CORTEX 44 (2008) 462–469

available at www.sciencedirect.com

ScienceDirect

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Special issue: Original article

Dissociation of numerosity and duration processing in the left intraparietal sulcus: A transcranial magnetic stimulation study

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ARTICLE INFO

Article history:
Received 3 April 2007
Revised 9 July 2007
Accepted 20 August 2007
Published online 23 December 2007

Keywords:
Numerosity
Duration
TMS
IPS

ABSTRACT

A possible dissociation of duration and numerosity processing was tested in an off-line repetitive transcranial magnetic stimulation (rTMS) design. Participants had to compare the numerosity of flashed dot sequences or the duration of single dot displays before and after 15 min of 1 Hz rTMS over one of three sites (the left or right intraparietal sulcus (IPS), or the vertex chosen as a control site). Compared to the control site, performance was only slowed down for the numerosity comparison task after the left IPS stimulation, whereas it was not affected for the duration comparison task for any of the parietal sites. These results show that the parietal area critically involved in numerosity processing is not involved in duration processing, revealing at least one cerebral site where duration and numerosity comparison processes dissociate.

1. Introduction

Various animal species can discriminate numerosities (Boysen and Capaldi, 1993; Breukelaar and Dalrymple-Alford, 1998; Davis and Perusse, 1988) and durations (Roberts and Church, 1978) in experimental as well as natural conditions. These results are well accounted for by a model where the numerosity and duration of sequential events are encoded into a single accumulator through different operative modes. The impulses produced by a generator can either be summed each time an event is encountered (for numerosity processing), or at a given frequency (for duration processing) (Meck, 1997; Meck and Church, 1983; Meck et al., 1985). Such a process accords with the early preverbal numerical abilities of infants, from which adult arithmetical abilities develop (Dehaene, 1992; Dehaene et al., 1998; Gallistel and Gelman, 1992). It has therefore been assumed that the adult brain is endowed with a common functional mechanism, underlain by a common cerebral substrate, to process numerosity and duration (Walsh, 2003).

We recently investigated the interaction between duration and numerosity processing at a functional level (Dormal et al., 2006). The duration and numerosity of a series of flashing dots were simultaneously and independently manipulated in a Stroop paradigm to create congruent, incongruent and neutral trials. The participants had to compare either the total duration or the number of dots in two series. The irrelevant numerical cues conveyed by the stimuli were found to influence the temporal judgement, as demonstrated by the presence of a facilitation effect in duration processing when numerosity and duration were congruent, and an interference

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doi:10.1016/j.cortex.2007.08.011

effect when they were incongruent. However, the temporal cues did not interfere with numerosity judgements. These results indicate that the interactions between numerosity and duration processing are limited to a unidirectional interference of numerosity on duration. Similar results were observed in adults and in 5- to 8-year-old children during a task which involved bisecting a series of dot displays flashed for 2–8 sec (Droit-Volet et al., 2003). This suggests a difference in the mandatory processing of numerosity and duration, but does not allow firm conclusions concerning a possible common mechanism or dissociation, and hence a common or different brain substrate, to be drawn.

The assumption that numerosity and duration processes share a common cerebral substrate is thus still under debate. On the one hand, brain imaging studies are converging towards the involvement of parietal areas, and more precisely the intraparietal sulcus (IPS), in the estimation of the numerosity of sequential series of visually- or auditory-presented stimuli (Piazza et al., 2006). Bilateral activations in the IPS were found in response to visual numerosity changes when participants were passively exposed to arrays of dots in event-related adaptation paradigms (Ansari et al., 2006; Cantlon et al., 2006; Piazza et al., 2004). A bilateral involvement of the posterior IPS was also demonstrated in dot enumeration or simple addition tasks (requiring explicit counting), irrespective of whether the stimuli were presented sequentially or simultaneously (Fink et al., 2001; Piazza et al., 2002, 2003; Sathian et al., 1999; Venkatraman et al., 2004). Finally, the critical role played by the left IPS in processing numerosities was demonstrated in a recent transcranial magnetic stimulation (TMS) study showing that the comparison of dot collections was slowed down after the stimulation of the left IPS (Cappelletti et al., 2007).

On the other hand, neuropsychological and brain imaging studies have suggested that duration processing involves a neural network including the frontal cortex, the cerebellum, the basal ganglia, the inferior part of the temporal lobes, the cingulate cortex, and parietal areas (Gibbon et al., 1997; Griffiths et al., 1999; Harrington, et al., 1998; Ivry and Keele, 1989; Ivry and Spencer, 2004; Jueptner et al., 1995; Matell and Meck, 2004; Nichelli, et al., 1996; Tracy et al., 2000). Activations of the parietal cortices, mainly in the right hemisphere, were found during time estimation and comparison (Lejeune et al., 1997; Maquet et al., 1996). A bilateral involvement of the parietal cortex was also observed during the processing of auditory and visually presented temporal rhythmic patterns (Schubotz et al., 2000). Moreover, the temporal allocation of attention (e.g., cued allocation of attention across delays) was found to produce a left-sided activation in the IPS (Coull et al., 2000; Coull and Nobre, 1998). Finally, increased latencies were found when TMS was applied over the right posterior parietal cortex as participants were judging whether a duration interval (from 960 to 1440 msec) was longer or shorter than a standard interval (1200 msec) (Alexander et al., 2005). To sum up, although activation in areas close to the IPS has been observed in studies concerned with either numerosity or duration processes, no direct evidence for a common cerebral substrate for numerosity and duration processing has been provided so far.

Whether numerosity and duration processes do or do not share the same mechanism and neuro-anatomical substrate in the parietal cortex thus remains an open question. The aim of the present study was to determine whether the IPS area(s) known to play a crucial role in numerosity processing is(are) also involved in duration processing. In order to test the causal relationship between numerosity or duration processing and the contribution of the IPS, a TMS off-line paradigm (Robertson et al., 2003; Walsh and Pascual-Leone, 2003) was used in which participants had to compare the numerosity of flashed dot sequences or the duration of single dot displays before and after repetitive transcranial magnetic stimulation (rTMS) over the left or right IPS. To exclude unspecific effects of the duration of the TMS, the two comparison tasks were also performed before and after rTMS over the vertex, chosen as a control site. Based on the results of previous functional imaging (e.g., Piazza et al., 2006) and TMS (Cappelletti et al., 2007) studies, we predicted that IPS stimulation would slow down responses in the numerosity comparison task. The performance in the duration comparison after parietal TMS should throw light on the existence of a shared mechanism for numerosity and duration processing in this region. Under the strong assumption that numerosity and duration are encoded into a single accumulator, a similar impairment should be observed in the duration task after rTMS over the IPS (i.e., slowing down the response latencies (RLs)). On the other hand, an absence of disruptive effects in the duration task is predicted if the IPS contribution to magnitude processing is specific to numerosity.

2. Materials and methods

2.1. *Participants*

Fifteen right-handed volunteers (three females, mean ± s.d. age: 22 ± 2.7 years) gave their informed consent to participate in this experiment. All had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. In particular, all of them were negative for the risk factors associated with TMS (Keel et al., 2002). The biomedical ethical committee of the Université Catholique de Louvain approved the rTMS protocol.

2.2. *Tasks and stimuli*

The participants had to perform two tasks: a numerosity comparison of two successive series of flashing dots and a duration comparison of two successive single dots. Stimuli in the numerosity task were composed of a black dot (diameter: 3.5 cm) rapidly flashed at the centre of the screen. The series were constructed using non-periodic signals so that temporal ratios did not constitute a potential confounding variable, and rhythm biases and pattern recognition were avoided (Breukelaar and Dalrymple-Alford, 1998; Dormal et al., 2006). The total duration of the series (i.e., the duration of the dots plus the inter-dot intervals) was constant (1500 msec). In the duration task, the stimuli were composed of pairs of single black dots (diameter: 3.5 cm) presented sequentially at the centre of the screen. To avoid as far as possible potential explicit or implicit counting strategies, non-subitizable numerosities (from 5 to 9 dots, excluding 7) and short durations (from 300 to 900 msec) were used. Pairs of series/dots were chosen to constitute two distances: a large distance (3 dots for numerosity, that is, pairs 5–8 and 6–9; 200 msec for duration, that is, pairs 300–500 and

700–900) and a small distance (1 dot for numerosity, that is, pairs 5–6 and 8–9; 100 msec for duration, that is, pairs 300–400 and 800–900). The order of presentation of the two series/dots within the pairs was also manipulated: half of the pairs began with the smaller/shorter series (S–L) and the other half with the larger/longer (L–S). The number of observations per subject in each cell of the design was 10.

2.3. *Experimental procedure and rTMS protocol*

Stimulus presentation and data collection were controlled by a Dell computer using a customised E-prime programme (Schneider et al., 2002) and equipped with a 17 inch screen (refresh rate: 85 Hz). The participants sat comfortably on a padded chair in a dark, quiet room, at 60 cm from the screen, and a response box (30 cm × 40 cm) with four horizontally aligned buttons lay on a cushion on their knees. At the beginning of each trial, a white rectangle (9.5 cm × 16 cm) was presented on a black background and the first series of flashing dots or a single dot was displayed in its centre for a given duration, after which the rectangle disappeared and was replaced by a black screen for 1000 msec. Then a new rectangle appeared and a second series or single dot was flashed. A black screen followed the second series/dot for a period of up to 1500 msec during which the participant could answer. As soon as the answer was given, the next trial started. In the numerosity comparison task, the participants were asked to press the furthest left button with the left index finger when the first series contained more dots than the second, and the furthest right button with the right index finger when it was the other way round; the two response buttons were 8 cm apart. In the duration comparison, participants had to decide which dot was displayed for longer, using the same key presses. The two tasks were designed to last approximately 5 min each.

rTMS was applied either over the left IPS, the right IPS, or the vertex (Cz) chosen as the control site (Fig. 1). Each site was stimulated on a separate day and the order of stimulation of the three sites was balanced across participants. At the beginning of each session, performance on the two comparison tasks was recorded in order to obtain a baseline measure. The rTMS was then delivered at 1 Hz for 15 min using a Magstim Super-Rapid stimulator (Magstim Co. Ltd., UK) and a 70 mm figure-of-eight coil. The coil was held over the targeted area by a mechanical arm, with the handle pointing downwards and forming an angle of 45° with the sagittal midline. TMS intensity was set at 65% of maximum stimulator output. This was selected on the basis of other TMS studies that had used 1 Hz TMS to interfere with cognitive tasks (e.g., Kosslyn et al., 1999), with particular interest in the parietal cortex functions (Ashbridge et al., 1997). Immediately after the end of the TMS train, participants were asked to perform the two comparison tasks again. Task order was balanced across subjects but, for a given subject, the two tasks were always presented in the same order before and after stimulation throughout the three TMS sessions. The vertex stimulation was used as a control condition in order to reveal non-specific effects due to prolonged exposure to the tactile and auditory sensations of TMS.

The localisation of stimulation sites was carried out with a frameless stereotactic system providing on-line information about the location of the coil (Noirhomme et al., 2004). Prior to the first session, a whole brain T1-weighted magnetic-resonance image (MRI) was acquired for each participant. The co-registration between the stimulation sites and the anatomical MRIs proceeded in three steps. First, the coordinates of about 200 points distributed randomly in the physical space over the participant's scalp were obtained using a digitized pen receiver connected to a forehead reference allowing for head movements (Polhemus Isotrak II System, Kaiser Aerospace Inc.). Second, the registration process created a transformation matrix that minimized the mean square distance between these points and a segmented scalp surface extracted from the individual MRI. Third, the figure-of-eight coil was placed over the target sites; three points were digitised at the intersection of the windings and converted within the transformation matrix; the position of the coil relative to the scalp was then indicated through the visualisation interface. A line normal to the plane of the coil was drawn from its centre to the brain, revealing the cortical impact point of TMS on both a segmented brain surface and the MRI slices.

This flexible method allowed the target sites to be visualised on individual brain images with a spatial accuracy close to a millimetre. The average location of the TMS sites in the left and right IPS was computed by normalising the individual brain images with reference to the MNI template provided by Statistical Parametric Mapping software (SPM2, Wellcome Department of Imaging Neuroscience, London, UK, <http://www.fil.ion.ac.uk/spm>; see Davare et al., 2006). As shown in Fig. 2, the parietal sites were located in the IPS (mean x, y, z ± s.d. for left IPS: −39 ± 4.6, −52 ± 8.6, 55 ± 5.5; for right IPS: 35 ± 6.2, −55 ± 7.3, 56 ± 5.9). This location is in good agreement

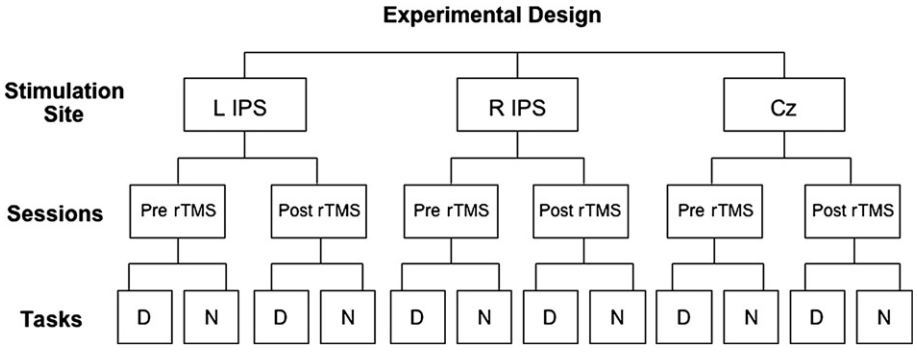

Fig. 1 – Experimental design using one possible counterbalancing order. L IPS = left intraparietal sulcus, R IPS = right intraparietal sulcus, Cz = Vertex; D = Duration task, N = Numerosity task.

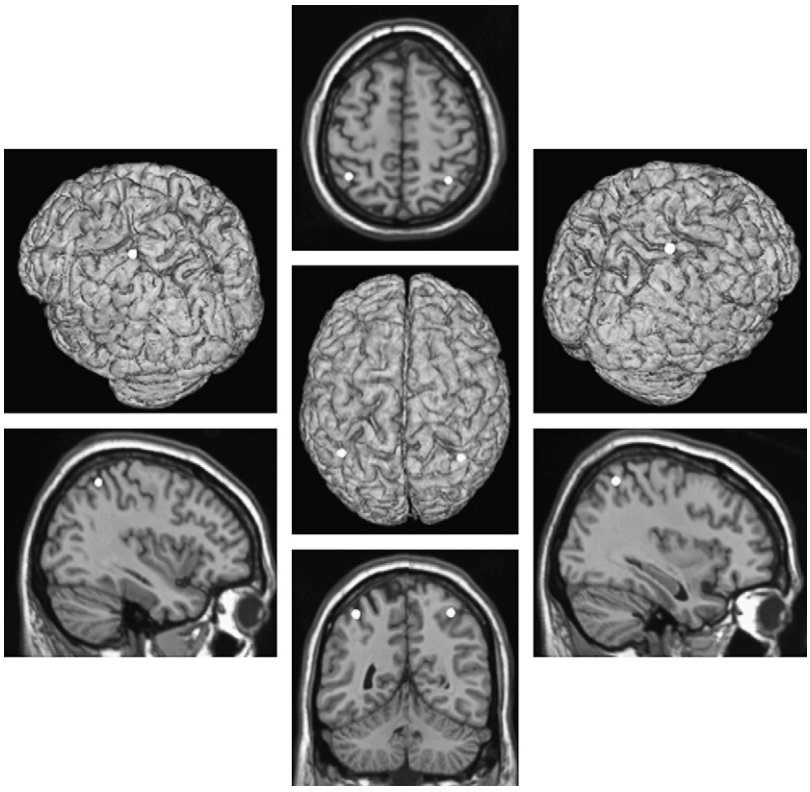

Fig. 2 – Location of the mean normalised left (−39, −52, 55) and right (35, −55, 56) IPS stimulation sites of the 15 participants on reconstructed standard brain surfaces and MRI slices. The left panels refer to the left hemisphere and the right panels to the right hemisphere. On the central panels, the axial and coronal views are oriented in the same way, following the neurological conventions.

with the results of brain imaging studies concerned with numerosity processing (e.g., Piazza et al., 2006).[1]

3. Results

Trials with RLs less than 100 msec (which were considered to be anticipatory responses), or more than 1000 msec were not included in the analyses (.8% of the data).

3.1. *Tasks and distance effects*

To assess the equivalence of the two tasks, and to test the distance effect, an analysis of variance (ANOVA) was performed on the RLs of correct pre-TMS answers with task (numerosity, duration) and distance (large, small) as within-subject variables. There was no difference between tasks (mean ± s.d. RLs for duration: 362 ± 56 msec; numerosity: 348 ± 69 msec; $F(1,14) < 1$). A significant main effect was found for distance (mean ± s.d. RLs: large distance: 342 ± 57 msec; small distance: 368 ± 66 msec; $F(1,14) = 26.238$, $p < .001$): large distances were responded faster than small distances. No significant interaction was observed ($F(1,14) < 1$).

The same ANOVA on error rates revealed significant main effects of task (mean ± s.d. percentage of errors: duration: 24 ± 11.5%; numerosity: 14 ± 13.2%; $F(1,14) = 29.649$, $p < .001$), and distance (mean ± s.d. percentage of errors: large distance: 9 ± 8.8%; small distance: 29 ± 7.6%; $F(1,14) = 248.315$, $p < .001$): more errors were produced in the duration task, and for small distances. No significant interaction was observed ($F(1,14) = 1.540$, $p = .235$).

3.2. *rTMS effects*

To investigate the rTMS effect on the various stimulation sites, an analysis was performed on the difference between the correct RLs in post- and pre-rTMS conditions with task (numerosity, duration), stimulation site (LIPS, RIPS, Cz) and distance (large, small) as within-subject variables.[2] There was a significant

[1] For example, the Euclidian distance between our left and right IPS stimulation sites and the IPS areas observed in numerosity processing in Piazza et al.'s (2006) study was 15 mm and 10 mm, respectively.

[2] In a separate analysis, the order of tasks (duration–numerosity *vs* numerosity-duration) was introduced as a supplementary between-subject variable. This was done to ensure that the interference effect of TMS applied uniformly throughout the experimental period, and to control for the presence of a possible temporal dissolution of this effect, as well as to assess a possible "priming" effect of one task over the other that could promote the use of a common neural code. Order had no main effect ($F(1,13) < 1$), but it interacted with task ($F(1,13) = 14.463$, $p < .002$). The RLs for the two tasks only differed significantly when duration was the second task ($t(7) = -5.128$; $p < .002$). Order did not appear in any significant interaction involving the stimulation site (all $F < 1$). The same analysis on the difference between the RLs in the post- and pre-rTMS sessions relative to the control site (Cz) showed no main effect and no interaction involving order. These analyses show that the order of tasks did not affect the interference effect of TMS.

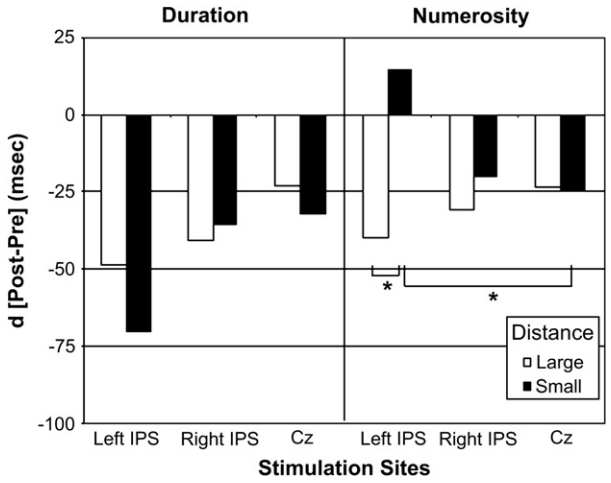

Fig. 3 – Difference in response latencies between post- and pre-rTMS session in msec for duration (left panel) and numerosity (right panel) tasks as a function of stimulation site (left IPS, right IPS or Cz) and distance (large or small). Asterisks indicate where the difference between two conditions was significant ($p < .05$).

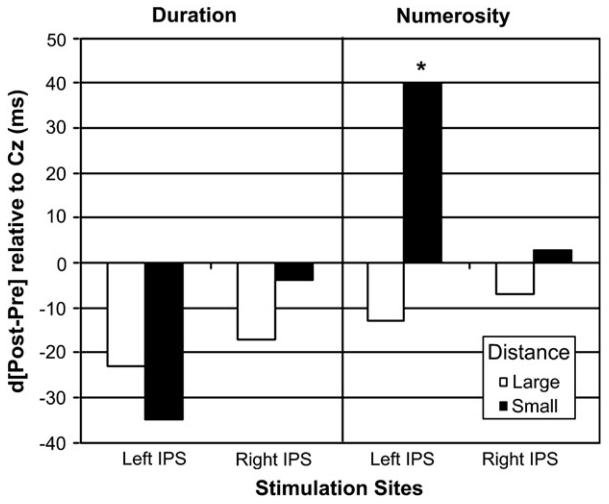

Fig. 4 – Difference in response latencies between post- and pre-rTMS session relative to the control site for duration and numerosity tasks as a function of stimulation sites and distance. Asterisks indicate which conditions were significantly different from zero ($p < .05$).

main effect of task (mean RLs difference ± s.d. for duration: −42 ± 52 msec; for numerosity: −21 ± 47 msec; $F(1,14) = 10.113$, $p < .008$): the overall decrease in the RLs observed after TMS was greater for the duration task. This effect interacted with distance ($F(1,14) = 15.101$, $p < .003$): no difference between small and large distances was found for the duration task (mean RLs difference ± s.d.: large distance: −38 ± 45 msec; small distance: −46 ± 59 msec; $t(14) = -1.17$, $p > .2$), while a significant difference was observed between the two distances in the numerosity task (mean RLs difference ± s.d.: large distance: −32 ± 36 msec; small distance: −10 ± 54 msec; $t(14) = 3.949$, $p < .001$). Moreover, a significant 3-way interaction between task, stimulation site and distance was found ($F(2,28) = 5.431$, $p < .02$).

Separate ANOVAs for duration and numerosity tasks with stimulation site and distance as within-subject variables revealed no RL difference in the duration task following stimulation over the parietal and control sites (all p values >.1),[3] whereas for the numerosity task, a main effect of distance was observed ($F(1,14) = 15.591$; $p < .002$), as well as a significant interaction between distance and stimulation sites ($F(2,28) = 3.430$; $p < .05$). *Post hoc* paired-sample t-tests indicated that close numerosity discrimination was impaired after rTMS over the left IPS compared to the control site ($t(14) = 2.248$, $p < .05$). No difference was observed between stimulation sites in far numerosity discrimination (left–right: $t(14) = -.597$, $p > .5$; left–Cz: $t(14) = -1.4$, $p > .1$; right–Cz: $t(14) = -.472$, $p > .6$) (see Fig. 3).

In order to investigate this effect further, we subtracted the difference between the RLs measured post- and pre-TMS over the left and right IPS from the difference between the RLs measured post- and pre-TMS over the control site. Then, we assessed the significance of this difference using t-tests. In this analysis, an RL decrease larger after left or right IPS stimulation than after stimulation of the control site resulted in negative dRLs, whereas positive dRL values indicated a greater slowing down of responses after left or right IPS stimulation than after the control site stimulation. Results showed that only the dRLs computed for the left IPS stimulation condition during the comparison of close numerosities were significantly different from 0 ($t(14) = 2.317$, $p < .04$). This indicates that the left IPS stimulation impaired numerosity discrimination when the numerical distance was small (see Fig. 4). The dRLs measured in the other conditions did not differ significantly from zero.[4]

Similar analyses performed on the difference in error rates between post- and pre-rTMS conditions showed no significant main effect or interaction (all p values >.1).

4. Discussion

In order to test a possible dissociation between numerosity and duration processing in the parietal cortex, we measured

[3] To ensure that the difference in error rates between the two tasks could not cause the absence of an interfering TMS effect in the duration task, a complementary analysis was carried out. The participants were divided into two groups according to their mean error rate (more than 20% of errors: 10 participants, less than or equal to 20%: five participants) in the duration task. An ANOVA showed no main effect (all p values >.2) and, most importantly, no group by site by distance interaction ($F(2,26) < 1$).

[4] In their study, Cappelletti et al. (2007) observed a facilitating effect of TMS after right IPS stimulation that was not observed here in the group analyses. At the group level, a slight facilitation tendency (7 msec) was observed after right IPS stimulation in the numerosity task; at the individual level, seven participants showed such a facilitation tendency, but this was only statistically significant for two of them. This absence of facilitation effect in our numerosity task could be due to several methodological differences with Cappelletti et al.'s study (i.e., a larger range of numerosities, simultaneous presentation, and lack of comparison to a standard task).

the performance of healthy subjects in tasks that required processing either the numerosity of flashed dot sequences or the duration of single dot displays, before and after off-line rTMS over the left or right IPS, a region known to be crucial for numerosity processing.

At the behavioural level, the results showed that in the range of selected durations and numerosities, the performance in the two comparison tasks was equally fast. Moreover, the presence of the classical distance effect (e.g., Moyer and Landauer, 1967) in both tasks showed that the participants actually performed the comparisons using the appropriate dimension. However, the two tasks were found to differ in terms of error rate. Although there was no interaction between tasks and distance, a closer look at the data clearly indicated that this difference was due to better discrimination between numerically distant sequences, approaching a ceiling effect and creating a disparity between the two tasks. The question arises whether the observed differential effects of rTMS in the numerosity and duration tasks can be explained by differences in attentional demands. Four reasons argue against this possibility. First, it is worth noting that rTMS was found to disrupt RLs but not error rates, a dissociation that has often been reported in previous studies (e.g., Alexander et al., 2005; Ashbridge et al., 1997). Second, whereas an interpretation in terms of attention allocation predicted impaired performance in the most difficult task, the disruptive effects of rTMS were observed in numerosity comparison, which was the easiest task. Third, the finding that the RL increase induced by rTMS over the left IPS was significantly larger than that induced by rTMS over the vertex strengthens the idea that the impairment was not due to unspecific task demands. Finally, TMS still had no effect when the analyses were performed on the subgroup of participants who had made the fewest errors in the duration task.

Our results thus support the idea that the IPS is involved in numerosity processing, as demonstrated by previous neuroimaging studies showing bilateral IPS activations (e.g., Piazza et al., 2003). Moreover, our findings specify that only the left IPS is necessary for numerosity processing, whereas the right IPS does not appear to be critically involved in this process. This interpretation is consistent with the results of a TMS study showing that left IPS stimulation induced an RL increase when participants had to compare the numerosity of random patterns of dots (Cappelletti et al., 2007). It is also consistent with two neuropsychological studies describing patients with focal lesion of the left parietal lobe. In the first study, the patient was impaired in number comparison tasks with Arabic digits and arrays of dots (Lemer et al., 2003); in the second study, the performance of the patient in dot comparison did not differ from the performance of controls in the subitizing range but it did in the counting range (Ashkenazi et al., 2008, this issue). Moreover, we show that the numerical distance modulated the impairment induced by rTMS over the left IPS, as only the dot sequences differing by a small numerical distance were affected. This supports the idea of a left hemispheric dominance for exact quantity judgement, whereas approximate judgements of numerosity would preferentially involve the right hemisphere (Dehaene and Cohen, 1991; Piazza et al., 2006). Indeed, the more the task needs a fine and precise judgement, the more the left IPS seems to be necessary for correct performance, as demonstrated by several studies showing a correlation between the degree of involvement of the IPS and the numerical distance between the stimuli (Andres et al., 2005; Cappelletti et al., 2007; Knops et al., 2006; Pinel et al., 2001). The absence of deficit following rTMS over the right IPS does not mean that this region is not involved in this judgement, but indicates that it is not crucial for processing numerosities in the range selected for this study. Indeed, the activation of a right-lateralised fronto-parietal network including the IPS was observed when participants had to estimate larger numerosities (i.e., 15 dots) of series of visually and auditory-presented stimuli (Piazza et al., 2006).

For the duration judgement, performance after stimulation of the left or right IPS was equivalent to performance after stimulation of the control site. This result contradicts a recent TMS study in which performance in a duration comparison task was impaired after rTMS over the right posterior parietal cortex (Alexander et al., 2005). However, the stimulation sites of that study were located more posterior in the IPS (above the angular gyrus) than our sites (above the supramarginal gyrus), and these areas could be involved in other aspects of duration processing than magnitude processing, such as attention orientation. Moreover, the functional procedure used to identify the stimulation site suggests that this site also participated in a visual search. Parietal activations, mainly right-lateralised, have also been reported in several neuroimaging studies (e.g., Lejeune et al., 1997), but the time course analysis of these activations suggested that the right inferior parietal cortex contributed to the early stages of duration processing (most probably reflecting encoding and maintenance operations). In contrast, the bilateral temporal, cerebellum and right dorso-lateral prefrontal activations were found to occur later on, at a time when the comparison process could take place (Rao et al., 2001). So, in these studies, the role played by parietal areas in duration could rather reflect attentional and mnesic processes not specific to the duration characteristics of the task in progress (Lewis and Miall, 2003; Pouthas and Macar, 2005).

Although the interpretation proposed by these authors may explain the discrepancies between our results and those found in fMRI studies, it may be argued that the absence of an rTMS effect in our duration comparison task could be due to the fact that duration processing can be performed by either the left or the right IPS, so that any unilateral rTMS-induced deficit can be compensated for by the non-stimulated hemisphere. However, the great majority of brain imaging results converge to show that duration processing is lateralised in the right hemisphere (Lejeune et al., 1997; Maquet et al., 1996; Rao et al., 2001). Only one study revealed a bilateral involvement of the parietal cortex in processing rhythmic patterns (Schubotz et al., 2000), a task in which duration may be confounded with numerosity. In other words, further neuroimaging studies are necessary to identify the brain areas dedicated to processing duration magnitude. The available evidence from neuropsychological studies points to the prefrontral cortex as a possible candidate for such processing. Indeed, its lesion often leads to impaired time perception (e.g., Harrington et al., 1998). A specific relationship between the prefrontal cortex and duration processing has also been

reported in an fMRI study (Rao et al., 2001). Our findings further stress the fact that the range of the selected durations is of particular importance in dissociating magnitude processing from attention allocation and memory. Finally, our experiment suggests that a double dissociation between numerosity and duration processing in the parietal and frontal cortex should be investigated, and highlights the contribution of TMS to such brain-function studies.

In conclusion, our results confirm the results of previous brain imaging and TMS studies which reported a left IPS involvement in numerosity processing. The absence of a deficit in duration comparison following TMS over the left and right IPS indicates that this region is not crucial for duration comparisons. So, if there is a common cerebral substrate for processing these two types of magnitude (Walsh, 2003), this region is not the specific IPS area involved in numerosity processing. Future studies combining fMRI and TMS should help us to clarify this issue.

Acknowledgements

This study was supported by Grant 01/06-267 from the Communauté Française de Belgique – Actions de Recherche Concertées (Belgium), and grant P5/04 from the IUAP Program of the Belgian Federal Government. MA is a postdoctoral researcher and MP is a research associate at the National Fund for Scientific Research (Belgium).

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