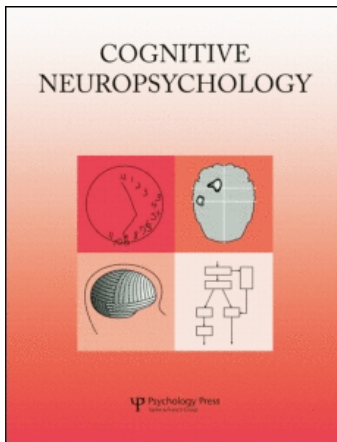


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THE RIGHT PARIETAL CORTEX AND TIME PERCEPTION: BACK TO CRITCHLEY AND THE ZEITRAFFER PHENOMENON

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We investigated the involvement of the posterior parietal cortex in time perception by temporarily disrupting normal functioning in this region, in subjects making prospective judgements of time or pitch. Disruption of the right posterior parietal cortex significantly slowed reaction times when making time, but not pitch, judgements. Similar interference with the left parietal cortex and control stimulation over the vertex did not significantly change performance on either pitch or time tasks. The results show that the information processing necessary for temporal judgements involves the parietal cortex, probably to optimise spatiotemporal accuracy in voluntary action. The results are in agreement with a recent neuroimaging study and are discussed with regard to a psychological model of temporal processing and a recent proposal that time is part of a parietal cortex system for encoding magnitude information relevant for action.

INTRODUCTION

The ability to register the temporal order and the temporal structure of events in the external world is important for coherent synchronous visual perception (Battelli, Cavanagh, Martini, & Barton, 2003; Nishida & Johnston, 2002; Walsh, 2002), in the timing of motor behaviour (Miall, 1996; Wing & Kristofferson, 1973), and in estimating the duration of intervals of time (Wearden, 1998, 1999). The brain areas identified as important for time perception have been associated with widely different ranges of time intervals: circadian rhythms depend on the suprachiasmatic nucleus; ultradian

cycles are abolished by lesions to the paraventricular and retrochiasmatic nuclei; and much shorter intervals of seconds or milliseconds variously require cortical structures such as motor and supplementary motor areas, right parietal cortex, prefrontal cortex, and also the cerebellum (Harrington & Haaland, 1999; Hazeltine, Helmuth, & Ivry, 1997; Ivry, 1996; Lacruz, Artieda, Pastor, & Obeso, 1991; Rao, Mayer, & Harrington, 2001; Theoret, Haque, & Pascual-Leone, 2001). Several lines of evidence indicate that one of these regions, the right inferior parietal cortex (rIPC), is indispensable for time perception. For example, Rao et al. (2001) have observed rIPC activity specific to

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prospective time judgements in fMRI experiments; patients with rIPC damage, but not left, have substantial time-related perception deficits (Battelli et al., 2003; Harrington, Haaland, & Knight, 1998); and electroencephalographic (EEG) recordings also implicate right posterior cortical areas in time perception (Mohl & Pfurtscheller, 1992). The occurrence of pure temporal deficits may be less salient or less common than spatial and visuomotor deficits following parietal lesions but, as Critchley (1953) noted, spatial and temporal deficits often coincide and parietal patients can display a wide range of errors in temporal experience. Such patients may be unable to judge the passage of time during a medical interview, time may appear to pass too quickly, objects may appear to move too quickly, too slowly, or too jerkily—phenomena that “may be merely a part of a more generalized distortion of the temporal sense, i.e. the ‘time-grabbing’ (*Zeitraffer*) phenomenon” (Critchley, 1953, p. 300; see also pp. 301–303). The parietal cortex is also emerging as an important locus of multimodal integration and some temporal phenomena hitherto regarded as purely visual have recently been shown to have auditory analogues (e.g., Hodinott-Hill, Thilo, Cowey, & Walsh, 2002), suggesting that time, like space, requires or involves multimodal algorithms. The association of time and spatial attributes in the parietal cortex has also recently been discussed in a wider context, also encompassing number (see Walsh, 2003a, 2003b).

In this experiment, to test competing predictions that the right and left parietal cortex are important for time perception, we disrupted the normal activity of right or left IPC by applying low-frequency (1 Hz), repetitive transcranial magnetic stimulation (rTMS) over these regions. Stimulation at 1 Hz has been shown to decrease blood flow and cortical excitability in the region targeted by TMS for several minutes following stimulation (Chen et al., 1997; Paus, Jech, Thompson, Comeau, Peters, & Evans, 1997) and to impair performance on behavioural tasks that depend on the region stimulated (e.g., Kosslyn et al., 1999; Theoret et al., 2001). To make our interference study as closely comparable as possible with a recent neuroimaging study

(Rao et al., 2001) we adapted the behavioural procedures described in that paper.

METHODS

Subjects

Six subjects, four male and two female, mean age 30.5 years, all right-handed, participated. All were screened for TMS exclusion criteria according to Wasserman (1998) and gave written informed consent to take part. All had previous experience as TMS subjects. They were paid for their participation. All procedures were approved by the Departmental Ethics Committee and by Oxford Research Ethics Committee (OXREC).

Experimental procedure

Subjects sat in a dark, quiet room 60 cm from a loudspeaker, which delivered the auditory discriminanda, and carried out a pitch discrimination task and a time discrimination task before receiving repetitive pulse TMS (rTMS). Magnetic stimulation was delivered for 10 minutes over the right or left parietal cortex or the vertex, as described below, and the subjects were then immediately retested on the two discrimination tasks. The order of tasks and TMS conditions was counterbalanced across subjects. Stimuli were generated from a Pentium II PC and delivered at 12dB[A] above background. All programs were written in E-Prime software and key-press responses for reaction times and accuracy were measured using a response box on which subjects made one of two presses with their right hand to indicate their decision of longer/shorter (time task) or higher/lower (pitch task). The motor demands of the two tasks were identical. There were 64 trials in each block and subjects carried out a control block per TMS block.

Time discrimination task

Two tones (700 Hz for 50 ms) separated by a standard interval of 1200 ms were followed by a delay of 1000 ms and by two further identical tones

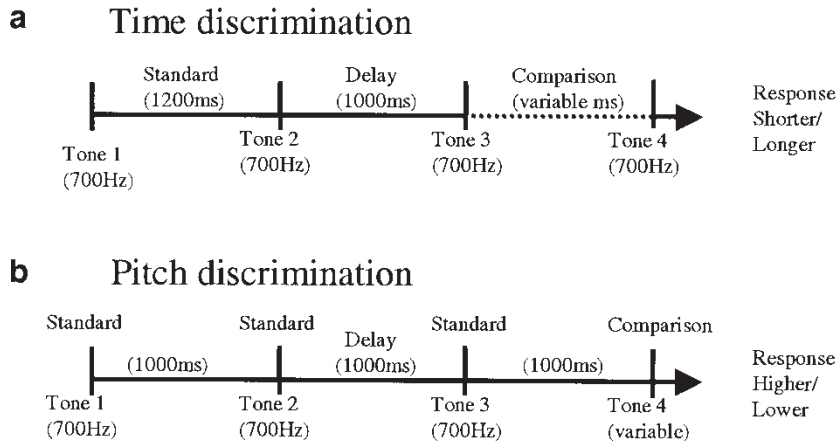


Figure 1. The tone sequences and responses of (a) the time and (b) the pitch tasks. In each task the subject heard four tones. In the time task the subjects judged whether the interval between tones 3 and 4 was longer or shorter than between tones 1 and 2 (the interval difference was $\pm 60, 120, 180,$ or 240 ms and the interval between tones 1 and 2 was always 1200 ms). In the pitch task, both intervals were 1000 ms and the subjects judged whether the fourth tone was higher or lower in frequency than the first three tones. Tones 1–3 were always 700 Hz and tone four was $700 \pm 4, 8, 12,$ or 16 Hz.

(700 Hz, 50 ms) separated by a comparison interval ($1200 \pm 60, 120, 180$ or 240 ms). The subject's task was to indicate, by a key press, whether the comparison interval between the third and fourth tones was shorter or longer than the standard interval between the first two tones (Figure 1a).

Pitch discrimination task

Subjects were presented with three standard tones (each 700 Hz for 50 ms) separated by 1000 ms followed by a fourth comparison tone ($700 \pm 4, 8, 12$ or 16 Hz), which subjects had to judge as either being higher or lower than the three standards (Figure 1b).

Magnetic stimulation

TMS was delivered at 1 Hz for 10 minutes using a Magstim Super-Rapid stimulator and a 70 mm figure-of-eight coil. The intensity was fixed at 65% of maximum stimulator output. In the TMS condition the behavioural task immediately followed the TMS. Before subsequent testing on a non-TMS or another TMS block the subjects had a 30 -minute break to preclude the possibility of

any TMS after-effects from having any effect on a subsequent block.

The parietal areas stimulated lie between the motor cortex and the visual cortex and it is difficult to select a level of TMS based on intrinsic excitability because there is no equivalent of a motor threshold or a phosphene threshold to use as a guide and the excitability of one region of cortex does not predict the level of stimulator output for another region of cortex (e.g., Stewart, Walsh, & Rothwell, 2000). Accordingly, the intensity and recovery periods were selected on the basis of other TMS studies that have used 1 Hz TMS in cognitive tasks (e.g., Kosslyn et al., 1999), disrupted parietal cortex function (Ashbridge, Walsh, & Cowey, 1997), or disrupted timing behaviour (Theoret et al., 2001).

The coil was fixed tangential to the skull with the handle pointing backwards at approximately 45° to the spinal cord. Subjects wore a tight-fitting lycra cap on which the relevant coordinates of the international 10/20 EEG system were marked. To select the region of stimulated parietal cortex, subjects first carried out a visual conjunction search task on a VDU at 60 cm distance, while receiving 10 Hz TMS for 500 ms over the P3 or P4 electrode

site (left and right parietal cortex respectively). The coil stimulated sites on and around these locations for blocks of 20 trials until one region was found that consistently and markedly increased mean reaction times on the search task. This region was usually within 1 cm of the marked electrode site. We have described this "hunting procedure" in detail in several papers (e.g., Ashbridge et al., 1997). To compare our functional identification of the posterior parietal cortex with a measure of anatomical accuracy, before proceeding to the time experiment, we used theBrainsight Frameless Stereotaxic system (Rogue Research, Montreal, Canada) to identify the regions stimulated and to allow comparison with the parietal areas localised by Rao et al. (2001). Each subject was scanned to provide MRI T1 structural images. We then localised the intended site of stimulation on each subject. Figure 2 shows the Brainsight localisations

of the parietal areas stimulated. As an additional control for nonspecific effects of TMS, the vertex was used as a stimulation site in four of the subjects to ensure that there were no effects due to the tactile or auditory sensations of TMS. Vertex was included purely as a check for nonspecific effects; the critical control condition was the IIPC stimulation. We thus carried out one analysis with IIPC vs. rIPC TMS and a separate analysis to ensure that behaviour following vertex TMS did not differ from no-TMS.

RESULTS

Reaction time data from correct trials were subjected to a two-factor Task (time/pitch) \times Stimulation (IIPC, rIPC and no-TMS) repeated measures ANOVA to compare the effects of TMS

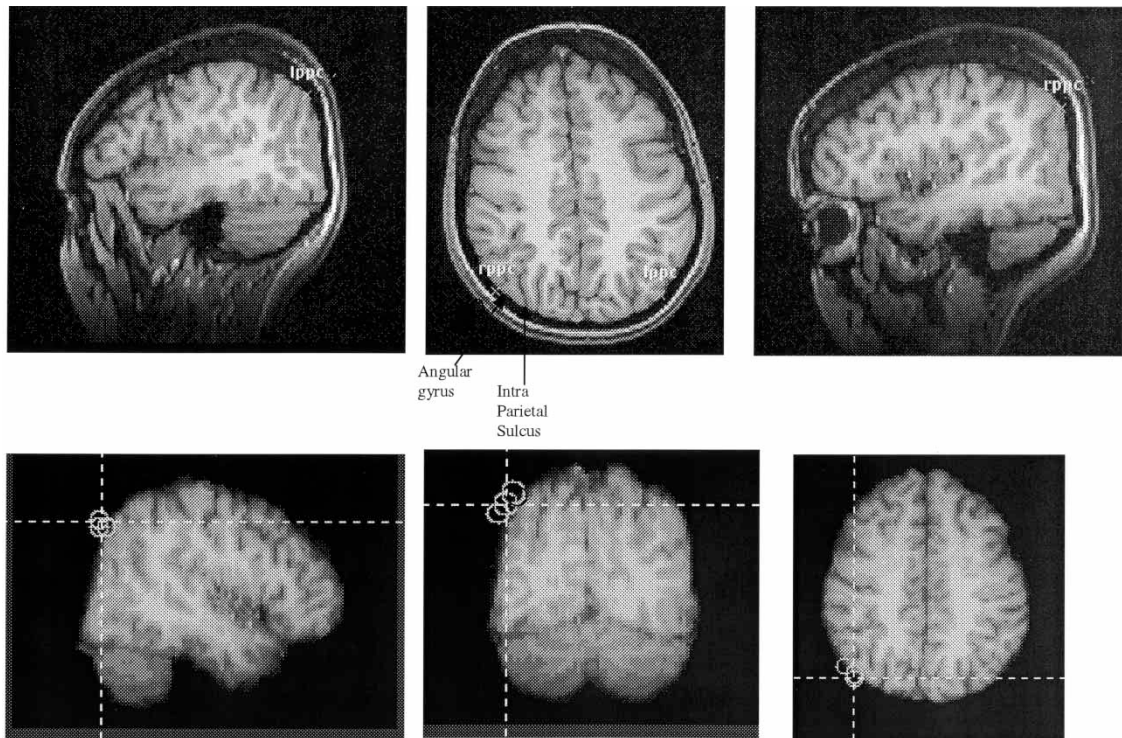


Figure 2. Localisation of the rIPC stimulation site with Brainsight. The stimulated areas were the left and right inferior parietal cortices, ventral to the intraparietal sulcus and on the angular gyrus.

on the two tasks, followed by post hoc tests to test directly the prediction that rIPC TMS would impair temporal discrimination. There was a significant main effect of stimulation, $F(2, 10) = 6.13$; $p < .02$, and a significant interaction effect between task and stimulation, $F(2, 10) = 5.128$; $p < .05$. There was a significant effect of TMS on time, $F(2, 15) = 5.56$; $p = .018$, but not pitch, $F(2, 15) = 0.323$; $p = .729$. Figure 3a shows that the mean reaction times on the time discrimination task increased significantly, by 166 ms, when TMS was applied over rIPC, relative to no-TMS (Dunnett's test, $p < .05$). Left IPC stimulation had no effect on reaction time relative to the no-TMS control (RT increase = 9 ms, $p > .05$).

Figure 3b shows the mean reaction time performance on the pitch discrimination task. In contrast to the time task, there was no significant effect of applying TMS over IIPC or rIPC compared to no-TMS controls ($p > .05$ in all cases), although left IPC stimulation slightly but insignificantly decreased reaction time (-20 ms), $p > .05$.

To examine the nonspecific effects of TMS, a two-factor Task (time/pitch) \times Stimulation (vertex and no-TMS) repeated measures ANOVA was carried out. There was no significant main effect of task, $F(1, 3) = 1.418$; $p > .05$, or stimulation,

$F(1, 3) = 1.841$; $p > .05$, and there was no significant interaction effect between task and stimulation, $F(1, 3) = 0.604$; $p > .05$.

The tasks were always performed at a high level of accuracy. Mean % correct responses in the pitch task were IIPC = 84.9%, rIPC = 83.55%, vertex = 93.6%, no-TMS = 91.2%. Mean errors in the time task were IIPC = 83%, rIPC = 89.6%, vertex = 84.37%, no-TMS = 92.8%. Error data were subjected to a two-factor Task (time/pitch) \times Stimulation (IIPC, rIPC and no-TMS) repeated measures ANOVA. There was no significant main effect of task, $F(1, 5) = 0.066$; $p > .05$, or stimulation, $F(2, 10) = 0.387$; $p > .05$, and there was no significant interaction effect between task and stimulation, $F(2, 10) = 3.072$; $p > .05$. A two-factor Task (time/pitch) \times Stimulation (vertex and no-TMS) repeated measures ANOVA on error data from vertex and no-TMS conditions revealed no significant main effect of task, $F(1, 3) = 0.273$; $p > .05$, or stimulation, $F(1, 3) = 6.618$; $p > .05$, and there was no significant interaction effect between task and stimulation, $F(1, 3) = 1.744$; $p > .05$.

In summary, 1 Hz rTMS over the right IPC impaired time perception and this effect was specific when controlled by task (pitch perception) and TMS stimulation site (IIPC). The results are

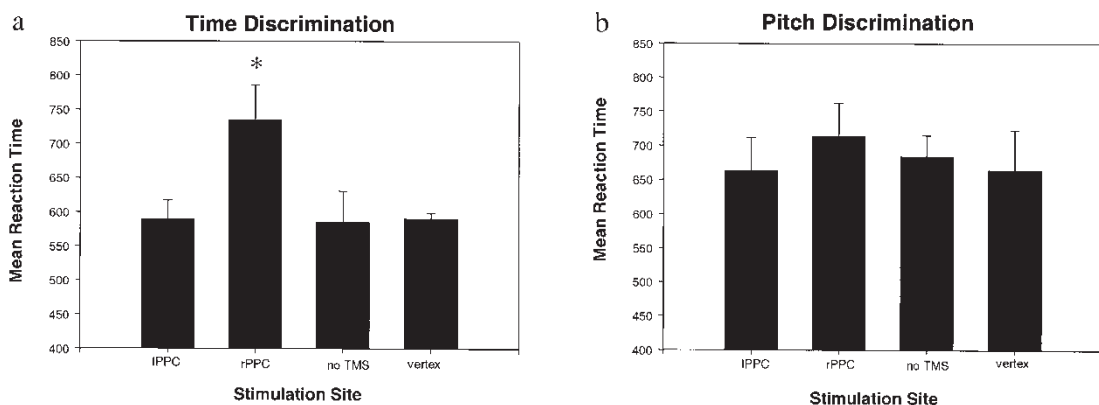


Figure 3. The effects of rTMS on reaction time when judging (a) time and (b) pitch. Time: rTMS over the rIPC significantly delayed the response to categorise a temporal interval as longer or shorter than a standard. Stimulation over the vertex or the IIPC on the time discrimination task did not delay reaction times significantly. There were no effects of rTMS over left or right parietal cortex or vertex on the ability to make pitch judgements.

not attributable to task difficulty. If time taken to reach a decision is taken as an index of difficulty, the pitch perception task was more difficult and therefore more likely to be disrupted by nonspecific aspects of magnetic stimulation. We can be sure that these effects of TMS are independent of motor effects because there was no effect of left parietal TMS even though all responses were made with the right hand. The effects were also specific to task, which is inconsistent with a motor artefact explanation of the data.

DISCUSSION

The effects of TMS show the right inferior parietal cortex to be necessary for rapid discrimination of temporal intervals. This is consistent with Critchley's observation of the judgement of time, the *Zeitraffer* phenomenon, following parietal cortex damage, with brain-imaging evidence (Rao et al., 2001), with temporal deficits observed in neuropsychological patients (Battelli et al., 2003; Harrington et al., 1998; Lacruz et al., 1991) and with EEG evidence (Mohl & Pfurtscheller, 1992).

Reaction time and error data were both analysed in this study. In several previous studies (e.g., Ashbridge et al., 1997) we have observed that tasks that are performed at a high level of correctness are likely to yield reaction time deficits rather than errors during TMS, whereas tasks close to the threshold of performance are also likely to produce increased errors in response to TMS. The reasons for this have been rehearsed at length in other publications (e.g., Walsh & Cowey, 1998; Walsh & Pascual-Leone, 2003), but before proceeding to our interpretation of the data it is perhaps worth stating what we understand a TMS disruption to mean in general terms. Briefly, if one considers the neural activity induced by TMS as highly unlikely to be organised in the pattern required for the brain area being stimulated to make its normal contribution to a task, the TMS can be considered to act as "neural noise." As a useful analogy, consider adding visual white noise to a display during, say, a visual identification task. With a little noise added, the subject might not

immediately make misidentifications but might take longer to identify the target. If the noise level is increased, then the time required to identify the target will increase. If the noise level is increased again, subjects may begin to make errors. In other words, introducing noise to a signal is more likely to slow down correct performance than to force errors. One referee of this article asked whether a RT deficit without an error deficit could be considered as evidence that the stimulated area is *necessary* to perform the task. What we mean by necessary is *necessary for normal performance*. If the induced neural noise slows down performance then we would consider it as having induced an abnormal performance and thus have demonstrated the necessity of the area in normal performance.

The role(s) of the parietal cortex, or of cortex in general, in time perception have been investigated far less than those of subcortical structures. As a consequence, cortical processes have been loosely associated with all stages of temporal processing. In one model, for example, cortex is allocated a comparator role (decision unit in Figure 4) (Hazeltine et al., 1997; Meck, 1996). Although we agree that comparator processes may be cortical (see below), Meck's model applies to longer intervals (20 seconds or more) than those with which we are concerned here. Gibbon, Malapani, Dale, and Gallistel's model (1997) differentiates between prefrontal and premotor components but posterior parietal regions are not included. Rao et al. (2001, p. 317) also suggest that the parietal cortex may be required to encode or maintain temporal intervals (the memory component in Figure 4). Several studies emphasise the attentional role of parietal cortex in timing functions (Coull & Nobre, 1998; Rao et al., 2001). Other proposals suggest that attention may act at the level of the pacemaker (Timer in Figure 4), the switch between the pacemaker and accumulator (Zackay & Block, 1995), the level of the accumulator itself (Burle & Casini, 2001), or attention to expected or unexpected intervals in motor preparation (Coull & Nobre, 1998). Given the psychophysical success of certain models of time perception and timing behaviour (Gibbon et al., 1997; Wearden, 1999; Wing & Kristofferson, 1973), attention is clearly too vague a parameter to

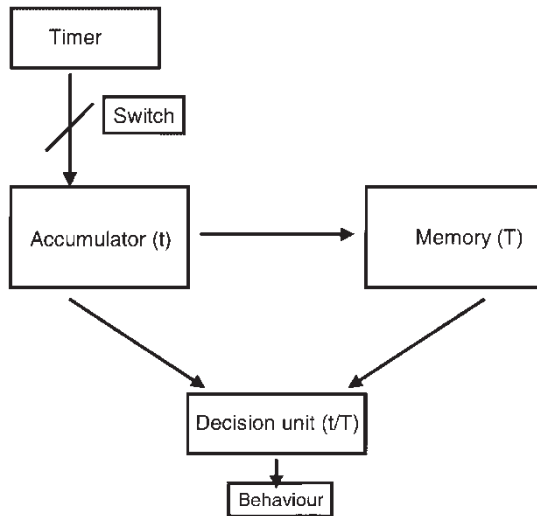


Figure 4. *A model of time perception containing the elements common to the major models of Gibbon, Meck, and Treisman. Terminology may change from paper to paper: the Timer is also termed “pacemaker” or “clock,” the Accumulator “integrator” or “working memory,” and the Memory Unit may sometimes be referred to as “reference memory.”*

be of use in constraining explanations. The many degrees of freedom allowed by an attention-based explanation permit it to be applied alike to pacemaker, gating, integrating, encoding, maintaining, comparing, and decision stages of temporal models indiscriminately (see Walsh, 2003b).

There is some inconsistency in neuroimaging studies regarding which hemisphere is activated by temporal information processing. Rao et al. (2001) reported rIPC activity in a prospective task whereas Coull and Nobre (1998) reported left parietal activity. Our data, using a task similar to that of Rao et al., support their observations. The left hemisphere activity reported by Coull and Nobre was elicited by a task that confounded motor preparation and time processing and, as the authors suggest, is likely to be due to the motoric elements of the task rather than to anything concerned with temporal processing. Our data, then, support the suggestion by Rao et al. that the rIPC is important for encoding and maintaining temporal intervals. We propose that the right parietal cortex uses representational systems, perhaps spatially encoded (Walsh, 2003b), that are common to time, space, and quantity as relevant to action and that this rep-

resentation is available to left hemisphere areas required for action selection and generation.

Figure 4 schematises a psychological model of time perception containing the core elements common to experimental studies (Gibbon et al., 1997; Meck, 1996; Treisman, 1963). The five elements of this model are Timer, Switch, Accumulator, Memory, and Decision Unit. In trying to account for the importance of rIPC in time perception, we have asked which of these functions seem to be closely related to already-known functions of the parietal cortex and also which known functions of parietal cortex might share computational or behavioural goals with some element of the time model.

In terms of temporal processing, being at the crossroads between perception and action places the role of the parietal cortex at the junction of central clock and peripheral effector processes. Hazeltine et al. (1997, p. 167) have observed that “in many cases, the distinction between time production and time perception is unclear” and where tasks fall within the range of motor decisions and actions (i.e., hundreds of milliseconds) this uncertainty may arise precisely because time information is used for

action. Treisman (1963, 2002) also noted that “The coupling between perceiving durations and acting in time requires that similar pacemakers mediate both” (2002, p. 220). The parietal cortex, in its pivotal role in the “where” and “how” of spatial vision (Milner & Goodale, 1993), may also use temporal information to ensure that the metrics employed in space are employed at the right moment, which requires accurate spatiotemporal integration.

Our emphasis on the parietal cortex, at the interface of temporal transformations to be used with spatial information, raises the question of which components of models of timing (Gibbon et al., 1997; Meck, 1996; Treisman, 1963) best encapsulate its function. Our proposal that its importance lies in the need for convergence of space and time predicts an effect late in the processing hierarchy (Figure 4). This question is currently being pursued by assessment of inaccuracies made during time production tasks following 1 Hz rTMS. The pattern of inaccuracies may be more compatible with rIPC being the last stage of clock processing (in which case rTMS will bias judgements rather than increase variability) or the first stage of post-clock processes (in which case rTMS will increase variability more than bias). One might also predict that the behavioural pattern will fall between clock-like (increased bias) and effector-like (greater variability) patterns (Wing & Kristofferson, 1973) precisely because rIPC disruption could interfere with incoming clock signals or outgoing signals transformed to employ a metric compatible with spatial requirements. There is a clear consensus that where to look and reach (Ungerleider & Mishkin, 1982), and how to grasp (Milner & Goodale, 1993), require the integrity of the parietal cortex. However, not all objects to be fixated, pointed to, or grasped are stationary (e.g., tracking someone in a crowd; shaking someone’s hand; catching something thrown; etc.), and behavioural accuracy often requires anticipation or temporal calculations: Behaviourally, space and time cannot easily be segregated (Campbell, 1994). In this context it is important to note that space and time processing are required in accurate motion perception and it is established that the right parietal cortex is involved in auditory spatial perception

and higher-level motion perception (Battelli et al., 2001; Bisiach, Cornacchia, Sterzi, & Vallar, 1984; Griffiths et al., 1998). It would not be surprising if the sensory sources to be temporally decoded in these tasks involved the same region concerned with localisation, movement, and duration. Our data do not preclude a role for the left parietal cortex in temporal information processing in tasks other than the simple judgements made in our experiment. Indeed, when temporal information processing may have more motoric implications than in our task the left hemisphere is likely to be very important. A recent experiment showing such left hemisphere involvement in spatiotemporal integration (Assmus, Marshall, Ritzl, Noth, Zilles, & Fink, 2003) is one such example and how the left and right hemispheres contribute to other tasks is clearly an important question.

An important feature of cortical organisation relevant to this proposed convergence of space and time in behaviour is that wiring distances are kept to a minimum (Cowey, 1979), a consequence being that related computations are often performed in overlapping cortical areas or by near neighbours. We therefore suggest that the production of a time discrimination deficit with rIPC TMS reflects the fact that the need for a common metric of time and space to ensure accurate action requires that time information (in temporal ranges relevant for action) be closely associated with the visuospatial transformations carried out by the right posterior parietal cortex. Half a century after Critchley’s comments concerning the *Zeitraffer* phenomenon, the parietal cortex has grabbed time back.

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