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Fast Forward: Supramarginal Gyrus Stimulation Alters Time Measurement

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Disciplines

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Comments

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Martin Wiener[1], Roy Hamilton[1], Peter Turkeltaub[1], Matthew S. Matell[2], and H. B. Coslett[1]

Abstract

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INTRODUCTION

Temporal perception, the ability to perceive the passage of time, is undeniably influenced by attention. The adages ''a watched pot never boils'' and ''time flies when you're having fun,'' are commonly used to describe the subjective effects of devoting attention toward, and away, from time. The neural systems underlying temporal perception and attention may include many of the same structures (Coull, 2004); however, the precise role of these neural structures with respect to timing remains unclear.

Scalar Expectancy Theory (SET) has framed the majority of temporal perception studies. Formally proposed by Gibbon (1977), and expanded into an information processing account by Gibbon, Church, and Meck (1984), SET consists of a three-stage process in which temporal intervals are judged (Figure 1). First, a pacemaker emits a series of pulses, which are summated by an accumulator mechanism during a to-be-timed interval. Second, at the offset of the timed stimulus, a memory stage encodes the duration into either working or reference memory, depending on the constraints of the task. Third, if the timed stimulus must be compared to a previously experienced duration, a decision stage monitors the relative similarity of the two durations and provides the appropriate output (e.g., ''Duration A is longer than Duration B''). Data from a wide range of tasks and species have demonstrated that the variability of responses increases with duration, adhering to Weber's law (Gibbon, Malapani, Dale, & Gallistel, 1997).

As a further development of SET, Zakay and Block's (1995) Attentional Gate Model addresses the role of attentional resources in temporal perception. Specifically, the perceived length of an interval depends upon the amount of attentional resources devoted to timekeeping. The Attentional Gate Model thus proposes that attention functions like a gate between the pacemaker and the accumulator. At the onset of a to-be-timed stimulus, the gate opens, allowing pacemaker pulses to enter the accumulator. If attentional resources are diverted away from the timed stimulus, the gate partially closes and fewer pacemaker pulses enter the accumulator. Numerous experiments have now demonstrated that when a concurrent, nontemporal task is introduced during a temporal task, the perceived duration is shortened, presumably by diverting attentional resources away from the gate (Zakay & Block, 2004; Casini & Macar, 1997; but see Lejeune, 1998). Conversely, increased attention to temporal tasks is hypothesized to widen the gate, increasing the amount of pacemaker accumulation and thereby increasing perceived duration (Wittman & Paulus, 2007; Mattes & Ulrich, 1998; Zakay & Block, 1997). The perceived duration of an interval, then, is modulated by the status of the gate during that interval. This balance of attentional resources between temporal perception and other mental operations is collectively known as ''time-sharing'' (Fortin, 2003).

Where might the neuroanatomical locus of time-sharing be? Right inferior parietal cortex has been shown to be part of the neural substrate of selective attention

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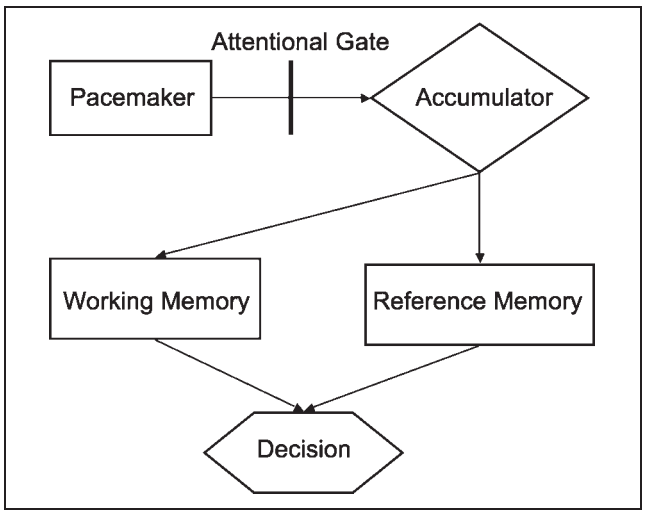

Figure 1. A schematic display of SET. A pacemaker and accumulator mechanism constitutes the ''internal clock'' stage, in which pacemaker pulses are passed into an accumulator. Working memory is recruited when the accumulated duration must be retained for a short period of time, whereas reference memory is necessary if a previously experienced duration must be retrieved. A decision stage mechanism serves as comparator between durations of different lengths. Attention influences temporal perception via a gate mechanism, which allows pacemaker pulses to enter the accumulator.

(Behrmann, Geng, & Shomstein, 2004). Additionally, recent studies demonstrate that dissociable regions of parietal cortex may mediate different types of attention. The right angular gyrus (AG) and supramarginal gyrus (SMG) are two such functionally dissociable regions of inferior parietal cortex. The AG has been implicated in the spatial reorienting of attention, in which attentional resources should be shifted to a new location (Rushworth, Ellison, & Walsh, 2001), as well as the spatial representation of number (Gobel, Walsh, & Rushworth, 2001). In contrast, the SMG has been implicated in the strategic orienting of spatial attention, in which attentional resources are covertly devoted to a peripheral source (Chambers, Stokes, & Mattingley, 2004; Perry & Zeki, 2000). Neuroimaging evidence also suggests that the SMG is recruited during counting tasks, when sustained attention is crucial (Ortuno et al., 2002).

In lesion and neuroimaging studies of temporal perception, both the right AG and the right SMG have been implicated (for reviews, see Lewis & Miall, 2003; Harrington & Haaland, 1999). For example, neuroimaging data have demonstrated inferior parietal cortex activity during the active measurement of duration (Harrington et al., 2004; Rao, Mayer, & Harrington, 2001), suggesting an involvement in clock processes, whereas lesion overlay analysis of stroke patients with temporal perception deficits has demonstrated the SMG as a common area of damage (Danckert et al., 2007; Harrington, Haaland, & Knight, 1998). These data are consistent with the claim that a right-hemispheric network of cortical structures is involved in temporal perception (Lewis & Miall, 2006; Buhusi & Meck, 2005; Harrington & Haaland, 1999). Not all data support this conclusion, however. A number of neuroimaging studies demonstrate left parietal involvement in temporal perception (Livesey, Wall, & Smith, 2007; Coull, 2004; Coull, Frith, Buchel, & Nobre, 2000; Coull & Nobre, 1998). Additionally, a recent study of 31 subjects with focal brain lesions found no difference in the temporal processing impairments associated with right or left hemisphere lesions (Coslett, Shenton, Dyer, & Wiener, in press). Finally, recent investigations involving subjects with brain dysfunction suggest that temporal perception may be supported by both hemispheres (Wiener & Coslett, 2008; Handy, Gazzaniga, & Ivry, 2003).

Several studies of temporal perception have employed repetitive transcranial magnetic stimulation (rTMS), a technique that disrupts discrete cortical regions and affords greater inferences regarding function than neuroimaging alone. Thus far, only the AG has been specifically targeted during temporal perception tasks. Bueti, Bahrami, and Walsh (2008) demonstrated that stimulation of the right, but not left, AG significantly increased variability on a temporal discrimination task, in which subjects were required to judge whether a comparison stimulus was longer or shorter than a standard stimulus. Although these results provide direct evidence for the involvement of the AG in temporal discrimination, they are ambiguous with regards to SET; increases in variability may be attributable to any stage in the timing process (Wearden, 1999). Furthermore, stimulation only occurred during the presentation of the comparison stimulus, in which clock, memory, and decision stage mechanisms are recruited. In the present study, we investigated the roles of the right and left SMG, a heretofore unexplored region in studies of TMS and timing, by administering stimulation in two experiments in which rTMS was delivered at different points in a temporal discrimination task.

EXPERIMENT 1

Methods

Subjects

Nine right-handed healthy volunteers (5 men, 4 women) aged 23–36 years, who met criteria for TMS, participated in Experiment 1. All subjects gave their informed consent as approved by the University Institutional Review Board. Subjects were seated on an adjustable chair facing a Dell Latitude laptop computer approximately 3 feet away. A USB keyboard was attached to the laptop and placed either on the subject's lap or on an extended platform, depending on which was more comfortable to the subject.

Repetitive Transcranial Magnetic Stimulation

Stimulation was administered with a Magstim Rapid magnetic stimulator (Magstim, Whitland, UK), connected

to a figure-eight air-cooled coil with a diameter of 70 mm. Motor thresholds were collected for each subject by determining the stimulation output that elicited a motor-evoked potential from the contralateral hand on at least 50% of pulses. Stimulation remained at this output for the remainder of the experiment. The coil was held tangentially to the scalp and secured in place with a mechanical arm, connected to a metal frame.

We utilized Brainsight Stereotaxic Frameless Software (Rogue Research, Montreal) to target brain sites for stimulation. A high-resolution MP-RAGE image was obtained for each subject and used to construct a 3-D image of his or her brain. A Polaris optical tracking system (Northern Digital, Waterloo, Ontario) was employed with Brainsight to coregister the subject's brain and coil.

The anterior aspects of the left and right SMG, as well as the vertex, were identified for each subject (approximate Talairach coordinates of 59, −34, 31; −59, −39, 31; and 0, −17, 65, respectively; see Figure 2). Subjects were stimulated at 100% of their motor threshold with three pulses of rTMS at 10 Hz (∼50 μsec pulse, 100 msec interpulse interval). Stimulation was elicited with a custom script, written in E-Prime (Psychology Software Tools, Pittsburgh, PA). Subjects sat with their heads in a chin rest in order to restrict movement. All subjects wore earplugs to reduce noise from coil stimulation.

Baseline

Prior to receiving rTMS, each subject performed a baseline temporal discrimination task. All baseline tests were carried out on a Macintosh Powerbook G4, and were programmed in Matlab (Mathworks, Natick, MA) using the Psychophysics Toolbox extensions (Brainard, 1997). We utilized the Parameter Estimation by Sequential Testing (PEST) algorithm (Pentland, 1980), an adaptive staircase psychophysical task, in which the threshold for determining the difference between two successively presented stimuli is derived by successively updating the set of tested values. At the onset of each trial, subjects were presented with a fixation point for 1 sec, followed by the presentation of a red square (4 × 4 cm) subtending ∼2° for 600 msec (standard duration). After the target interval was reached, the red square extinguished for a 1-sec ISI. A second red square was then presented for a variable duration of time (comparison duration) as determined by the adaptive staircase procedure of the PEST algorithm. The comparison duration boundaries were set not to go below 50%, or exceed 150%, of the standard interval for determining lower and upper thresholds, respectively. Subjects were required to indicate on the keyboard whether they judged the second stimulus to be shorter (by pressing the ''S'' key) or longer (by pressing the ''L'' key) than the first stimulus. Once a response was detected, the next trial began immediately. All subjects were given 30 practice trials with a standard interval of 1000 msec, and then completed 60 trials of the baseline task with the 600-msec standard interval. Subjects were not told the range of stimulus durations and were not given feedback regarding accuracy.

The probability of each subject making a ''longer'' response choice was plotted as a function of the comparison interval. These data were then fit with a sigmoidal, psychometric curve (see Figure 3 for a representative function) using the psignifit version 2.5.6 software package (see http://bootstrap-software.org/psignifit/) for Matlab, which implements the maximum likelihood method described by Wichmann and Hill (2001a).

Lower and upper thresholds, the approximate points at which the subject is 25% and 75% likely to judge the stimulus as longer, were calculated by using the BC bootstrap method implemented by psignifit, based on 4999 simulations (Wichmann & Hill, 2001b). The results of this analysis yield the point of subjective equality (PSE; the time value when subjects were equally likely to judge the stimulus as shorter or longer), the difference limen (DL; upper − lower thresholds/2), and the coefficient of variation (CV; DL/PSE).

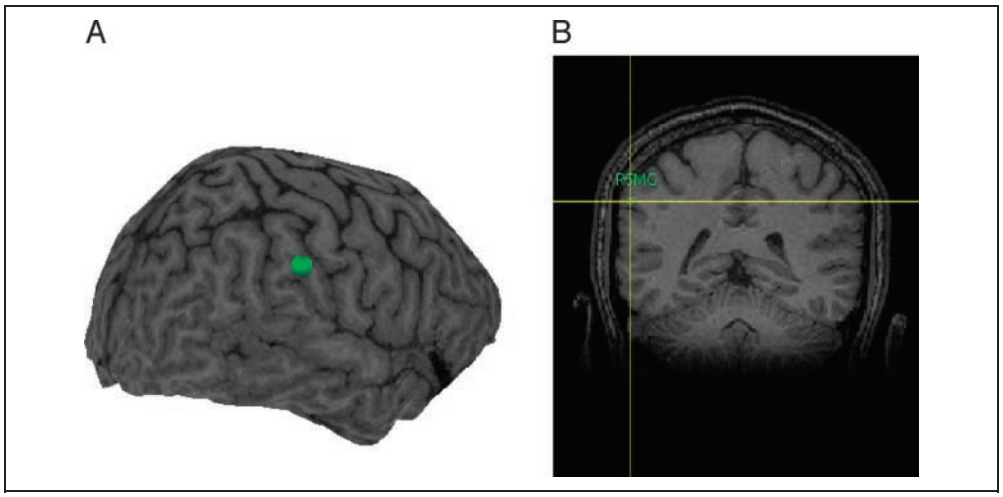

Figure 2. Two images constructed in Brainsight of a representative subject. (A) A 3-D image with the right SMG marked. (B) A coronal image; crosshairs indicate the anatomical location of the right SMG.

Experimental Protocol

Once baseline performance using the PEST algorithm was complete, subjects participated in the stimulation procedure. Two durations were chosen for each subject: 600 msec and the individually determined upper threshold (UT) value at which they were 75% likely to respond ''longer'' on the PEST temporal discrimination task (mean UT = 718 msec, *SD* = 60 msec). At the onset of each trial, subjects viewed a fixation point for 1 sec, followed by the presentation of a red square (4 × 4 cm) for either 600 msec or the subject's UT (VS1; Visual Stimulus 1). After a 4-sec ISI, the second red square was presented for 600 msec or the subject's UT (VS2; Visual Stimulus 2). After the second square was extinguished, subjects responded by depressing the ''S'' key if they believed VS2 to be shorter or the ''L'' key if they believed VS2 to be longer in duration than VS1. There were four possible trial types generated by crossing the standard duration and the subject's UT: 600–600, 600–UT, UT–600, and UT–UT. A single session consisted of 96 trials, with 24 trials for each trial type. Subjects received rTMS on half of the trials in a given session (48 trials), with 12 trials for each presentation order. Administration of rTMS was synchronous with the onset of VS1 (see Figure 4 for sample stimulation protocol).

Subjects were tested on two separate days, with two sessions on the first day and one session on the second day. Only one site was stimulated per session. The left and right SMG were always stimulated on the first day; the vertex was stimulated on the second day. The order of left versus right SMG stimulation was counterbalanced between subjects.

Data Analysis

Subject performance was calculated by dividing the total number of ''longer'' responses by the total number of trials for each trial type, expressing the proportion of trials in which subjects judged the second stimulus to be longer than the first. All analyses were carried out by repeated measures ANOVAs. Post hoc pairwise comparisons, when necessary, were conducted with a Bonferroni correction.

Results

Performance on trials in which stimulation was absent (No TMS) in all three sessions was first analyzed separately, in order to evaluate for differences by session. A repeated measures ANOVA with site (right SMG, left SMG, vertex) and trial type (600–600, 600–UT, UT–600, UT–UT) as within-subject factors was performed using SPSS ($\alpha = .05$ for all analyses). There was no effect of site [$F(2, 16) = 0.271$, $p = .766$] for No-TMS trials, but a significant effect of trial type [$F(3, 24) = 66.085$, $p = .0001$]. Post hoc pairwise comparisons between trial type demonstrated that all trial types were significantly different from each other (all $p < .05$) with the exception of 600–600 versus UT–600 ($p = .109$). There was no interaction between site and trial type [$F(6, 48) = 0.985$, $p = .446$]. Data from No-TMS conditions were collapsed across site for subsequent analyses.

Performance during stimulation of all three sites was characterized by a decrease in the proportion of trials on which subjects reported that the comparison stimulus was longer than the standard. The effect of site was

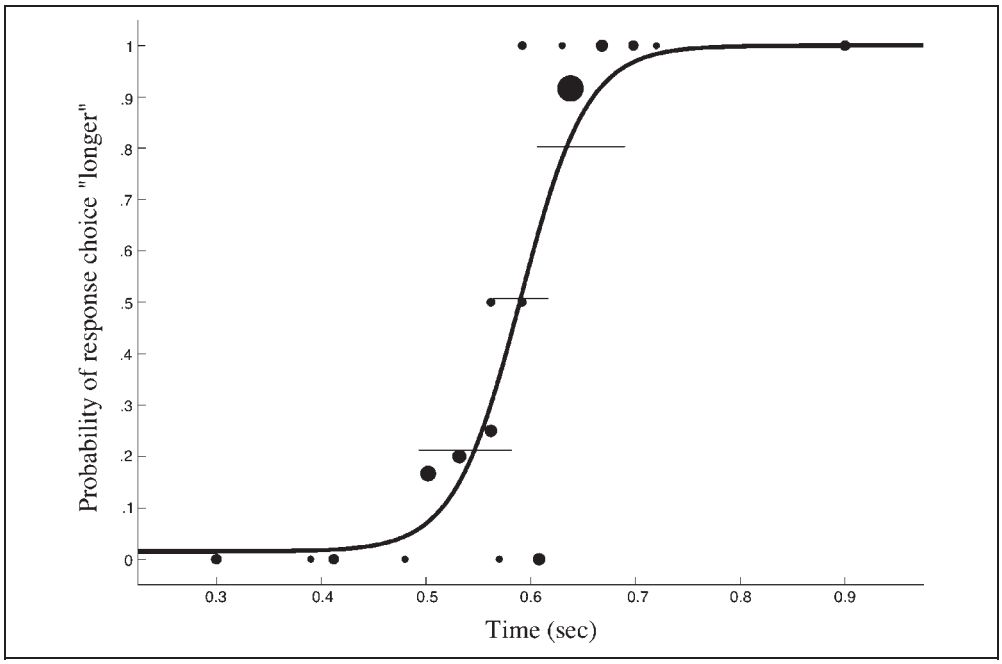

Figure 3. Baseline data from a representative subject performing a temporal discrimination task utilizing the PEST algorithm. Plotted points represent the range of comparison durations tested, and the probability of responding longer for those durations. The size of the plotted points represents the number of trials tested with that comparison duration.

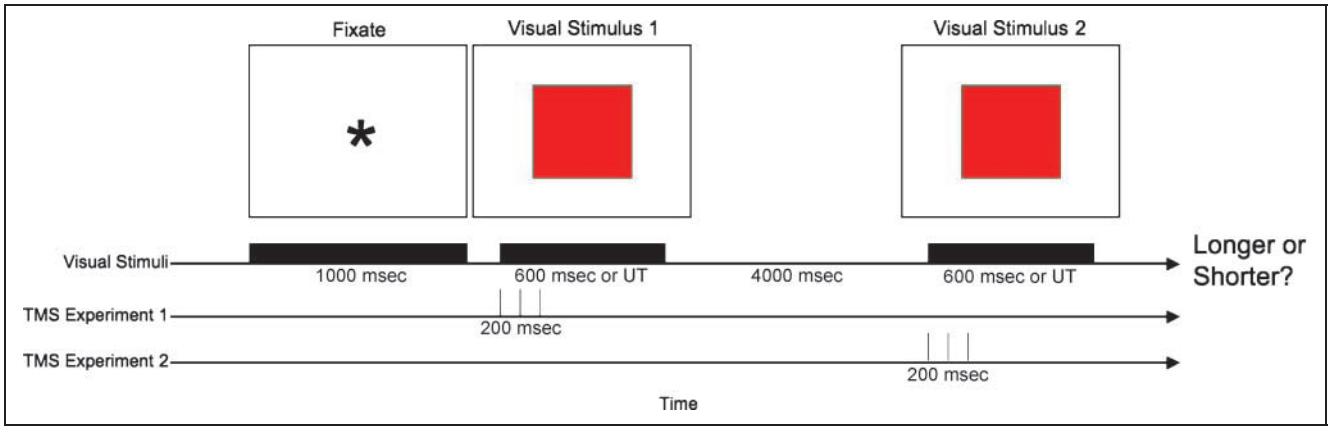

Figure 4. Task design for Experiments 1 and 2. Subjects viewed a red square for either 600 msec or their upper threshold (UT) duration, taken from their baseline performance. After a gap of 4000 msec, a second red square was presented for either duration again. Subjects were required to judge whether the second red square persisted for shorter or longer than the first. Stimulation was administered in Experiment 1 at the onset of the first visual stimulus, and at the onset of the second visual stimulus in Experiment 2.

assessed with a repeated measures ANOVA with condition (No TMS, vertex, right SMG, left SMG) and trial type (600–600, 600–UT, UT–600, UT–UT) as within-subject factors. There was a significant main effect of condition [$F(3, 24) = 10.857$, $p = .0001$] and trial type [$F(3, 24) = 67.087$, $p = .0001$], but no interaction [$F(9, 72) = 0.925$, $p = .509$] (see Table 1 and Figure 5A). Post hoc pairwise comparisons between trial type demonstrated that all trial types were significantly different from each other (all $p < .05$) with the exception of 600–UT versus UT–UT ($p = 1.00$). A planned repeated contrast on condition revealed that vertex stimulation was associated with a significantly lower proportion of trials on which subjects responded ''longer'' than No-TMS trials [$F(1, 8) = 25.288$, $p = .001$] but not left SMG trials [$F(1, 8) = 0.342$, $p = .575$]; right SMG stimulation was associated with a significantly lower proportion of ''longer'' trials than both vertex [$F(1, 8) = 6.780$, $p = .031$] and left SMG stimulation [$F(1, 8) = 9.751$, $p = .014$]; post hoc tests additionally revealed that right SMG stimulation was associated with a significantly lower proportion of trials on which subjects said ''longer'' than No-TMS stimulation ($p = .003$).

Discussion

rTMS during the presentation of a visual stimulus decreased the proportion of trials on which subjects responded ''longer.'' These data suggest that rTMS causes an *increase* in the perceived duration of a stimulus. The effect was observed at all sites, suggesting that the presence of the auditory clicks and/or the tactile stimuli associated with the coil discharge increased the perception of the duration of the event. A number of studies have previously reported that the presentation of a rapid series of auditory clicks alone are capable of leading to the subjective lengthening of perceived duration, possibly by increasing arousal, thereby increasing the speed of the pacemaker (Burle & Casini, 2001; Wearden, Philpott, & Win, 1999; Penton-Voak, Edwards, Percival, & Wearden, 1996). In these experiments, a rapid series of auditory clicks—ranging from 5 to 25 Hz—were presented to the subject either prior to or during the active measurement of duration. The results of numerous experiments across a range of temporal perception tasks revealed that the effect is dependent on both the intensity and duration of the clicks, but not on the frequency (although see Treisman, Cook, Naish, & MacCrone, 1994 for evidence of nonlinearities in the frequency response). Although the duration of the TMS clicks in the present study is shorter (~200 msec) than those used in explicit investigations of click trains (~1–5 sec), this, perhaps in conjunction with the tactile effect of

Table 1. Proportion of Trials on Which Subjects Judged the Second Stimulus to Be Longer for Each Stimulation Condition, in Each Experiment

	600–600	*600–UT*	*UT–600*	*UT–UT*
Experiment 1				
Left SMG	0.21	0.56	0.19	0.57
Right SMG	0.15	0.44	0.11	0.40
Vertex	0.22	0.55	0.11	0.54
No TMS	0.35	0.77	0.28	0.60
Experiment 2				
Left SMG	0.41	0.65	0.36	0.60
Right SMG	0.47	0.70	0.41	0.69
Vertex	0.45	0.70	0.33	0.61
No TMS	0.27	0.50	0.21	0.48

No-TMS values constitute the aggregate of all trials on which TMS was absent, across sessions.

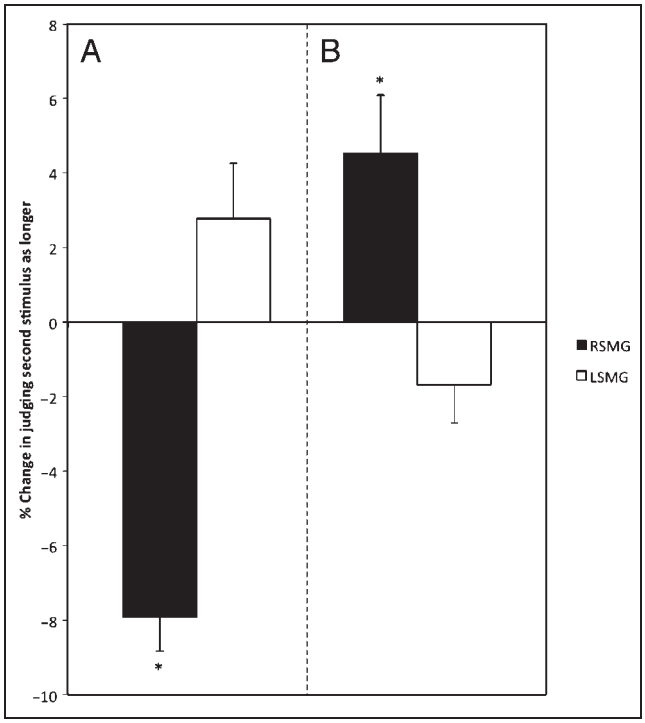

Figure 5. Changes in the proportion of trials on which subjects judged the second stimulus to be longer after receiving rTMS to the right supramarginal gyrus (RSMG) or left supramarginal gyrus (LSMG), as compared to vertex stimulation in (A) Experiment 1 and (B) Experiment 2. Plotted values were obtained for each subject by subtracting the average proportion of trials on which subjects judged the second stimulus to be longer for both sites from the vertex. Asterisks represent significant differences versus vertex stimulation in repeated measures ANOVAs.

rTMS, appears to have been sufficient to cause a subjective increase in duration of the associated visual stimulus. The use of noise-canceling headphones (Bueti, van Dongen, & Walsh, 2008), or the continuous exposure to recordings of TMS clicks during experimental protocols (Bueti, Bahrami, et al., 2008), has recently been implemented in order to diminish interference during temporal perception tasks.

In addition to this nonspecific finding observed across all conditions, we documented a site-specific effect of rTMS: Stimulation of the right SMG caused subjects to respond ''longer'' on a significantly lower number of trials than stimulation of the left SMG or vertex. Thus, in our investigation, rTMS produced a significant prolongation of the subjective duration of the paired visual stimulus. Before considering the mechanisms by which such an effect could be generated, we sought to replicate and extend this finding in Experiment 2. We reasoned that if rTMS to the right SMG is associated with an increase in the apparent duration of a paired stimulus, then rTMS during the second stimulus should produce results that are in the opposite direction of those reported here. That is, with rTMS during the second stimulus, subjects would be expected to perceive the second stimulus as longer, thereby *increasing* the number of trials on which they respond ''longer.''

There is one final finding from Experiment 1 that warrants comment. On trials with no rTMS, subjects were expected to respond ''longer'' on approximately 50% of trials. Instead, subjects exhibited a bias to respond ''shorter'' in 600–600 conditions, and to respond ''longer'' in UT–UT conditions; such biases are respectively known as positive and negative time-order errors (Hellström, 1985). One possible explanation for this result, as suggested by previous research (e.g., Lapid, Ulrich, & Rammsayer, 2008; Nachmias, 2006), is that subjects had generated a running average (i.e., internal standard) of the first (VS1) stimulus that reflected the average contribution of the 600 and UT trials.

EXPERIMENT 2

Methods

Seventeen right-handed healthy volunteers (8 men, 9 women), aged 23–35 years, participated in Experiment 2. Seven subjects had participated in Experiment 1. One subject was unable to participate in their vertex session but was included in comparisons of the right SMG and the left SMG. All baseline testing, experimental testing, TMS protocols, and analyses were the same as Experiment 1, except that stimulation was administered at the onset of VS2 (mean UT = 715 msec, SD = 46 msec).

Results

Once again, a repeated measures ANOVA demonstrated no significant difference between sessions for No-TMS trials [$F(2, 30) = 0.679$, $p = .515$]; consequently, these data were combined. Additionally, we compared No-TMS performance between naïve subjects and those that had participated in Experiment 1; no significant differences were detected [$F(3, 45) = 0.590$, $p = .625$]. There was a significant effect of trial type [$F(3, 45) = 38.608$, $p = .0001$] as observed in Experiment 1 but no interaction [$F(6, 90) = 1.602$, $p = .156$]. Post hoc pairwise comparisons between trial type demonstrated that all trial types were significantly different from each other (all $p < .05$) with the exception of 600–600 versus UT–600 ($p = .693$) and 600–UT versus UT–UT ($p = 1.000$).

Stimulation of all sites was associated with an increase in the proportion of trials on which subjects responded ''longer.'' The effect of site was again assessed with a repeated measures ANOVA with condition (No TMS, vertex, right SMG, left SMG) and trial type (600–600, 600–UT, UT–600, UT–UT) as within-subject factors. There was a significant effect of condition [$F(3, 45) = 15.593$, $p = .0001$], as well as an effect of trial type [$F(3, 45) = 60.667$, $p = .0001$], but no interaction [$F(9, 135) = 0.409$, $p = .928$] (see Table 1 and Figure 5B). Post hoc pairwise comparisons between trial type demonstrated

that all trial types were significantly different from each other (all $p < .05$) with the exception of UT–600 versus UT–UT ($p = .516$). Additional ANOVAs evaluated the differences between sites. Right SMG stimulation produced a significantly higher proportion of trials on which subjects responded ''longer'' than either left SMG [$F(1, 16) = 4.935$, $p = .041$] or vertex stimulation [$F(1, 15) = 4.596$, $p = .049$], whereas vertex stimulation was associated with a significantly higher proportion of trials on which subjects responded ''longer'' than No TMS [$F(1, 15) = 20.905$, $p = .0001$] but not left SMG stimulation [$F(1, 15) = 0.075$, $p = .788$]; post hoc pairwise comparisons also demonstrated that right SMG was significantly higher than No TMS ($p = .0001$).

Discussion

Stimulation of all sites was associated with a change in response probabilities; rTMS was associated with a tendency to judge the stimulus as longer. Critically, as in Experiment 1, this effect was significantly greater with stimulation of the right SMG as compared to the left SMG or vertex. Furthermore, as predicted, the effect was in the opposite direction of that observed in Experiment 1. Whereas rTMS during the standard stimulus in Experiment 1 led to a decrease in the proportion of trials in which subjects indicated the standard (first) stimulus was longer, rTMS during the comparison stimulus led to an increase in the proportion of trials in which subjects indicated that the comparison (second) stimulus was longer.

As in Experiment 1, differences were noted in the No-TMS 600–600 and UT–UT conditions; in contrast to Experiment 1, however, only 600–600 trials exhibited a positive time-order error, whereas UT–UT trials exhibited a near equal proportion of shorter and longer responses.

GENERAL DISCUSSION

Data from two experiments demonstrate that rTMS is associated with a subjective prolongation of a concurrent visual stimulus. These data are in line with previous studies demonstrating the involvement of right parietal cortex in temporal perception (Lewis & Miall, 2006; Harrington & Haaland, 1999). Although several studies also demonstrate left parietal activity during temporal perception (for a review, see Coull, 2004), in the present study, left SMG stimulation did not result in any significant changes in performance versus vertex stimulation.

Combining our results with another recent rTMS study of parietal cortex suggests dissociable functions of the right AG and right SMG in temporal perception. Bueti, Bahrami, et al. (2008) investigated the role of parietal cortex in timing by administering on-line rTMS to the left and right AG, and vertex as a control site. Subjects performed a temporal discrimination task with auditory and visual stimuli in separate experiments. Standard stimuli were 600 msec in duration, whereas comparison stimuli ranged 435–765 msec. Stimulation occurred at the onset of the comparison (second) stimulus. For visual stimuli, stimulation of the right AG significantly increased variability (but not the point of subjective equality) as compared to the vertex and No-TMS conditions. For auditory stimuli, right AG stimulation was associated with significantly increased variability as compared to the No-TMS condition; the effect was significant in comparison to vertex stimulation only when the comparison durations were restricted to a smaller range of 520–680 msec.

Dissociations between stimulation of the AG and the SMG have been reported in other domains as well. Rushworth et al. (2001) demonstrated that rTMS to the right AG, but not the SMG, selectively disrupted spatial reorienting to a peripheral target on invalidly cued trials. In contrast, Chambers et al. (2004) demonstrated that disruption of the right SMG, but not the AG, disrupted covert orienting to a peripheral target.

Supramarginal Gyrus and Scalar Expectancy Theory

Stimulation of the right SMG selectively increased perceived duration. As this increase occurred during stimulation of either the standard (first) or comparison (second) stimulus, disruptions of memory or decision stage mechanisms are unlikely to explain our results. Memory processes are assumed to be relevant to the maintenance of a measure of the duration of a stimulus; the fact that rTMS altered performance during the first stimulus—that is, at a time at which memory demands are minimal—strongly suggests that the effects were not attributable to an alteration in retention of knowledge of stimulus duration. Similarly, as decision processes in this task would be primarily active during and/or following presentation of the comparison (second) stimulus, the fact that stimulation was effective during the first stimulus makes altered decision processes an unlikely explanation. Finally, neither hypothesis offers a principled explanation for the most striking aspect of the data, the fact that there was consistent directional effect of rTMS; that is, ''longer'' responses decreased in Experiment 1 and increased in Experiment 2.

We suggest that rTMS influences the clock mechanism. There are several possible mechanisms by which this could occur. First, rTMS could have directly influenced the speed of the pacemaker; an increase in the pacemaker rate during rTMS would yield the obtained results. A second possibility is that rTMS may have modulated the accumulator; an increase in the efficiency of accumulation would lead to a subjective prolongation of a time interval as a greater number of ''pulses'' would result for a given duration.

Finally, an alteration in the attentional gate could explain these data; for example, if rTMS is associated with an ''opening'' of the gate such that more pulses were directed to the accumulator, the accumulation would progress more rapidly and the interval would appear to be longer. The Attentional Gate Model (Zakay & Block, 1995) proposes that attentional resources are divided between temporal and nontemporal processes, a phenomenon known as time-sharing (Fortin, 2003). As the right SMG has been implicated in the covert orienting of spatial attention (Chambers et al., 2004; Perry & Zeki, 2000) and other operations for which ''attention'' is thought to be crucial (Ortuno et al., 2002; Driver & Mattingley, 1998), disruption of the right SMG may have disrupted the flexible, on-line process by which attention is allocated to timing and other operations relevant to the organism's current state. Although one might expect subjects in this experiment to be orienting attention primarily toward the timing task, some proportion of their attention is likely directed toward nontask elements. If rTMS to the right SMG results in disruption in directing covert attention to these nontask elements, then by the time-sharing account, a greater amount of attention would be allocated to the judgment of temporal duration. This would cause faster accumulation of ''pulses'' because the gate is operating more efficiently for a greater proportion of the stimulus. By this account, the right SMG is not crucial for timing per se, but any operation in which attentional resources must be flexibly and quickly reallocated between tasks. Unfortunately, given the complex interactions of the putative elements of the clock, our data do not permit one to adjudicate between the pacemaker, accumulator, and attentional gate accounts described above.

The results of the present experiment provide support for neural models of temporal perception that postulate a right hemispheric network mediating temporal perception (Lewis & Miall, 2006). Furthermore, this study highlights the importance of attentional resources in shaping judgments of temporal intervals, and provides support for neural models of timing that suggest right parietal cortex is involved in temporal attention.

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