



Are low and high number magnitudes processed differently while resolving the conflict evoked by the SNARC effect?

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ABSTRACT

In the brain, numbers are thought to be represented in a spatially organised fashion on what is known as the Mental Number Line (MNL). The SNARC (Spatial-Numerical Association of Response Codes) effect refers to the faster responses to digits when the reaction side is congruent with the digit position on the MNL (e.g. a left-handed response to a small magnitude) and the slowing down of responses (inhibition) in the case of incongruity. We examined the electrophysiological correlates of conflict, which are linked to that of inhibition, to shed light on the relationship between the SNARC effect and executive attention. Event-related potentials (ERPs) were recorded from twenty-nine participants during a parity-judgment task. The participants responded more quickly on congruent than on incongruent trials. The congruency effect was reflected in early sensory (N1, N2) components above parieto-occipital and frontal regions, as well as in the later P3 component above centro-parietal areas. Moreover, both the N1 amplitude and N2 latency were greater with high than low magnitude digit targets. P3 amplitude modulation implies that the SNARC effect is the result of first evoking the parallel processing of digit magnitude categorisation (in the occipital and central areas) and numeric conflict detection (in the parieto-occipital and frontal areas) and secondly conflict monitoring and resolution localised in the centro-parietal and frontal sites. These results also suggest that the left hemisphere specialises in conflict processing of high magnitude digit targets, while the right hemisphere of low digit magnitudes.

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1. Introduction

The SNARC (Spatial-Numerical Association of Response Codes) effect (Dehaene et al., 1993) is an example of the relationship between number magnitude and the spatial organization of mental representations. This effect arises for example in parity judgment task, where the participant's response to larger magnitude digits like “8” or “9” are faster with the right than with the left hand, and the opposite occurs for smaller magnitude digits like “1” or “2”. This phenomenon leads to faster responses with the left hand. This effect occurs even when the processed numbers are totally irrelevant to the task (e.g. Fias et al., 1996; Fias et al., 2001; Lammertyn et al., 2002), and is independent of the stimuli modality (Fischer et al., 2009; Nuerk et al., 2005) and of the notation of the numbers (Ganor-Stern and Tzelgov, 2008; Jiang et al., 2010; Nuerk et al., 2005; Reynvoet and Brysbaert, 2004). On the basis of these studies and several other findings, it has been established that numbers are spatially organised along the Mental Number Line (MNL).

Despite extensive research in this field, the relationship between numerical cognition and attentional processing is still debated. The neural architecture for numbers and visuo-spatial attention may be partially shared (for reviews, Dehaene et al., 2004; Hubbard et al., 2005). For example, the quantity representational system of numbers is thought to be located in the horizontal segment of the intraparietal sulcus (HIPS), which plays an important role in the interactions between numerical and spatial processing (for review, Hubbard et al., 2005). Simon et al. (2002, 2004) suggested that numerical processing activates the IPS area that is surrounded by and is functionally linked with regions involved in language, attentional and spatial processes. The review of data leads to the view that this portion of the parietal cortex is responsible for mediating spatial-numerical associations, such as the SNARC effect, because of its relationship with orienting attention, which have been localised in the aforementioned brain regions. This is why the spatial-cueing detection task is the most frequently used experimental paradigm to examine attentional engagement of the SNARC effect (Dodd et al., 2008; Fischer et al., 2003; Ranzini et al., 2009; Ristic et al., 2006; Salillas et al., 2008), where a number is employed as a spatial cue that influences attentional allocation. In contrast, less is known about the engagement of executive attention (Posner and Petersen, 1990) in spatial-numerical relationships, despite an obvious conflict that originates from the incongruity between the response effector side and the supposed location of the displayed digit on

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the MNL, or between the localisation of the presented stimulus in the external space and the MNL locus of the digit cueing this stimulus. This is why we used the parity judgment task to evoke the conflict between the position of a digit on the MNL and a response side. We reasoned that the digit might evoke, in parallel, a shift of orienting attention according to the organisation of MNL, as well as the engagement of executive functions necessary for conflict processing. Thus, how could this be interpreted in light of the discussion on independence vs. integration of attentional networks, especially in orienting and executive attention? (e.g. Chen et al., 2006; Fan et al., 2009; Fan et al., 2002; Green et al., 2008). Executive attention is involved during such operations as conflict monitoring and resolution, planning, decision-making and error detection, and it is required for novel responses, which are not well-learned and can be difficult, complex or dangerous (Fan and Posner, 2004). Its neuronal underpinnings have been anatomically separated using the Attention Network Test (ANT) (Fan et al., 2002) from orienting and alerting networks and have been localised mainly in the anterior cingulate cortex (ACC), which is responsible for conflict resolution, as well as in the dorsolateral prefrontal cortex (DLPFC) (Botvinick et al., 2001; Bush et al., 2000; Fan et al., 2003; Fan et al., 2005; MacDonald et al., 2000), which is engaged in conflict monitoring and is either bound up with the beginning of the response phase or is involved in inhibiting the wrong answer. Several neuroimaging studies (e.g. Bench et al., 1993; Peterson et al., 1999) have also shown activation in the inferior and/or superior (Adleman et al., 2002) parietal areas evoked by conflict, while others have shown activation in the prefrontal regions (including the ACC) together with the parietal areas (e.g. Hazeltine et al., 2000; Kaufmann et al., 2005).

Using event-related potential (ERP) measurements and the ANT paradigm, Neuhaus et al. (2007) obtained the congruency effect on P3 recorded from the parietal and central electrodes. Source localization performed with LORETA identified two regions of activation evoked by incongruent stimuli: the left inferior temporal cortex and ACC. One subsequent study (Neuhaus et al., 2010) also suggested that the fronto-parietal P3 amplitude modulations were not only a sign of response inhibition, but also of target stimuli detection. Moreover, these studies also emphasised a clear separation of the brain temporal and spatial indices of particular attentional components; alerting and orienting processes are visible in early stages of visual processing, namely, in the N1 amplitude that increased at posterior sites, while P3 amplitude modulation was linked to executive attention involvement. It should be stressed, however, that P3 is not a unitary phenomenon. In the literature there is well known a distinction regarding the P3; more anteriorly located P3a is separated from P3b, which is located in parietal regions. This was confirmed among others by Verleger et al. (2005) or Conroy and Polich (2007). Verleger and collaborators suggest that P3b is a reflexion of the link between perception and response, which signals a monitoring process of the decision concerning stimulus classification and action according to the appropriate steps of processing. Polich (2007) argues that the frontal P3a is a sign of the stimulus-driven attention mechanism, while the temporo-parietal P3b is associated with attention engaging subsequent memory processing. Furthermore, Nikolaev et al. (2008) observed the conflict effect on earlier sensory components (P1 and P2) that were interpreted as the reflexion of the stimulus evaluation and conflict detection. These researchers also found longer latencies for the response-locked lateralized readiness potential (LRP), indicating an extended motor reaction. These researchers concluded that in conflict tasks, a link between perception and execution is established, in the context of anticipation of action consequences. We also know that stimuli requiring inhibition (e.g. in No-Go tasks) usually evoke enhanced negativity in the N2 component and a later positivity in P3 at fronto-central electrodes, which are interpreted as the manifestation of conflict monitoring (in N2 modulation) and response inhibition (in the P3 differences) (Jonkman, 2006). The source of the N2 component in conflict tasks has been localised in the ACC (e.g.

Bekker et al., 2005; Nieuwenhuis et al., 2003), and the source of P3-modulated response inhibition has been localised in left fronto-central areas (Bokura et al., 2001). This brain localisation of conflict processing is compatible with the neuroimaging data mentioned above.

Parity judgment, magnitude assessment and other experimental paradigms have been used to unravel the spatial organisation of digits (Dehaene and Cohen, 1995; Fias et al., 1996), which reflect the SNARC effect. However, to study the psychophysiological correlates of conflict evoked by numbers, rather different type of tasks is typically used (e.g. numerical Stroop-like task) when participants have to select the larger number from a pair of presented digits, but an irrelevant physical size and the numeric representation may be in conflict (e.g. Pansky and Algorn, 1999). Neuroimaging data confirmed the brain locus of activation, typical for conflict processing, by using this type of task and stimuli (Ansari et al., 2006; Kaufmann et al., 2005). However, it should be stressed that this is not precisely a conflict task evoked by the SNARC effect.

Electrophysiological investigations of the SNARC effect are focused also on the stage of processing, at which spatial-numerical association occurs, indicating on the response selection stage as the locus of the described effect (Keus et al., 2005; Szucs and Soltesz, 2007; Gevers et al., 2006). In contrast, Salillas et al. (2008) investigated the orienting attention engagement by measurement of ERPs induced by lateral presentation of targets that were preceded by digit cues, and they demonstrated congruency effects in the larger amplitude of both sensory P1 and cognitive P3. A similar paradigm was used in Ranzini et al. (2009), where they found the same effect of spatial orienting, both with digits and with arrows as cues, but in ADAN and EDAN components, which are typically linked to attentional control.

In summary, in spite of the consistency in neuroimaging findings on the brain localisation of executive attention, ERPs studies do not lead to such clear conclusions. Different findings point to different ERP components, which are modulated by congruency. The view is additionally complicated by the lack of consistency in the type of tasks used for examining this problem. The SNARC effect, which obviously generates conflict, is not investigated in the context of executive attentional processing, but is linked mainly to orienting attention (with the use of Posner's paradigm). This is why our goal was to focus on the executive attention evoked by the parity judgment task, to examine the congruency effect in various components and compare our results with the reports concerning temporal and spatial loci of the SNARC effect on the one hand and executive attention on the other hand. We were also interested in hemispheric effects. Lateralisation of executive attention has been extensively investigated (e.g. Matsumoto and Tanaka, 2004; Casey et al., 2000; Fan et al., 2003; Fan et al., 2005; MacDonald et al., 2000), but there are no current reports focused on brain asymmetry of the SNARC effect. Despite well-known right hemisphere dominance in spatial-numerical processing, it is worth noting that this asymmetry could be dependent on the number magnitude of the stimulus. It would be in accordance with the right hemisphere role in the comparison or estimation, rather than, e.g. the exact calculation, which is the role of the left hemisphere (Cohen and Dehaene, 1996).

2. Method

2.1. Participants

After giving their informed consent, 29 subjects (mean age = 24.6; range 19–45; 24 females and 5 males) participated in the experiment. All of the participants were healthy, had no history of neurological problems, were right-handed and had normal or corrected-to-normal vision. In addition, participants were unaware of the purpose of the study. The experimental procedures used in this study were

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