



## Note

# Contribution of the right intraparietal sulcus to numerosity and length processing: An fMRI-guided TMS study

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## ABSTRACT

The critical involvement of the left and right intraparietal sulci (IPS) in numerosity and length processing was tested with neuro-navigated repetitive transcranial magnetic stimulation (rTMS). Participants had to categorize linear arrays of dots as containing “few” or “many” dots, and filled rectangles as “short” or “long”. The stimulation sites were determined for each individual participant by identifying the IPS areas showing peak activity during a number comparison task in earlier functional magnetic resonance imaging (fMRI) studies. Compared to the stimulation of the vertex chosen as a control site, rTMS over the right IPS increased the error rate in both tasks. This result indicates that the integrity of the right IPS is a necessary condition not only for discriminating numerosities but also for performing accurate judgements of lengths. We propose that these two processes rely on a common representation and/or mechanism in the right IPS.

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## 1. Introduction

Numerosity and space are often linked in the descriptions people give of their mental representation of numbers (Galton, 1880; Seron et al., 1992) and in the representations left by primitive cultures (Ifrah, 2000). Moreover, one well-known method of teaching arithmetic operations relies on the manipulation of sticks of various lengths (the Cuisenaire rods; Cuisenaire and Gattegno, 1954). This relationship between numerosity and length has also generated a long tradition of research in cognitive neurosciences. Several behavioural studies have shown a functional interaction through the presence of facilitation and interference effects between numerosity and length. In numerosity comparison tasks, it

has been shown that long arrays of elements are numerically overestimated by children (Houdé and Guichart, 2001; Pufall and Shaw, 1972) and even by adults (Dormal and Pesenti, 2007), and that non-symbolic numerical cues interfere with performance in length bisection (de Hevia and Spelke, 2009) and length comparison (Dormal and Pesenti, 2007) tasks.

The neural substrate of numerosity and length estimation has long been investigated in separate experiments that showed right or bilateral parietal activations during non-symbolic numerosity (e.g., Dormal et al., 2010; Piazza et al., 2004) and length comparison judgements (e.g., Fink et al., 2000). Importantly, even for bilateral activations, a right-hemispheric dominance for non-symbolic numerosity processing is frequently observed in children (Holloway and

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Ansari, 2010; Hyde et al., 2010) and in adults (Dormal et al., 2010; Holloway et al., 2010; Piazza et al., 2006). Neuronal recordings in monkeys and neuroimaging studies in humans have contributed to showing the existence of a shared cerebral network. For example, the activity of single neurons in the intraparietal sulci (IPS) and prefrontal cortices was recorded while monkeys were comparing either the number of dots in visual displays or the length of filled rectangles (Tudusciuc and Nieder, 2007, 2009). The results showed that anatomically intermingled neurons responded selectively to either the numerosity or the length of the stimuli, or to both, supporting the idea that representations of discrete numerosities and continuous quantities share a fronto-parietal network. In humans, comparing Arabic numerals, lengths of line or amplitudes of angles activates the left IPS (Fias et al., 2003). Using numerosity and length comparison with non-symbolic materials (i.e., linear arrays of dots and horizontal rectangles) in a functional magnetic resonance imaging (fMRI) study, we recently showed that whereas bilateral IPS activations were found in numerosity comparison, only the right IPS was activated in both tasks, suggesting that this area underlies a common mechanism or representation for numerosity and length processing (Dormal and Pesenti, 2009).

Functional imaging techniques reveal the changes in cerebral activation correlated to a cognitive task, but they do not demonstrate causal links between task performance and the activated region. To assess the causal role of the IPS in numerosity and length processing, we coupled TMS with an fMRI neuro-navigation method. For each participant, the TMS coil was placed over the left or right IPS sites showing the greatest increase in activity during a numerosity comparison task performed in earlier fMRI experiments. In the numerosity task, participants had to categorize linear arrays of dots as containing “few” or “many” dots; in the length task, they had to categorize filled rectangles as “short” or “long”. The present study aimed to determine the critical involvement of these bilateral IPS areas in numerosity processing and whether these IPS areas are also causally involved in length processing.

## 2. Methods

### 2.1. Participants

Ten young healthy male adults<sup>1</sup> (mean age:  $24 \pm .5$  years) took part in this experiment after giving their informed consent. All the participants were right-handed [range of right handedness percentage: (80–100)] according to the Edinburgh Handedness Inventory (Oldfield, 1971), had no history of neurological or psychiatric disorder, had normal or corrected-to-normal vision, and were unaware of the purpose of the study. All of them were negative for the risk factors associated with TMS (Keel et al., 2002). The procedures were non-invasive and were performed in accordance with the ethical standards laid down in the 1964 Helsinki Declaration; the experimental

protocol was approved by the Biomedical Ethical Committee of the Université Catholique de Louvain.

### 2.2. Tasks and stimuli

Two categorization tasks were used: a numerosity categorization of linear arrays of dots (hereafter N, for numerosity), and a length categorization of continuous filled rectangles (hereafter L, for length; Fig. 1). In the N task, the participants had to decide if the arrays contained “few” (i.e., 5 or 6) or “many” (i.e., 8 or 9) dots by pressing respectively the furthest left button on a response box with the left index finger, or the furthest right button with the right index finger. In the L task, they had to decide if the rectangles were “short” (i.e., 7.5 or 8 cm) or “long” (i.e., 9 or 9.5 cm) using the same two-choice button-press.

To avoid as far as possible the use of explicit or implicit counting strategies, only non-subitizable numerosities were presented in the N task, with a very short presentation time. The stimuli were composed of linear arrays of 5, 6, 8 or 9 black dots. Non-periodic signals were used so that spatial ratios were not confounded with numerosity, the size of dots did not constitute a numerical cue, and pattern recognition was avoided (for methodological details, see Dormal and Pesenti, 2007). The total length of the arrays was held constant (at 10 cm), while the diameter of each dot ( $e_j$ ) and the interdot spacing ( $i_j$ ) varied from .33 to 1.5 cm. The total blackened surface covered by the dots was held constant in all arrays. In the L task, the stimuli were black rectangles 1 cm wide and 7.5, 8, 9 or 9.5 cm long.

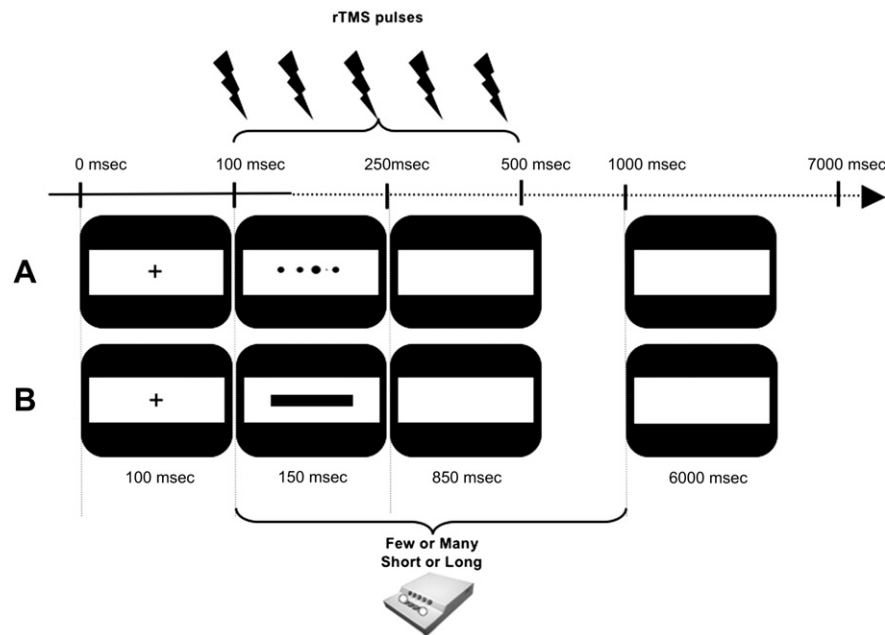
### 2.3. Experimental procedure

Stimulus presentation and response recording were controlled using the e-Prime software (Schneider et al., 2002). The participants sat comfortably on a padded chair in a quiet, dark room, 60 cm from the screen, and a response box (30 cm × 40 cm) with four horizontally aligned buttons laid on a cushion on their knees. A white rectangle (9.5 × 16 cm) was presented on a black background throughout the experiment. At the beginning of each trial, a cross was presented for 100 msec, and a linear array of dots or a black rectangle was then displayed for 150 msec. The stimulus was followed by a blank rectangle for 850 msec during which the participants answered, and then an intertrial interval of 6000 msec to preclude TMS carry-over effects across trials (Fig. 1).

Based on the individual fMRI results obtained during comparison or categorization of linear arrays of dots in previous studies, we defined two parietal sites for each participant in the sulcal walls of the IPS of each hemisphere. We used the coordinates of the voxels showing the greatest increase of activity during the numerosity task, compared to the reference colour detection task (see Fig. 2A and Table 1 for individual coordinates). The vertex (Cz) was used as a control site as it has been shown to strictly reproduce the somatosensory effects of parietal stimulations and it is considered as a better control than other solutions (e.g., sham stimulation; Robertson et al., 2003).

Before the TMS experiment, each participant undertook a practice session to reach a stable performance level. The stimulation sites were then localized with a frameless

<sup>1</sup> All the volunteers had participated in one of our previous fMRI experiments [as described in Dormal and Pesenti, 2009 ( $n = 6$ ), or Dormal et al., 2010 ( $n = 4$ )] and the present TMS experiment took place within 24 months of the acquisition of the fMRI data.



**Fig. 1 – Schematic representation of the temporal structure of the (A) numerosity and (B) length categorization task. Each trial was composed of a fixation cross, followed by a stimulus (i.e., linear array of dots or black filled rectangle). The participants had to decide whether the array contained “few” (left-button response) or “many” (right-button response) dots in the numerosity task and whether the rectangle was “short” or “long” (same response buttons) in the length task. In each trial, rTMS was applied at 10 Hz for 400 msec (i.e., 5 pulses) over the left or right IPS or the vertex (as a control stimulation site), starting at stimulus presentation. (Note that the time line is not represented with a continuous scale).**

stereotactic system providing on-line information about the position of the coil (Noirhomme et al., 2004). Prior to the first session, a whole brain T1-weighted magnetic-resonance image (MRI) had been acquired for each participant. The co-registration between the stimulation sites and the anatomical MRI proceeded in three steps. First, the coordinates of about 200 points randomly distributed 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 minimizing 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 digitized 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 the 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.

There were 2 blocks of each task (N and L) for each stimulated area. Each block contained 24 trials; at the beginning of each block, the instructions were repeated and examples from each category (“few” and “many”, “short” and “long”) were presented. The order of the stimulation sites and the order of the experimental tasks were counterbalanced across participants. Five TMS pulses (10 Hz; 65% of the machine's output)

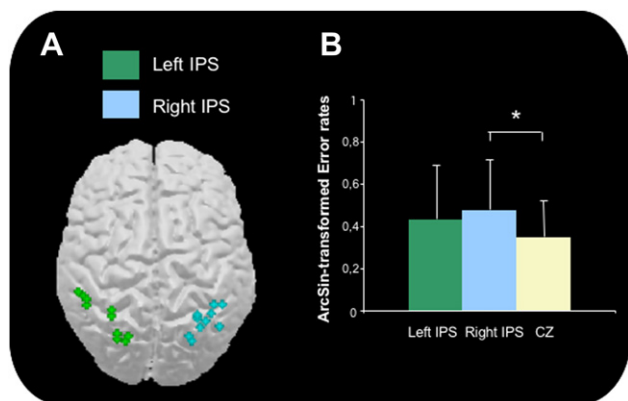
were delivered at the stimulus onset using a Rapid Magstim 200 stimulator (Magstim Co. Ltd., UK) through a 75-mm outer diameter figure-of-eight coil.

### 3. Results

An analysis of variance (ANOVA) was performed on the response latencies of correct answers with task (N vs L), site (left IPS vs right IPS vs Cz) and magnitude (small: few/short vs large: many/long) as within-subject variables. Significant main effects of task [ $F(1,9) = 20.007, p < .002, |\eta^2| = .69$ ] and magnitude [ $F(1,9) = 8.191, p < .02, |\eta^2| = .476$ ] were observed. The participants responded faster overall to the L task ( $463 \pm 78$  msec) than to the N task ( $499 \pm 76$  msec), and faster to large ( $462 \pm 76$  msec) than to small ( $500 \pm 72$  msec) magnitudes. Moreover, a significant interaction between task and magnitude was found [ $F(1,9) = 7.952, p < .02, |\eta^2| = .469$ ]. No significant difference was observed in the length task [small:  $474 \pm 77$  msec; large:  $451 \pm 75$  msec;  $t(9) = 1.701, p > .1$ ], whereas small ( $527 \pm 68$  msec) and large ( $472 \pm 76$  msec) magnitudes differed in the numerosity task [ $t(9) = 3.453, p < .008$ ]. No significant effect of site was observed [ $F(2,18) = 3.079, p > .1, |\eta^2| = .255$ ], and there were no other significant interactions (all  $p$  at least  $> .3$ ).

A similar ANOVA on arcsine-transformed error rates revealed a significant main effect of site [ $F(2,18) = 5.844, p < .012, |\eta^2| = .394$ ]<sup>2</sup>: the participants made more errors after

<sup>2</sup> For the sake of comprehension, untransformed error rates are presented.



**Fig. 2 – (A)** Representation of the individual left and right IPS stimulation sites on a glass brain. **(B)** Mean ArcSin-transformed error rate ( $\pm$ SE) during the two categorization tasks, while rTMS was applied over the left (green), right (blue) and control (yellow) sites. The asterisk indicates where a significant increase was observed relative to the control condition ( $*p < .05$ ).

TMS over the right IPS ( $10.3 \pm 8.8\%$ ) than over the control site ( $7.2 \pm 6.3\%$ ) [one-tailed  $t(9) = 3.721$ ,  $p < .007$ ; Fig. 2B]. There were no significant differences between the left ( $9.8 \pm 8.0\%$ ) and the right IPS conditions [one-tailed  $t(9) = -1.675$ ,  $p > .19$ ] or between the left IPS and the control conditions [one-tailed  $t(9) = 1.669$ ,  $p > .19$ ]. There was also a marginal effect of magnitude [ $F(1,9) = 4.189$ ,  $p = .072$ ,  $\eta^2 = .317$ ], indicating that the participants tended to make more errors for small ( $11.4 \pm 9.84\%$ ) than for large ( $6.8 \pm 6.13\%$ ) magnitudes. A significant interaction between task and magnitude was also found [ $F(1,9) = 10.095$ ,  $p < .012$ ,  $\eta^2 = .529$ ]: no difference was present in the length task [small:  $7.9 \pm 7.8\%$ , large:  $9.1 \pm 7.3\%$ ;  $t(9) = -.731$ ,  $p > .4$ ], whereas small magnitudes ( $14.8 \pm 11.9\%$ ) were more error prone than large ones ( $4.4 \pm 4.9\%$ ) in the numerosity task [ $t(9) = 3.3$ ,  $p < .01$ ]. There was no main effect of task [ $F(1,9) = .698$ ,  $p > .4$ ,  $\eta^2 = .072$ ], and no other significant interaction was observed (all  $p$  at least  $> .3$ ).

#### 4. Discussion

In order to test the causal role of the left and right IPS in numerosity and length processing, we carried out an rTMS experiment in which participants had to discriminate the numerosity of linear arrays of dots or the length of filled rectangles. Disrupting the right IPS led to inaccurate judgements<sup>3</sup> of both magnitudes, which extends previous results in two ways.

Firstly, our results show that the right IPS is involved in processing both numerosity and length. Indeed, at the level of precision available with this rTMS technique, the right IPS

<sup>3</sup> As noted by an anonymous reviewer, TMS had no effect on response latencies contrarily to what was observed in previous studies. The reason may be that the present study uses a categorization task: TMS may have affected the way the decision criterion is set and/or taken into account to take a decision, hence increasing the error rate but leaving the speed of responding unaffected.

**Table 1 – Normalized MNI coordinates (x, y, z) for the TMS sites selected as a function of the fMRI activations revealed at the individual level by the subtraction of the activations during a reference colour detection task from those obtained during a numerosity task. Left and right IPS sites were defined at a corrected threshold ( $p < .05$ ), except for three participants (Participants 5, 6 and 10) for which the threshold was set at an uncorrected level ( $p < .001$ ) for the left IPS. Individual coordinates of the peak are provided for the left and right intraparietal sulcus (IPS).**

| Participant | Study <sup>a</sup> | Left IPS |     |    | Right IPS |     |    |
|-------------|--------------------|----------|-----|----|-----------|-----|----|
|             |                    | x        | y   | z  | x         | y   | z  |
| 1           | A                  | −20      | −66 | 44 | 24        | −66 | 42 |
| 2           | A                  | −22      | −68 | 60 | 48        | −42 | 54 |
| 3           | A                  | −52      | −36 | 50 | 42        | −42 | 54 |
| 4           | A                  | −32      | −50 | 56 | 32        | −58 | 60 |
| 5           | A                  | −56      | −34 | 40 | 40        | −48 | 56 |
| 6           | A                  | −50      | −38 | 54 | 26        | −68 | 56 |
| 7           | B                  | −28      | −66 | 62 | 36        | −54 | 54 |
| 8           | B                  | −32      | −46 | 52 | 30        | −50 | 46 |
| 9           | B                  | −50      | −42 | 56 | 46        | −58 | 52 |
| 10          | B                  | −28      | −62 | 66 | 30        | −52 | 54 |
| Mean        |                    | −37      | −51 | 54 | 35        | −54 | 53 |
| SD          |                    | 14       | 14  | 8  | 8         | 9   | 5  |

a Study A: Dormal and Pesenti (2009); Study B: Dormal et al. (2010).

area involved in numerosity processing was also critically implicated in length categorization. This fits with deficits observed in patients with right parietal damage who show impairments in numerical and spatial bisection tasks (Cappelletti et al., 2007a; Marshall and Halligan, 1989; Zorzi et al., 2002), with TMS studies pointing the causal role of right parietal areas in length judgement (Fierro et al., 2006; Oliveri and Vallar, 2009; Pourtois et al., 2001), and with fMRI results showing that the right IPS is activated in numerosity and length comparison (Dormal and Pesenti, 2009). These findings thus suggest that numerosity and length may be processed and represented by a common magnitude-processing system located in right IPS areas (Buetti and Walsh, 2009; Dormal and Pesenti, 2009; Walsh, 2003). Future studies will show whether this system is composed of intermingled sets of neurons coding separately numerosity and length as observed in monkeys or truly shared neurons coding both dimensions.

Secondly, our results indicate that the right IPS plays a critical role in non-symbolic numerosity categorization. While several fMRI studies have shown increased activity in the right IPS during non-symbolic numerosity estimation (Dormal and Pesenti, 2009; Holloway et al., 2010; Piazza et al., 2006), the causal relationship between this region and numerosity processing remained undetected in previous TMS studies (Cappelletti et al., 2007b; Dormal et al., 2008). So far, indeed, the only pieces of evidence of numerical deficits after right parietal lesions came from group studies where the description of the lesions was not well documented and the tasks sometimes involved additional reasoning processes (e.g., Warrington and James, 1967), or from TMS studies using symbolic notations in numerical tasks including some spatial



components (e.g., mental bisection of numerical intervals: Göbel et al., 2006; Oliveri et al., 2004; physical–numerical size judgements in Stroop paradigms: Cohen Kadosh et al., 2007a; space–number association in parity tasks: Rusconi et al., 2007). Our original finding could stem from the use of a categorization task that implies approximate rather than exact judgements. Indeed, several studies suggested a right-hemispheric dominance for approximate judgements of numerosity, whereas exact judgements would depend on the integrity of the left hemisphere (Dehaene and Cohen, 1991; Piazza et al., 2006). It is unclear, however, why an exact processing in the left IPS would not compensate the disruption of approximate judgements in the right IPS. Another plausible explanation is that the numerical processes or representations supported by each hemisphere are qualitatively different and that the left IPS cannot systematically take over the role of the right IPS after a lesion. Accordingly, it has been proposed that each hemisphere is initially endowed with a ratio-limited magnitude-processing system, available early in life and shared with other species, but that, as children start using number words or fingers to represent numerosities, a refinement takes place in the hemisphere dominant for verbal and manual abilities, that is the left hemisphere in right-handed people (Andres et al., 2005; Piazza et al., 2004, 2007). This refinement would stem from the development of a more elaborate numerical system in the left IPS, each magnitude being represented by sharper (i.e., with less variability around the target value) tuning curves than in the right IPS (Verguts and Fias, 2004). Such an account fits with behavioural (Notebaert and Reynvoet, 2008), functional (Piazza et al., 2004, 2007), and TMS (Andres et al., 2005; Dormal et al., 2008) findings. We therefore suggest that the developmental trajectory of numerical learning leads to a specific lateralization of numerical abilities in the adult brain, with a privileged relationship between exact numerosity processing in the left IPS and numerosity discrimination tasks, whereas the ratio-limited system available in the right IPS would be particularly suited to perform numerosity categorization. Although further research is necessary to characterise hemispheric lateralization in numerosity processing, the present finding extends previous results to show that the representations available in the right IPS are complementary to the exact representations of the left IPS in categorization tasks. To our knowledge, this provides the first demonstration of a necessary contribution of the right IPS in numerosity processing.

The human IPS is a complex cerebral structure showing large inter-individual variability both anatomically (Molko et al., 2003; Zilles et al., 2003) and functionally (Cohen Kadosh et al., 2007b). A greater right-hemispheric IPS variability was also reported in a recent meta-analysis of numerosity processing (Dormal et al., 2010). The use of the classical stereotactic system does not take this variability into account, which might explain the absence of impairing effects of right IPS stimulations in previous studies (Cappelletti et al., 2007b; Dormal et al., 2008), as the stimulation sites were not functionally defined but rather corresponded to normalized mean coordinates, and this uncontrolled variability might have been greater in the right IPS. The neuro-navigation method we used allowed us to capture most of the

inter-individual variability (Sparing et al., 2008), since the position of the TMS coil was coregistered with the brain anatomy of each participant, and the stimulation sites corresponded to the projection of the individual IPS sites showing the highest BOLD response in numerosity comparison. This does not make the inter-individual variability disappear, but makes it ineffective by ensuring that functionally relevant areas are stimulated. Neurophysiological recordings in monkeys suggest that, within these areas, the sets of neurons coding specific numerosities are intermingled (Tudusciuc and Nieder, 2007, 2009), and the on-line stimulation paradigm used here does not allow these sets to be dissociated, which may explain the lack of site by magnitude interaction. TMS-adaptation paradigms, in which sets of neurons are adapted to a specific feature before TMS is applied (e.g., Cattaneo et al., 2009; Cohen Kadosh et al., 2010; Silvanto et al., 2008), may clarify this issue.

It is worth noting that, although the effect of the left IPS stimulation differed significantly neither from the right IPS nor from the vertex stimulations, it was closer to the former than to the latter. Hence, one cannot exclude a moderate effect of the left stimulation, suggesting a possible bilateral involvement of the IPS in numerosity and length processing. This would, in fact, be compatible with fMRI results showing sub-threshold activations in this area in numerosity categorization tasks (Dormal et al., 2010), and a left IPS impairment in numerosity comparison after TMS (Cappelletti et al., 2007b; Dormal et al., 2008). The role of the left IPS in length comparison is less well established as a right-hemispheric dominance is generally observed in spatial processing (Sack, 2009). As no activation of the left IPS was found in a similar length comparison task (Dormal and Pesenti, 2009), extreme caution is required before concluding that this region has any specific involvement in length judgements. A possible account of this result is that homologous areas in the left and right parietal cortices are transcallosally connected (Knops et al., 2006), thereby allowing propagation of left IPS stimulation to the right hemisphere via interhemispheric connections, as suggested by recent combined fMRI-TMS studies (Bestmann et al., 2008; Driver et al., 2009). This could explain the possible moderate effect of TMS over the left IPS in the present study. Further investigation is required to resolve this issue.

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