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Space, time, and numbers in the right posterior parietal cortex: Differences between response code associations and congruency effects

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The mental representations of space, time, and number magnitude are inherently linked. The right posterior parietal cortex (PPC) has been suggested to contain a general magnitude system that underlies the overlap between various perceptual dimensions. However, comparative studies including spatial, temporal, and numerical dimensions are missing. In a unified paradigm, we compared the impact of right PPC inhibition on associations with spatial response codes (i.e., Simon, SNARC, and STARC effects) and on congruency effects between space, time, and numbers. Prolonged cortical inhibition was induced by continuous theta-burst stimulation (cTBS), a protocol for transcranial magnetic stimulation (TMS), at the right intraparietal sulcus (IPS).
Our results show that congruency effects, but not response code associations, are affected by right PPC inhibition, indicating different neuronal mechanisms underlying these effects. Furthermore, the results demonstrate that interactions between space and time perception are reflected in congruency effects, but not in an association between time and spatial response codes. Taken together, these results implicate that the congruency between purely perceptual dimensions is processed in PPC areas along the IPS, while the congruency between percepts and behavioral responses is independent of this region.

1. Introduction

Temporal and numerical information is strongly related to our concept of space. From a theoretical perspective, these interrelations have been pointed out by Bergson (1888), who argued 'that the very idea of the number [...] involves the idea of a juxtaposition in space' (p. 89) and 'that we are compelled to borrow from space the images by which we describe what the reflective consciousness feels about time' (p. 91). Many psychophysical studies confirmed the interactions between the perception of time, space, and numbers (Bonato et al., 2012; Bueti and Walsh, 2009; Burr et al., 2010; Dehaene and Brannon, 2011; Fabbri et al., 2012; Walsh, 2003). Thinking about large vs. small numbers increases attention to the right vs. the left side of space (Cattaneo et al., 2009; Fischer et al., 2003; Loetscher et al., 2010; Ruiz Fernandez et al., 2011), and these shifts of spatial attention in turn affect the perception of temporal intervals (Di Bono et al., 2012; Frassinetti et al., 2009; Santiago et al., 2007; Vicario et al., 2008). Finally, large vs. small numbers are perceived as longer in duration (Lu et al., 2009; Oliveri et al., 2008; Vicario et al., 2008; Xuan et al., 2007).

A growing body of evidence suggests that the interactions between perceptual dimensions are mediated by neuronal structures in the parietal cortex (Basso et al., 1996; Bueti and Walsh, 2009; Burr et al., 2010; Coull and Nobre, 1998; Hubbard et al., 2005; Magnani et al., 2010; Oliveri et al., 2009; Oliveri et al., 2004; Walsh, 2003). The role of parietal structures for spatial, temporal, and numerical processing was also confirmed by single cell studies in non-human primates (Janssen and Shadlen, 2005; Nieder, 2004; Nieder et al., 2006; Sawamura et al., 2002; Thompson et al., 1970). Moreover, Leon and Shadlen (2003) observed that spatially tuned neurons in the right posterior parietal cortex (PPC) of rhesus monkeys were concurrently sensitive to temporal characteristics of stimuli. Together, these findings suggest that not only the processing of different magnitudes, but also their mutual interactions might be mediated by the parietal cortex (Göbel et al., 2006; Göbel et al., 2001; Hayashi et al., 2013; Rusconi et al., 2007). Imaging studies in humans similarly showed that the right PPC, especially the posterior part along the intraparietal sulcus (IPS), might contain the neural substrate of a generalized magnitude system for space, time, numbers and other magnitudes (Bueti and Walsh, 2009; Cohen Kadosh et al., 2007a; Cohen Kadosh et al., 2007b; Walsh, 2003). Interference with neuronal processes in the PPC by using transcranial magnetic stimulation (TMS) causes deficits in space (Bjoertomt et al., 2002; Fierro

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et al., 2000; Muggleton et al., 2006), time (Hayashi et al., 2013; Magnani et al., 2010; Oliveri et al., 2009; Wiener, 2014), and number processing (Cattaneo et al., 2009; Göbel et al., 2006; Göbel et al., 2001). Therefore, TMS provides a promising method to investigate the interactions between these dimensions.

Interactions between perceptual dimensions have often been investigated in terms of response code associations and congruency effects. For example, the spatial–numerical association of response codes (SNARC) denotes the phenomenon of faster reactions with the right hand in response to relatively large numbers, while the left hand reacts faster to relatively small numbers (Dehaene et al., 1993; Hubbard et al., 2005; Wood et al., 2008). This indicates that numbers are spatially represented along a mental number line (i.e., small numbers to the left and large numbers to the right).[1] The SNARC effect represents an analog of the Simon effect, which denotes that stimuli appearing on either side of egocentric space facilitate reactions with the ipsilateral hand (Hommel, 1993; Simon and Wolf, 1963). Importantly, Simon and SNARC effects occur despite the fact that stimulus position and number magnitude are irrelevant for the task. There have been various attempts to find evidence for an analogous effect of a spatial–temporal association of response codes (STARC). Although an association between short vs. long durations and left vs. right response buttons has been confirmed (Fabbri et al., 2012; Ishihara et al., 2008; Vallesi et al., 2008), it is unknown whether this response code association applies as well for early vs. late events. As stressed by Bonato et al. (2012), however, a spatial representation of moments in time (rather than duration magnitudes) is a key aspect for the theory of spatialized time.

Congruency effects denote the phenomenon that stimuli are processed faster when they possess congruent characteristics across different dimensions. For example, congruency effects between space and numbers would be reflected by shortened reaction times to large numbers, which are presented in the right hemifield (as compared to large numbers presented in the left hemifield). Thus, an important difference between response code associations and congruency effects is that the former relate to interactions between perceived dimensions and associated motor responses, whereas the latter relate to interactions between two perceived dimensions independent from response selection.

There is converging evidence that cross-dimensional congruency effects are mediated by neuronal structures within the right PPC, predominantly in the IPS (Cattaneo et al., 2009; Cohen Kadosh et al., 2007a; Cohen Kadosh et al., 2007b; Oliveri et al., 2009). In contrast, evidence for a PPC involvement in response code associations is rather scarce (one example is Rusconi et al., 2007). Lesions in the right PPC often result in neglect of the left spatial hemifield (Halligan et al., 2003). While congruent neglect symptoms can extend to numerical and temporal cognition (Basso et al., 1996; Oliveri et al., 2009; Priftis et al., 2006), response code associations like the SNARC effect are not affected in the same patients (Priftis et al., 2006). Instead, prefrontal areas have been suggested to underlie the association between perceived numbers and specific motor responses (Rusconi et al., 2011). Furthermore, single cell recordings in non-human primates indicate that stimulus–response compatibility, which is assumed to underlie Simon and SNARC effects, is encoded by neurons in the premotor cortex (Kalaska and Crammond, 1995).

In the present study, we investigated the relative impact of right PPC inhibition on response code associations and congruency effects within the same paradigm, enabling a direct comparison between these effects (Fig. 1). In a two-alternative forced-choice task, participants were asked for odd–even judgments on numbers, which were either small or large (numerical magnitude), appeared either on the left or the right side of a screen (spatial position), and occurred either early or late within a predefined time interval (temporal position). Inhibition of the right PPC was induced by continuous theta-burst stimulation (cTBS; Chaves et al., 2012; Huang et al., 2005; Nyffeler et al., 2008). If response code associations and congruency effects are both mediated by the right PPC, they should decrease after TMS compared to sham stimulation. Furthermore, if the interrelations between space, time, and numbers are based on the PPC, TMS-induced inhibition should reduce all interactions to a similar degree.

[1] The SNARC effect depends on relative rather than absolute number magnitude and on the culturally defined writing direction, but not on handedness or hemispheric dominance (Dehaene et al., 1993).

2. Methods

2.1. Participants

Twenty-two healthy participants (7 males, mean age was 25.9 years, ranging from 21 to 35) were recruited from the local community. All but one were right-handed. Exclusion criteria were metallic objects in the body, auditory impairments or previous occurrences of epileptic seizures, and advanced skills in languages that use right-to-left or top-to-bottom writing directions. Participants received monetary compensation and gave written informed consent to the experimental protocol, which was approved by the local ethics committee.

2.2. Stimuli and task

Participants sat in front of a computer monitor (24 in. diagonal) and a centrally arranged standard German keyboard. Two buttons at the left and the right side of the keyboard were used as response buttons (button codes '<' and 'num_3'). Participants were instructed to align their body midline with monitor and keyboard and to maintain a distance of approximately 1 m between their head and the monitor.

A light blue rectangular frame (47 × 8 cm; [0.6,1,1] in rgb space) was presented for 4 s in the center of the monitor (gray background) with a black fixation cross in the middle. One of four numbers (1, 2, 8, or 9) was presented for 250 ms either 13 cm to the left or to the right of the fixation cross, either 1 or 3 s after frame onset. In a reaction time task, participants had to press the right button for an even number and the left button for an odd number. Each of the possible combinations (4 numbers × 2 positions × 2 onsets) was repeated five times in randomized order, resulting in 80 trials per block. In the second block of each session, the meaning of buttons was reversed. The order of assignment was counterbalanced across participants. Previous to each block, participants performed eight practice trials to get accustomed to the specific button assignment.

During the whole experiment, the frame was always presented for exactly 4 s. To familiarize participants with this duration, the frame was shown three times and participants were asked to attend to its presentation time. They were explicitly told that the frame would always appear for exactly this duration. However, the numerical value of 'four seconds' was not announced. In the following ten frame presentations, participants were instructed to press the space bar when half of its duration was over. No feedback was given. This method provided information on general timing abilities (no differences between experimental sessions were found) and enabled familiarization with the frame duration. Presentation of stimuli was controlled by PsychoPy (v1.80.01).

2.3. Experimental sessions

The experiment was performed during two experimental sessions, conducted on different days. In the TMS session, transcranial magnetic stimulation (TMS) was applied over the right PPC according to the TMS protocol described in Section 2.4. In the sham session, the coil was turned upside down and no TMS was applied. Due to this procedure, acoustic disturbance and vibrations of the coil were comparable during both sessions. Importantly, given that our aim was to test for interactions between spatial, temporal, and numerical dimensions, the left PPC was not considered as control stimulation site because of its

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