effects or interactions reached significance.

In Experiment 2, we sought to investigate the critical moment in time when processing of words and pseudowords is carried out in the visual cortex of the LH and RH. This was achieved using single pulses of TMS delivered at a variable SOA after the onset of the visual stimulus. Once again, our results showed clear differences on how the hemispheres process words. A single pulse of TMS delivered to the left occipital cortex had an effect on RVF processing only when it occurred 80 msec after visual stimulus onset, at which point a length effect was created in the RVF. On the other hand, TMS of the right occipital cortex had no reliable effect on LVF processing. These results are consistent with those obtained in Experiment 1, and once again support the notion of LH specialization in visual word recognition. This support for LH specialization comes from two main observations: First, that the LH is able to process five- and eight-letter words with equal efficiency; and second, that LH performance levels are similar under conditions of TMS-induced impairment to RH performance in the baseline (no TMS) condition. This latter point will be discussed further in the following section.

GENERAL DISCUSSION

The primary aim of our study was to investigate the comparative efficiency with which the cerebral hemispheres

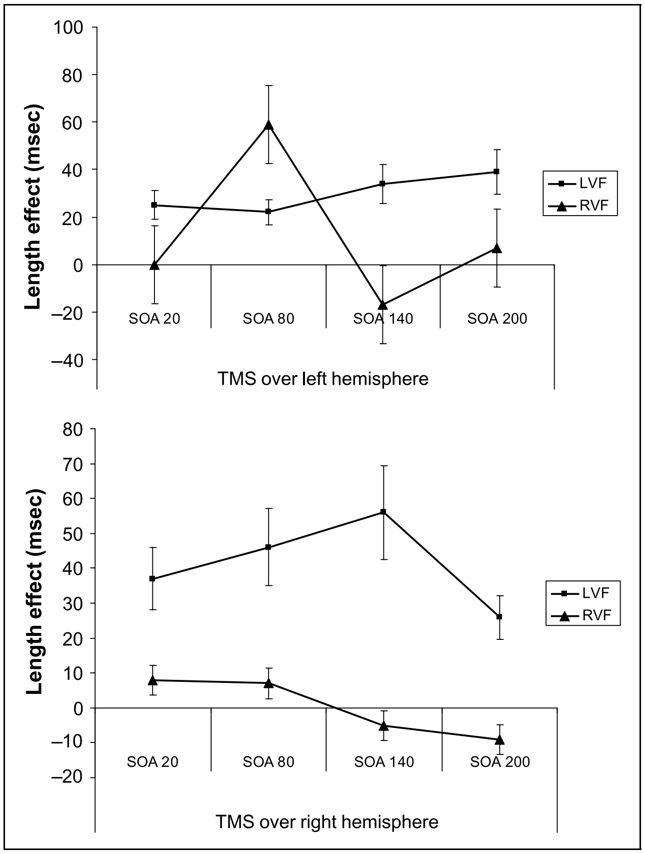

Figure 2. Word length effect size for response times for words as a function of visual field and magnetic stimulation timing and location (Experiment 2). Length effects were calculated as in Figure 1. Top: Length effects due to TMS of the LH. Bottom: RH TMS trials. For RVF words, a length effect was observed only when TMS was delivered to the left occipital cortex 80 msec postword onset. For LVF words, length effects were apparent under all stimulation conditions.

can process visually presented words. We carried out two experiments in which lexical decision responses to short and long words were compared under TMS-induced suppression of left and right hemispheric visual functioning. In the baseline (no rTMS) condition of Experiment 1, we replicated the usual length-dependent and length-independent effects observed in the left and right visual hemifields, respectively (Ellis, 2004). The application of TMS to the left and right occipital cortex allowed us to further investigate these differences in lexical processing efficiency. We found that left occipital rTMS created a length effect that is not normally present in the RVF. By contrast, right occipital rTMS had little effect on LVF processing, apart from subjecting absolute RTs to a marginal slowing. Together, these findings show that with respect to lexical processing, TMS impairment of the left occipital cortex is selective in nature, whereas impairment of the right occipital cortex is absolute. This distinction on how the two hemispheres function under conditions of TMS clearly shows differences in their ability to process lexical information. Inspection of Table 1 reveals that LH processing of the RVF remains as effective under conditions of TMS-induced impairment as does unimpaired RH processing of the LVF in the baseline (no TMS) condition. This claim is illustrated by comparing RTs to five- and eight-letter words in the RVF under LH stimulation (636 and 689 msec), with those in the LVF with no RH stimulation (640 and 696 msec, respectively). This provides us with a clear and novel measure of just how specialized the LH is for visual word recognition in comparison to the RH.

Experiment 2 was carried out to investigate when visual lexical processing takes place in the occipital cortex of the LH and RH. We delivered single pulses of TMS to the left or right occipital sites either 20, 80, 140, or 200 msec after visual stimulus onset. The results of Experiment 2 showed clear differences in the time course of visual lexical processing in the two hemispheres. Left occipital TMS created a length effect in the RVF, but only at 80 msec postvisual stimulus onset. Right occipital TMS showed no discernible influence on the size of the length effect naturally present in the LVF. These results are consistent with those from Experiment 1, showing again that TMS of the left and right occipital cortex can produce selective and absolute suppression of visual processing, respectively. They also concur with results from previous studies, which have also shown TMS-induced visual suppression at 80 msec after visual stimulus onset (Potts et al., 1994; Amassian et al. 1989). As the thalamocortical volley from the lateral geniculate nucleus is thought to arrive at the primary visual cortex between 80 and 140 msec after visual onset, the TMS effects we observed are likely to have occurred due to V1 stimulation. However, we cannot rule out the contribution that other visual areas adjacent to V1 might make to word length processing. This is because V1 is tucked into the calcarine fissure in humans, meaning that TMS of V1 can also provide artifactual stimulation of areas V2 and V3 (Marzi et al., 1998). Despite this, the possibility that the primary visual cortex is the major contributor to expert word recognition is in line with the findings of a recent PET study (Whiting et al., 2003), which showed that word length effects (as measured with RT) were associated only with posterior activation (BA 17) and not with other areas. Thus, our finding that left occipital TMS created a length effect in the RVF suggests that impairment occurring relatively early in the visual cortical pathway can inhibit expert word recognition later on. Similar impairments have been reported in several previous non-TMS experiments in which the visual pattern of common words was distorted by changing word orientation (Lavidor et al., 2001) or using mixed case (Ellis, Brooks, & Lavidor, 2005). Such manipulation selectively affected LH performance and abolished, or at least decreased, the LH advantage in visual word recognition.

Prior to carrying out a TMS procedure, it was necessary to obtain reliable baseline effects with the behavioral task. Word and pseudoword targets were briefly presented in the center of the monitor while right-handed participants made lexical decision judgments. The results were compatible with those of numerous previous lateralization experiments (Iacoboni & Zaidel, 1996; Chiarello, 1988; Ellis et al., 1988); words were responded to faster and more accurately than pseudowords, and we found the predicted word length and visual field interaction for the control conditions.

The rTMS effects we found for briefly presented targets are consistent with other rTMS findings with occipital stimulation in which TMS is only able to disrupt perceptual judgments if the relative duration of presentation is short (e.g., Amassian et al., 1989), stimuli are close to luminance detection thresholds (Miller, Fendrich, Eliassen, Demirel, & Gazzaniga, 1996), or both (see Kammer & Nusseck, 1998; see also Walsh & Pascual-Leone, 2003; Walsh & Cowey, 2000, for details of the relationship between stimuli and the temporal duration of TMS effects). In the present study, we did not find significant TMS effects on error rates. Although errors may be a useful measure of performance close to threshold, it has been difficult to obtain errors in cognitive tasks with TMS (see Walsh & Pascual-Leone, 2003; Walsh & Cowey, 1998, for methodological details).

This work confirms the expertise of the LH in its ability to recognize words. However, we might ask whether our results offer insight into the origin of the LH advantage in visual word recognition. One theory is that the specialization can be explained by the neuroanatomical arrangement of the visual system, in which RVF stimuli are projected directly to the LH (Ellis, 2004; Gazzaniga, 2000; Brysbaert, 1994; Young & Ellis, 1985). Alternatively, other explanations, such as attentional bias toward the right side of space (Kinsbourne, 1970) and cultural differences in reading habits (Nazir et al., 2004; Deutsch & Rayner, 1999), may also explain visual field differences associated with word recognition. We feel that our findings support the structural rather than other accounts, as the differential interference that TMS has on left and right occipital processing suggests differences in functioning at the cortical level. We do not claim that lexical processing occurs in the visual cortex, however; rather, that there are structural differences in the way the LH and RH visual pathways feed lexical information to the language-specialist areas. We feel this is best demonstrated by the selective nature of the impairment shown with TMS of the left occipital cortex. The fact that TMS impairs only some, rather than all, words in the RVF suggests an efficient pathway which links the left visual cortical areas to those directly involved in lexical processing. That the word length effect in the LVF is not modulated by right occipital TMS indicates that the pathway linking the RH visual areas to the specialist language areas is markedly less efficient. Although we would argue that these findings are perhaps best explained by differences in LH and RH brain architecture, we cannot rule out the possibility that attentional or cultural differences in reading behavior might also contribute to the length-by-visual field effect. Such factors might also impress upon low-level cortical connectivity in an asymmetric fashion. If this is the case, these factors might also be differentially affected by magnetic stimulation of the left and right visual cortex.

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