Brain activity underlying response induced by SNARC-congruent and SNARC-incongruent stimuli

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At least three well-documented phenomena indicate a relationship between numbers and the internal representation of space. They are shifting attention in accordance with the localization of numbers on the mental number line (MNL); the spatial-numerical association of response codes (SNARC) effect, which manifests as faster responses to high numbers with the right hand than with the left, and *vice versa* for low numbers; and the processing of both numbers and space primarily in the parietal cortex. Some EEG studies have pointed to the response selection stage as a locus of this effect. However, this explanation has yet to be corroborated by the fMRI experiments. The goal of this study was to investigate the functional anatomy underlying response selection induced by SNARC-congruent and SNARC-incongruent stimuli in a spatial visual cueing task. Healthy adult volunteers responded to a pair of target stimuli consisting of digits, non-digit symbols, or a mix of both. In each trial, the stimuli were preceded by a centrally presented numerical or non-numerical cue stimulus which was required to be memorized. One of the target stimuli that then appeared would be identical to the cue; the task was to determine which side it was presented on, within the pair. In the case of numerical stimuli, the side was congruent with its localization on the MNL in one-half of the trials. In the other half of the trials, it was incongruent. The behavioral results revealed the SNARC effect, as well as a faster reaction to low numbers than to high numbers. The fMRI responses to the target stimuli showed engagement of regions implicated in number processing but also in sensory-motor areas. This suggests that the motor response selection or execution stage may be the locus of the SNARC effect. Yet, the activation pattern obtained in the congruent and incongruent conditions did not allow us to determine, indisputably, the neural correlates of the mechanisms involved in the SNARC effect. Moreover, we did not observe any stimulus-specific responses to cues.

Key words: SNARC effect, attention, motor functions, spatial-numerical association, fMRI

INTRODUCTION

Various neuroimaging, behavioral, and clinical studies have highlighted the parietal cortex as a crucial region involved in creating and maintaining abstract representations of quantity, irrespective of number format and type of task (Dehaene et al., 2003, 2004; Hubbard et al., 2005; Wood et al., 2006; Ansari et al., 2006; Cantlon et al., 2006; Cohen Kadosh et al., 2007; Piazza et al., 2007; Ashkenazi et al., 2008; Sandrini and Rusconi, 2009). Along with the parietal area, number processing seems also to engage the frontal cortex. As evidenced by fMRI (Arsalidou and Taylor, 2011) and TMS studies (Rusconi et al., 2011), these regions also become active during more complex tasks, like calculation.

Research has also shown that the mental representation of numbers involves a spatial component (Fias and Fischer, 2005; de Hevia et al., 2008; Wood et al., 2008; Fischer and Shaki, 2014). Importantly, neural circuits involved in both spatial attention and number representations are located in the parietal cortex (reviewed by Hubbard et al., 2005). The literature sup-

ports the view that the spatial representations of number magnitudes are mapped onto the so-called mental number line (MNL), where numerically lower numbers are internally represented on the left side, while higher numbers are represented on the right side (Dehaene, 1992; Restle, 1970). One of the widely reported manifestations of this relationship is the spatial-numerical association of response codes (SNARC) effect (Dehaene et al., 1993). The effect is based on the observation that low numbers evoke faster left-side reaction times (RTs), whereas high numbers accelerate right-side RTs. Thus, RT is prolonged in the case of incongruence between the position of the number's representation on the MNL and the location of the motor response. The SNARC effect has been replicated using of several types of tasks, different number formats (Fias, 2001), and different modalities (Nuerk et al., 2005). The most common methods that induce this spatial-numerical association in RTs and the correctness of responses are parity judgment and magnitude comparison tasks. Other methods reported in the literature are based on stimulus detection; line bisection tasks; pointing (related to assessing a number's location on the line flanked by reference numbers, for example); random number generation tasks; or counting behavior (Fischer and Shaki, 2014). The SNARC effect has also been demonstrated as spatial attention shifting, induced by numbers. In a study by Fischer et al. (2003) using an adapted Posner paradigm (1980), the task involved replacing centrally presented symbolic directional cues with Arabic digits. Low-magnitude cues resulted in faster reactions to targets displayed on the left, while high-magnitude cues resulted in slower reactions (and *vice versa*, in the case of targets presented on the right). Yet, a very recent paper aiming to replicate the results of this experiment, which was performed in 17 labs, on data from more than 1100 participants (Colling et al., 2020), failed to replicate the original results. This is a sign indicating, that an attentional SNARC effect does not exist, and thus cannot be viewed as evidence supporting the relationship between number and spatial attention.

The SNARC effect can be observed even when the magnitude information is irrelevant to the task and the numerical magnitude is not intentionally processed (Fias et al., 2001). This suggests that the SNARC effect is an index of automatic access to the spatial representation of numerical magnitudes. On the other hand, it is possible that numbers and space have no intrinsic and obligatory relationship but that this association is instead constructed during the task, on the basis of the instructions or the context of stimuli during the performance. This means that the spatial-numerical association is not robust and that the SNARC effect is modifiable and dependent on several factors. This may

include, for example, the range of numbers used in the experiment (Dehaene et al., 1993) and the magnitude of a reference number (Nathan et al., 2009). Other researchers have demonstrated that the SNARC effect can be easily modulated by task instruction (Bächtold et al., 1998) and by the activity preceding the SNARC task (Shaki and Fischer, 2008). These facts all seem to indicate that the relationship between numbers and space is at least partially created during a task; this has an important contribution to the SNARC effect profile (i.e., whether this effect is clearly pronounced, rather indistinct, or even reversed). It is also a probable explanation for the problem of why it is so difficult to reveal the hemodynamic markers of this behavioral effect (Cutini et al., 2012; Weis et al., 2015).

Uncovering the neural mechanisms of the SNARC effect may extend our understanding of the neural basis of number processing. The functional MRI (fMRI), with its high spatial resolution, seems a perfect fit for this purpose. To our knowledge, the mechanisms underlying the SNARC effect have not yet been extensively investigated by fMRI studies. Amongst the few studies was one conducted by Weis et al. (2015), who showed that – despite an evident SNARC effect obtained in the behavioral data – spatial-numerical incongruence was not manifested in neuronal correlates. In another study, Cutini et al. (2012) used functional near-infrared spectroscopy (fNIRS), which, similar to the fMRI, enables the registering of hemodynamic changes, to indicate the bilateral intraparietal sulcus and left angular gyrus as the regions whose activation was modulated by spatial-numerical incongruence. Some reports from transcranial magnetic stimulation (TMS) studies have confirmed the roles of the parietal and frontal regions, in the induction of the SNARC effect (Sandrini and Rusconi, 2009; Rusconi et al., 2011). Moreover, the relationship between number processing and spatial attention evoked by numbers has been demonstrated in event related potentials (ERP) studies. These have investigated the spatial-numerical association manifested in sensory and cognitive components modulated by perception and the processing of numerical cues preceding laterally displayed targets (Salillas et al., 2008; Ranzini et al., 2009; Gut et al., 2012).

Several studies have focused on the motor control component of the spatial-numerical association. The SNARC effect occurs even in experimental conditions requiring participants to react with crossed hands (Dehaene et al., 1993). This means that the effect does not depend on hand-centered coordinates, and that the numbers' representations are associated with the side in extracorporeal space. Moreover, the SNARC effect occurs during tasks performed by pointing (Fischer, 2003), *via* eye movements (Schwarz and Keus, 2004),

and by pressing left/right response keys with the same finger (Vuilleumier et al., 2004). Current research suggests that the spatial-numerical relationship arises in a spatial-coordinate frame that is effector-independent, and it is even observed in the case of verbal responses to stimuli (Nicholls et al., 2008). This means that the SNARC effect emerges from the incongruence between the side of response (regardless of which hand is responding) and the side of the number's representation position on the MNL. Thus, one may ask at what stage of processing this spatial-numerical interaction occurs: is it stimulus perception, response selection, or response execution? Keus and Schwarz (2005) manipulated the congruence between the position of the presented number and its localization on the MNL, as well as between the position of the number and the position of the effector. They showed that only the second type of manipulation can produce the SNARC effect. In a series of experiments they revealed a significant interaction between the number magnitude (and its location on the MNL) and the side of response, which reflected the SNARC effect. Meanwhile, they did not observe a similar relationship between number magnitude and the side of number presentation on the screen. Some electrophysiological investigations of this issue pointed to the response selection stage as a locus of this effect (Keus et al., 2005; Gevers et al., 2006; Szucs and Soltesz, 2007). However, these observations have not yet been corroborated in fMRI and fNIRS studies.

In sum; in some studies the SNARC effect may be explained by an attentional shift evoked by number perception (see however, Colling et al., 2020), which is independent of the hand performing the reaction. The SNARC effect may also arise at a later stage of effector response selection. According to the so-called "effector hypothesis" (Müller and Schwarz, 2007), which describes the SNARC effect in terms of spatio-anatomical mapping (i.e., the relation between spatially represented sides of the body and number magnitude), low numbers are represented in the right hemisphere, which is dominant for left-hand movements (congruent with the locus of these magnitudes on the MNL). This explains why the left hand reacts faster to small numbers. Accordingly, the same relationship pertains to high numbers and the left hemisphere.

In the current study, the goals were twofold. First, we aimed to identify the regions activated during spatial-numerical incongruence (manifested in behavioral data as the SNARC effect). We presented the low- and high-magnitude numbers either on the left or the right side of the visual field, and the task was to determine the side of the target presentation with a corresponding hand. At the same time, in one-half of the trials, the side of number presentation (and the hand responding

to the stimulus) was incongruent with its location on the MNL. This enabled us to assess the effect of congruency between the side of the target presentation (which is here linked to the side of response) and its position on the MNL. Thus, by looking at the contrast between the congruent and incongruent trials, we aimed both to reveal the brain areas involved in the cognitive conflict associated with the SNARC effect and to compare them with the results reported in studies using tasks inducing executive attention (cognitive conflict). Second, we sought to verify the explanation for the SNARC effect, which is based on the effector hypothesis, by analyzing the asymmetry of activations resulting from reactions to numbers. This gave us the opportunity to address the question of whether the evoked brain responses would be determined by the spatial position of a number stimulus within the visual field (and the responding hand) or, alternatively, its position on the MNL. Namely, we aimed to determine whether the activation clusters in sensory-motor areas would be found in the hemisphere, that was contralateral to the side on the MNL where the number (low or high) is mentally represented. According to this hypothesis, small numbers should evoke a response selection in the right hemisphere (which mainly controls left-hand movements), while high numbers should evoke the same for the left hemisphere. Importantly, since the stimulus requires a motor response on the side compatible with the side of its presentation, we should also observe the brain activation referring to the response execution process; this should occur mainly in the hemisphere contralateral to the hand pressing the button (= the side of the stimulus). In one-half of the trials, this response selection was in conflict with the hand reaction required by the instruction, which in turn manifested in the SNARC effect. In the other trials, the response selection was congruent. Hence, a comparison of the asymmetrical brain activation patterns, reflecting responses to congruent numbers with the pattern linked to incongruent numbers (probably more bilateral), should result in a lateralized activation, related solely to the incongruence of the displayed number and the conflict processing. This enabled us to infer the possible processing stage where this effect occurs.

METHODS

Participants

After providing informed consent, 19 adult volunteers (mean age=24 years; range 20-38 years; 16 women and 3 men) participated in the experiment. All participants were declared healthy, with no history of neu-

rological problems. They were right-handed (their handedness was assessed by self-declaration) and had normal or corrected-to-normal vision. The participants were unaware of the purpose of the study, and they took part in the experiment for course credit. The experimental procedures used in this study were approved by the Ethics Committee of the University of Finance and Management in Warsaw, Poland. The data gathered from one subject were rejected, due to problems with synchronization of the stimulus presentation with the acquisition of functional images.

Stimuli

The cue stimulus consisted of a single centrally displayed one-digit number or non-digit symbol. The target stimulus consisted of a pair of two digits, two symbols, or one digit with a non-digit symbol. Both digits and non-digit symbols were presented in Arial font (size: 48-point) on a light gray background (RGB value 190, 190, 190). The digit stimuli set included digits 1, 2, 8, and 9; the non-digit symbol set included the following characters: %, &, #, and §. The characters had the following dimensions: 1.15° vertically and 1° horizontally. Each pair of digits/symbols (or mixed) had the following dimensions: 1.15° vertically and 5.72° horizontally.

Throughout the whole procedure, an orange fixation point (size 3 point, RGB value 255, 127, 0) was presented in the center of the screen. Screen resolution was set to 1920 x 1080 pixels, with a vertical refresh rate of 60 Hz. Stimuli were back-projected by the multimedia projector onto the screen located behind the scanner gantry (103 cm from the participant head) and were visible through a mirror system mounted in the head coil, 10 cm above the participants' eyes.

Experimental task

The whole experimental procedure was divided into three acquisition runs, each lasting 15 min. Each run started with the presentation of an information screen. Each trial within the experimental procedure then started with a cue-stimulus (a single digit or a non-digit symbol), which was presented centrally for 100 ms (Fig. 1). The participants were asked to remember this stimulus. The next stimulus, a target stimulus, was presented with SOA=2000 ms for 150 ms. The target stimulus consisted of a pair of characters, of which one was the digit or non-digit symbol that had been presented previously as a cue-stimulus during the same trial. The targets consisting of two numbers of the same magnitude (e.g.,

low) displayed in the one target stimulus set (for example, "1" in the right location and "2" in the left location) were excluded from the experimental procedure.

Participants were asked to press the appropriate response key to indicate, as quickly and accurately as possible, the spatial location of this digit/symbol (left or right). The left key on the response pad corresponded to the left position, and the right key corresponded to the right position. According to the MNL organization, the numbers represented by the digit stimuli were defined as left/low-magnitude ("1" and "2") and right/high-magnitude numbers ("8" and "9"). We used these four digits because we were most interested in the effect observed for the numbers positioned in the numerical distances that were at the far left and right (similar to the study by Fischer et al. (2003), which used only the numbers "1", "2", "8", and "9").

A trial was defined as congruent when the side of the digit in the target-stimulus presentation (left/right) corresponded to its location on the MNL
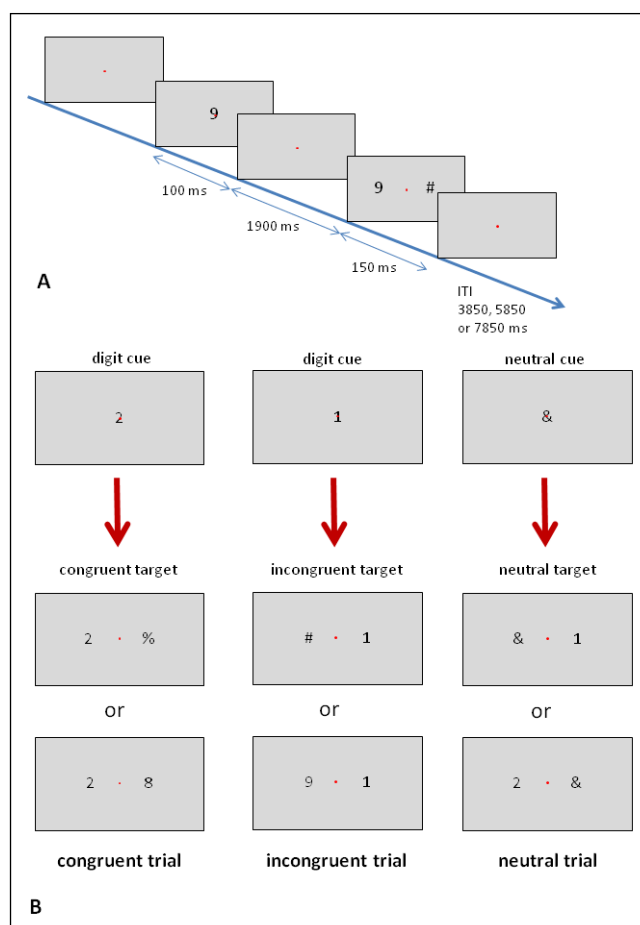

Fig. 1. (A) The structure of the experimental trial. The cue-only trials had the same temporal structure, with target stimuli screen replaced by the blank screen with the fixation point. (B) The examples of three different trial types.

(left-right). It was defined as incongruent in the opposite case (e.g., if the digit "2" had been presented on the right side of the target-stimulus). Thus, there were four types of trials (experimental conditions): congruent with a low-magnitude number ("1" or "2" on the left side of the target-stimulus), congruent with a high-magnitude number ("8" or "9" in the right location), incongruent with a low-magnitude number (with "1" or "2" on the right side), and incongruent with a high-magnitude number ("8" or "9" in the left location). The presentation of the target-stimulus set was followed by an inter-trial interval lasting for 3850, 5850, or 7850 ms (its duration was randomly selected). Trials with the non-digit symbols as cue-stimuli were labeled as neutral trials, and these symbols were also displayed in one of two locations in the target-stimulus set. To determine BOLD response to the cue stimulus, twenty percent of all trials were defined as cue-only trials. These consisted of only a cue-stimulus, with no target-stimulus presented after it; the other temporal parameters were identical to those in the trials with the target present. The experimental procedure, with examples of stimuli, is shown in Fig. 1.

The whole experimental session included 360 trials and lasted approximately 45 min. Of these, 72 trials were congruent, 72 were incongruent, 144 were neutral, and 72 were cue-only trials. An equal number of trials had low- and high-magnitude numbers used as the cue-stimuli. The order of the trials, and the magnitudes of numbers presented as the cues and targets, were randomized between subjects.

Before the experiment, the participants familiarized themselves with the task and stimuli by performing a short training block of 30 trials outside the MRI scanner. The task was controlled *via* a standard PC computer, using Presentation software (Neurobehavioral Systems Inc., Albany, CA, USA).

Acquisition of fMRI data

A Magnetom Avanto 1.5T scanner (Siemens, Erlangen, Germany), equipped with a 32-channel phased array head coil, was used to acquire whole-brain images. Head movement was restricted with foam cushions. Detailed whole-head structural images were acquired in the sagittal plane with the T1-weighted (TR=1720 ms, TE=2.92 ms, flip angle=15°) and T2-weighted (TR=3200 ms, TE=381 ms, flip angle=120°) MPRAGE scanning sequence with isotropic voxels (1 × 1 × 1 mm). Functional images were acquired with the T2*-weighted scanning sequence with the following parameters: TR=2000 ms, TE=50 ms, flip angle=90°, in-plane resolution=2.5 × 2.5 mm, field of view=240 mm, 23 axial slices, with 6-mm slice thickness and no gap between slices. One functional run consisted of 490 (8 subjects) or 505 (10 subjects) volumes. Each subject had three functional runs, with the exception of one subject, which had two runs with 607 volumes.

Behavioral data analysis

Behavioral data, including the timing and accuracy of responses, were used in the analysis of the median reaction time (RT) and the mean percentage of correct responses (PC). Custom MATLAB scripts (MathWorks, Inc., Natick, MA, USA) were used to calculate the median RTs and mean PCs, based on the raw data for each experimental condition. The median RTs and mean PCs for each participant and experimental condition were analyzed using SPSS software.

The incorrect responses and missed responses were all treated as errors (1.24% and 1.95% of all motor reactions, respectively) and were not included in the RT analyses. Statistical analyses concerning the effect of all factors on RTs were performed only on the RT data for the correct responses.

To examine the effect of the congruence of the number (digit) on RTs and PCs, as well as the lateralization of motor responses to all types of stimuli, the data (median RTs and mean PCs of all participants) obtained for numerical and non-numerical stimuli were submitted into a two-factor repeated-measures analysis of variance (ANOVA). We used the type of target stimulus (3 levels) and the side of target stimulus presentation (2 levels) as within-subject factors, and the RTs and PCs as dependent variables. More precisely - due to the use of numerical and neutral target stimuli - a two-factor ANOVA was performed, with the three-category factor defined as type (low number/high number/symbol) as the one within-subject factor and the side (left/right) as the second within-subject factor. This enabled us to examine the effect of number congruence on RT and PC (= the SNARC effect), since, we could thus compare reactions to small numbers presented on the left (= congruent) with those presented on the right (= incongruent), and the same comparison could be made for high numbers.

fMRI data analysis

The neuroimaging data were preprocessed and analyzed using the SPM12 (Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, UK) toolbox, running on MATLAB (MathWorks, Natick,

MA). During the preprocessing procedure, the functional images were corrected for shifts in acquisition time (slice-timing) and head motion (spatial realignment). Anatomical images (T1-weighted) were co-registered to the mean functional volume, and functional images were normalized to the MNI template, using a new unified normalization-segmentation procedure (Ashburner and Friston, 2005). The resulting functional volumes were spatially smoothed, using an 8-mm full-width half-maximum (FWHM) Gaussian kernel. First-level linear model (GLM) analysis was performed by entering into the design matrix regressors representing all experimental events (a separate regressor for each condition) with subject-specific onset timing as well as additional regressors of no interest, representing six head movement parameters and incorrect or missed responses. The model parameters were then estimated for each condition and corresponding first-level temporal derivative. A one-sample T-test was performed for contrasts of interest: the main effect of congruent numbers, the main effect of incongruent numbers, incongruent *vs.* neutral targets, congruent *vs.* neutral targets, incongruent *vs.* congruent and congruent *vs.* incongruent targets (which were also calculated separately for low magnitude numbers and for high magnitude numbers), the main effect of high-magnitude numbers, and the main effect of low-magnitude numbers. The same analysis was performed for the main effect of numerical and neutral cues. The resulting statistical maps were corrected for multiple comparisons, using a family-wise error (FWE) rate threshold (corrected < 0.05). To verify the hypothesis of more bilateral response patterns in the primary motor cortices to the incongruent target stimuli, we also compared evoked responses to incongruent target stimuli with the responses to incongruent target stimuli in the primary motor cortex. To do this, we extracted and averaged beta values from the voxels, comprised of the left and right motor cortex ROIs defined with Juelich histological atlas (ROI ID: "GM Primary motor cortex BA4p"). We inspected histograms of the beta value differences between the left and right hemisphere ROIs.

RESULTS

Behavioral results

The mean response PC rate and the mean RT (calculated for all trials with targets) were 96.81% and 469 ms, respectively.

In terms of median RT, the two-factor ANOVA was performed for the side and the stimulus type (low number/high number/neutral symbol) as the within-subject factors, and the RTs and PCs as the dependent variables. This revealed a significant effect for the side ($F_{1,17}$=9.95, P<0.01, η_p^2=0.369) – with faster reactions to stimuli displayed on the right side of the stimuli set (M_{right}=460.76 ms; SEM=19.07 ms) than on the left side (M_{left}=481.3 ms; SEM=18.53 ms; t_{17}=3.154, P<0.01) – and type of stimuli ($F_{2,34}$=10.7, P<0.01, η_p^2=0.386). The RT was significantly shorter for the low-magnitude numbers than for the high-magnitude numbers (M_{low}=457.29 ms; SEM=19.52 ms; M_{high}=473.56 ms; SEM=18.99 ms; t_{17}=3.218, P<0.01) and for neutral symbols (M_{symbol}=476.63 ms; SEM=18.08 ms; t_{17}=3.912, P<0.01).

Moreover, a significant interaction was found between stimulus type and the side of the target stimulus presentation ($F_{2,34}$=3.512, P<0.05, η_p^2=0.171). In the case of low-magnitude numbers, the side of digit presentation in the stimulus set was insignificant, as illustrated in Fig. 2. Meanwhile, in the case of high-magnitude numbers and neutral symbols, it was significant.

When the high-magnitude numbers were displayed on the right (M_{right}=457 ms; SEM=20.46 ms), the RTs were faster than when they were presented on the left (M_{left}=490.11 ms; SEM=18.7 ms; t_{17}=3.417, P<0.01). A similar difference, though less pronounced, was obtained for neutral symbols (M_{right}=467.72 ms; SEM=18.51 ms; M_{left}=485.55 ms; SEM=18.39 ms; t_{17}=2.409, P<0.05).

Moreover, in the case of incongruent trials (small numbers presented on the right, and high numbers presented on the left), the mean RT for the low-magnitude numbers (M_{low}=450.59 ms; SEM=20.04 ms) was faster than for the high-magnitude numbers (M_{high}=490.11 ms; SEM=18.7 ms; t_{17}=3.907, P<0.01). The RTs for congruent numbers, on the other hand, did not show a significant difference between mean RTs to low and high numbers.

To analyze the main effect of congruence in terms of median RT, we performed an additional two-factor ANOVA, with number magnitude (2) and congruence of stimuli (2) as the factors. This revealed a significant main effect of number magnitude (with the same profile of differences as described above) ($F_{1,17}$=10.356, P<0.01, η_p^2=0.379). It also showed a significant main effect of congruence (the SNARC effect), ($F_{1,17}$=7.407, P<0.05, η_p^2=0.303) with faster reactions to congruent stimuli (M_{cong}=460.5 ms; SEM=19.63 ms) than to incongruent stimuli (M_{incong}=470.35 ms; SEM=18.71 ms; t_{17}=2.722, P<0.05). Moreover, a significant interaction was found between magnitude and congruence of stimuli ($F_{1,17}$=9.653, P<0.01, η_p^2=0.362), confirming the interaction illustrated in Fig. 2.

Similar ANOVAs, with the mean PC used as the dependent variable, did not reveal a statistical significance of any factor or interactions between them.
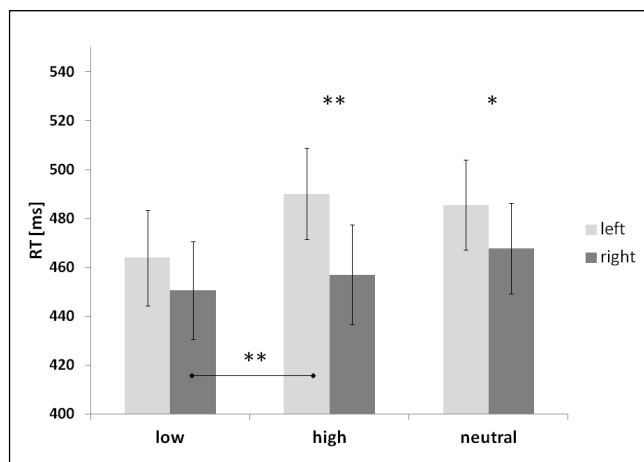
Fig. 2. The interaction between the side of target stimuli presentation and the type of stimulus (low number/high number/neutral) in the mean reaction time (RT; represented by bars). The error bars represent the SEM values. Since the side of the number presentation was congruent (right side for high and left side for low numbers) in half of trials and incongruent (right for low and left for high) in the other half, this graph also presents the differences between the congruent and incongruent trials. These were calculated separately for low and high numbers, which illustrates the effect of congruence on RTs (the SNARC effect), pronounced mainly in case of high magnitude numbers.

fMRI results

In the case of target stimuli presentation, the fMRI scans revealed a number of areas that were consistently activated during a low number condition and a high number condition as well as during congruent trials and incongruent trials. Fig. 3 and Fig. 4 illustrate the main effects for these conditions (main effects for these two factors). The list of suprathreshold voxels with their anatomical descriptions and their MNI coordinates grouped by condition is presented in Tables I and II.

Main effects of number congruence

To identify the brain areas involved in the cognitive conflict (namely, the conflict between the side of response and the side of number localization on the MNL) defined as the SNARC effect (along with its behavioral markers, reflected as an increased RT to incongruent stimulus), we analyzed the main effect of congruent trials and the same for incongruent trials. The results for the presentation of targets with congruent numbers (Fig. 3A) showed the bilateral pattern of activation. More precisely, in the frontal lobe they revealed significant activation in the right and left supplementary motor area (SMA), right Rolandic

operculum, and middle frontal gyrus, as well as in the left insula and middle cingulum. In the parietal lobe, activations were found in the right postcentral gyrus and inferior parietal lobule. Active locations in the temporal lobe were found in the right middle and superior temporal gyri. Active locations in the occipital lobe were found in the left inferior occipital gyrus. The congruent stimuli also evoked activation in the right thalamus and in the cerebellum, bilaterally. The data presented in Table I suggest lateralization with a predominance of the right hemisphere, which is manifested in the larger cluster identified in the right SMA and thalamus. However, as we can see in Fig. 3A, this brain activation region covers both hemispheres and the number of activation voxels is in fact a bit higher in the left hemisphere. To answer this question about lateralization, additional analyses have been performed. An inspection of the histogram representing the beta value differences between the left and right primary motor cortex ROIs showed more incidences of extreme asymmetric motor responses in the congruent condition, than in the incongruent condition. In the latter, the L-R beta difference values were clustered around zero. This indicates more less-lateralized responses in the primary motor cortex.

The incongruent trials (Fig. 3B) also evoked a bilateral activation pattern. In the case of incongruent condition, the cluster size also clearly suggests a broader activation of the right hemisphere, yet this was not the case. Again, an activation area in the SMA was expanded in the two hemispheres, as illustrated in Fig. 3B. Specifically, the suprathreshold activation was shown in frontal activation in the left insula, right and left SMA, precentral gyrus, inferior frontal operculum, and Rolandic operculum. Parietal activations were found in the left superior parietal lobule, as well as in the right inferior parietal lobule. In the occipital lobe, suprathreshold clusters were observed in the left middle occipital gyrus. The incongruent condition also evoked significant activation in the middle temporal and fusiform gyri of the right hemisphere; in the bilateral cerebellum; and in the right caudate nucleus, pallidum, and thalamus.

We did not observe any statistically significant differences in the whole-brain activation pattern, however, when comparing the congruent *vs.* the incongruent trials. We also designed congruent > neutral and incongruent > neutral contrasts. When investigating the uncorrected data, the first contrasts did not reveal any brain regions involved in the congruent condition compared to the neutral condition. Meanwhile, stronger responses in the incongruent trials – as compared to neutral trials – were found in the left middle occipital and angular gyri (Fig. 3C).

Table I. The list of suprathreshold clusters in trials with congruent and incongruent numbers. The cluster size threshold was 7 contiguous voxels and the FWE-corrected threshold was p<0.05 (FWE). In case of the contrast incongruent trials > neutral trials the table presents uncorrected data. The cluster size parameter indicates the number of voxels within the given cluster.

Condition or contrast	Hemisphere	Anatomical label	MNI coordinates	Z-score	Cluster size
Congruent number targets	Left	Inferior occipital gyrus	-48, -70, -4	5.74	181
		Insula	-30, 22, 6	5.69	191
		Cerebellum	-38, -48, -26	5.67	500
		Middle cingulum	-10, -24, 40	5.12	19
	Right	Supplementary motor area	2, 4, 50	7.03	7934
		Thalamus	12, -14, 2	6.03	1884
		Middle temporal gyrus	54, -66, 8	5.82	98
		Rolandic operculum	56, -18, 18	5.69	161
		Cerebellum	34, -50, -28	5.64	555
		Superior temporal gyrus	60, -34, 20	5.57	89
		Postcentral gyrus	44, -22, 40	5.56	111
		Middle frontal gyrus	32, 38, 24	5.34	26
		Superior parietal lobule	30, -58, 56	5.20	60
		Inferior parietal lobule	46, -34, 54	4.97	19
Incongruent number targets	Left	Middle occipital gyrus	-48, -66, 0	5.68	134
		Superior parietal lobule	-26, -66, 50	5.41	48
		Cerebellum	-38, -50, -30	5.28	132
		Insula	-30, 22, 4	5.21	73
	Right	Supplementary motor area	2, 2, 52	6.72	5353
		Caudate nucleus	10, 8, 4	6.31	82
		Cerebellum	26, -54, -28	6.26	424
		Precentral gyrus	34, -18, 54	6.06	546
		Inferior frontal operculum	60, 12, 22	6.01	480
		Thalamus	10, -18, 4	5.78	170
		Rolandic operculum	44, -2, 8	5.74	99
			58, -18, 16	5.57	203
		Inferior parietal lobule	34, -54, 52	5.23	28
			48, -32, 54	5.0	26
		Middle temporal gyrus	48, -62, 4	5.08	22
		Fusiform gyrus	32, -72, -12	5.04	34
		Pallidum	24, 2, 0	5.01	22
Incongruent *vs.* neutral targets	Left	Middle occipital gyrus	-40, -68, 26	4.05	250
		Angular gyrus	-48, -70, 26	3.88	

Main effect of number magnitude

To determine which brain areas were specifically activated by low (or high) magnitude numbers, we analyzed the effect of the second factor – number magnitude, as it was done on the behavioral data. Analyses done for low-magnitude numbers (independent of their congruence) revealed frontal brain regions involved in small number processing in the left middle and anterior cingulum, but also in several right
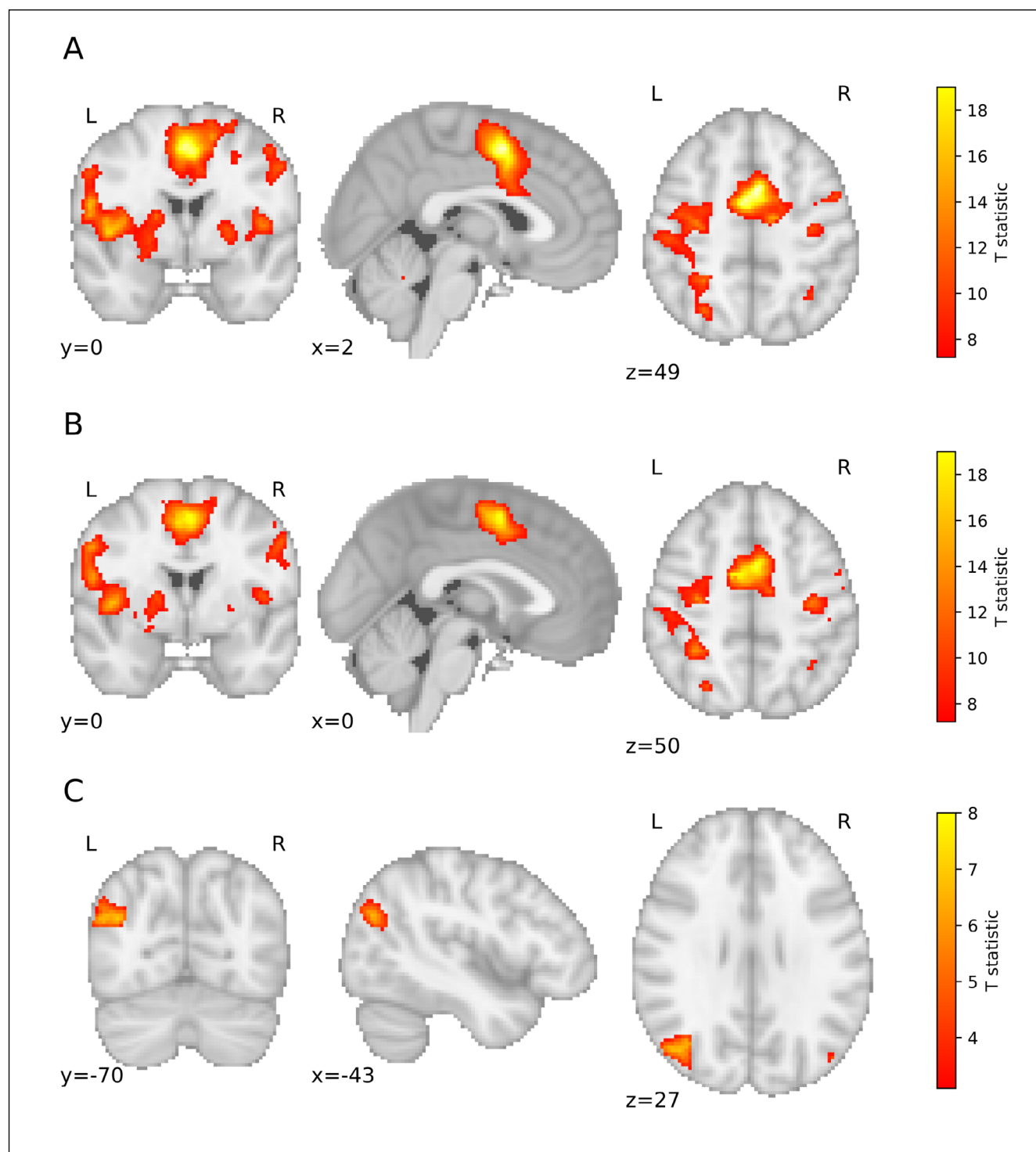

Fig. 3. Activation maps for trials with congruent (A) and incongruent (B) conditions. The bottom part (C) presents the activation patterns revealed in the case of contrasts: incongruent > neutral condition.

hemisphere regions. These included the insula and, bilaterally, the SMA (where we observed small right hemisphere prevalence, as illustrated in Fig. 4A), as well as in the Rolandic operculum. The number of suprathreshold voxels presented in Table II may suggest right-side lateralization in SMA. However, when looking at the brain activation pattern in Fig. 4A, there is very clearly one extensive activation cluster that covers both hemispheres almost equally. Significant foci for small number targets in the parietal lobe were observed, bilaterally, in the superior parietal lobules and in the right inferior parietal lobule; while in the occipital region, the suprathreshold clusters were observed in the left inferior occipital gyrus. In the temporal lobe, we obtained significant activations in the right middle and superior temporal gyri. Small number targets also evoked significant activation bilaterally (with a small right-side domination that manifested in a larger activation area), in the cerebellum and in the left thalamus.

The brain activation pattern during exposure to high numbers was very similar to the result obtained in the small number condition: a bilateral distribution of activation clusters, yet with more suprathreshold voxels in some regions of the left hemisphere. The frontal areas engaged in high number processing were localized in several brain areas. The biggest significant clusters of activation were found in the left and right SMA (this is identified as an activation localized in the left

hemisphere; see Table II. Yet, the scope of activation is strongly bilateral, as we can see in Fig. 4B). The frontal activation clusters were also shown in the inferior frontal operculum, Rolandic operculum, middle frontal gyrus of the right hemisphere, and bilaterally (with predomination of activation in the left hemisphere) in the insula. Parietal activations were observed in the right inferior and left superior parietal lobules. Significant foci for high number targets in the temporal regions were observed only in the left fusiform gyrus. The high number stimuli also evoked bilateral activation in the cerebellum, the right caudate nucleus, the thalamus, and the left pallidum. Brain scans depicting the distribution regions observed in these conditions (for low and high number targets) are presented in Fig. 4 and are listed in Table II.

No suprathreshold voxels (when applying such contrasts as low numbers > neutral and high numbers > neutral, as well as the opposite ones) were observed. Four additional analyses were performed, to investigate the localization of the activation evoked by congruent and incongruent stimuli, separately, for low and high magnitude numbers. Specifically, we obtained significant (FWE corrected) activation clusters in case of contrasts: incongruent low > congruent low numbers, congruent low > incongruent low numbers, and the same for high magnitude numbers. The lists of suprathreshold voxels – with their anatomical descriptions
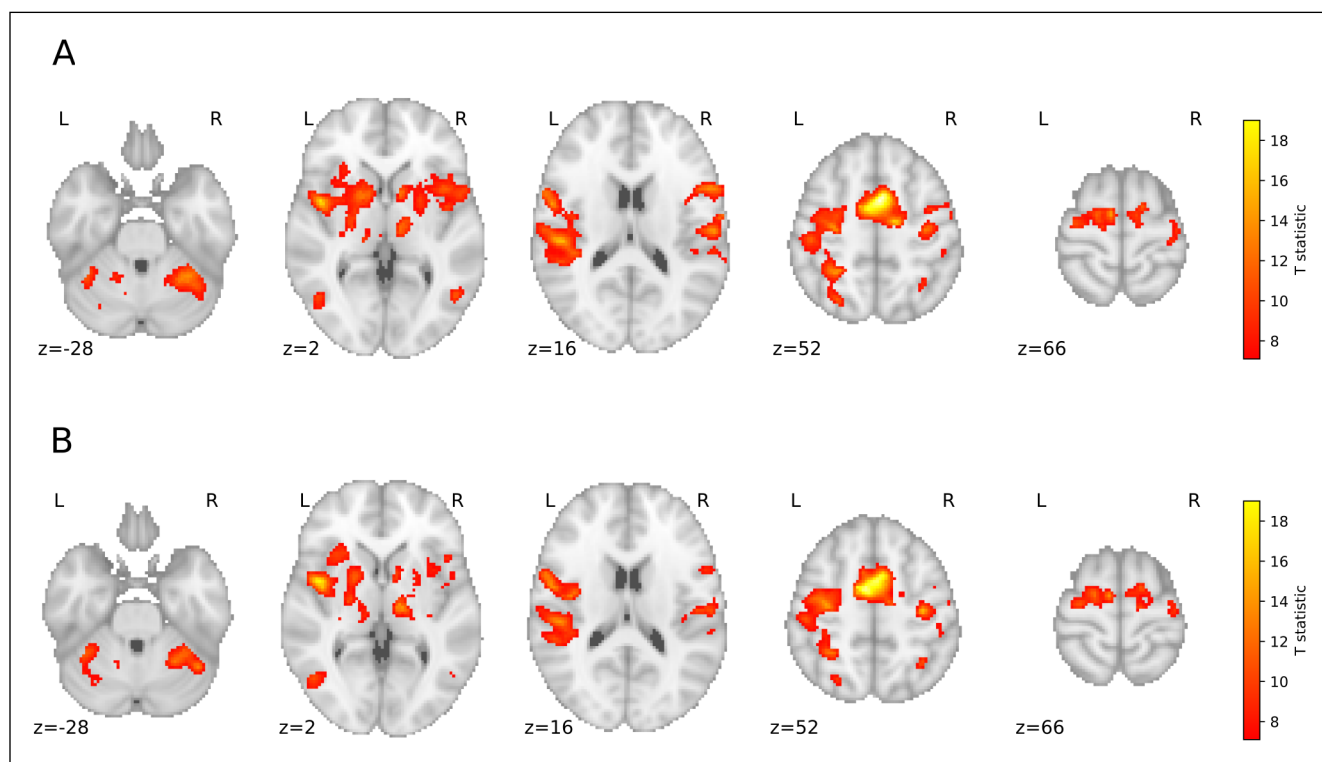

Fig. 4. Activation maps for trials with high-magnitude number targets (A) and low-magnitude targets (B).

Table II. The list of suprathreshold clusters in trials with low and high number stimuli. The cluster size threshold was 7 contiguous voxels and the FWE-corrected threshold was p<0.05 (FWE). The cluster size parameter indicates the number of voxels within the given cluster.

Condition	Hemisphere	Anatomical label	MNI coordinates	Z-score	Cluster size
Low number targets	Left	Superior parietal lobule	-34, -62, 56	5.0	110
		Inferior occipital gyrus	-48, -70, -4	5.7	123
		Cerebellum	-38, -52, -30	5.57	159
			-30, -72, -26	5.43	165
			-8, -62, -18	5.18	66
			-18, -50, -30	5.16	19
		Thalamus	-18, -24, 6	5.55	89
		Middle cingulum	-10, -24, 38	5.44	33
		Anterior cingulum	-6, 26, 22	5.38	30
	Right	Supplementary motor area	2, 2, 52	7.10	6946
		Insula	42, -2, 6	6.07	2064
		Rolandic operculum	58, -18, 18	5.99	252
		Cerebellum	30, -50, -30	5.88	618
			14, -48, -18	5.17	25
		Middle temporal gyrus	56, -62, 6	5.72	104
		Superior temporal gyrus	60, -34, 18	5.29	70
		Superior parietal lobule	32, -56, 54	5.12	42
		Inferior parietal lobule	48, -34, 54	5.11	44
High number targets	Left	Supplementary motor area	-6, -4, 54	6.95	5511
		Insula	-44, 2, 2	6.48	1176
			-30, 22, 6	5.66	175
		Middle temporal gyrus	-48, -66, 0	5.73	166
		Pallidum	-18, 4, 8	5.69	447
		Superior parietal lobule	-26, -66, 50	5.59	71
		Cerebellum	-36, -48, -28	5.53	263
		Fusiform gyrus	-38, -72, -18	5.24	61
	Right	Cerebellum	42, -58, -30	6.02	427
			4, -52, -8	5.42	25
		Thalamus	12, -16, 4	5.94	213
		Inferior frontal operculum	60, 12, 24	5.88	417
		Insula	42, 0, 10	5.51	95
			38, 8, 0	5.25	122
		Rolandic operculum	48, -18, 14	5.48	156
		Inferior parietal lobule	34, -54, 54	5.48	73
		Caudate nucleus	10, 8, 4	5.46	37
		Middle frontal gyrus	32, 40, 26	5.23	22

Table III. The list of suprathreshold clusters in contrasts: incongruent > congruent and congruent > incongruent trials separately for low and high magnitude numbers. The cluster size threshold was 7 contiguous voxels and the FWE-corrected threshold was p<0.05 (FWE). The cluster size parameter indicates the number of voxels within the given cluster.

Condition	Hemisphere	Anatomical label	MNI coordinates	Z-score	Cluster size
Incongruent *vs.* congruent low number targets	Left	Precentral gyrus	-36, -24, 66	6.74	262
		Precentral and postcentral gyrus	-44, -22, 60	5.83	
	Right	(no significant activation clusters)			
Incongruent *vs.* congruent high number targets	Left	Cerebellum	-20, -52, -24	5.31	59
	Right	Precentral and postcentral gyrus	46, -20, 48	6.17	831
			38, -22, 50	6.04	
			46, -26, 62	5.98	
Congruent *vs.* incongruent low number targets	Left	Cerebellum	-18, -52, -24	5.22	52
	Right	BA48, Precentral gyrus	34, -22, 46	6.38	1175
			44, -16, 48	6.24	
			30, -26, 54	6.10	
Congruent *vs.* incongruent high number targets	Left	Precentral and postcentral gyrus	-32, -26, 58	5.26	137
			-34, -22, 48	5.13	
			-28, -22, 72	5.04	
	Right	(no significant activation clusters)			

and their MNI coordinates grouped by those particular conditions – are presented in Table III. In all contrasts, the activation clusters were focused only in the sensory-motor regions (BA3, BA4, BA6) and mainly in the hemisphere contralateral to the hand performing the response to the target, as well as in the ipsilateral hemisphere of the cerebellum.

The lack of responses to numerical cues

To verify whether the number magnitude of a centrally displayed digit evokes a shift of attention toward its location on the MNL (accordingly to Fischer et al., 2003) or not (Colling et al., 2020), we also analyzed the main effect of a numerical cue as well as of a low number cue, a high number cue, and contrasts between a numerical *vs.* neutral cue. The activation pattern showing the involvement of an orienting attention process, as a result of number-cue presentation, would rather confirm the early, response-independent mechanism responsible for the SNARC-effect. It would be in line with an effect showed by Fischer and coworkers (2003). However, we did not observe a significant effect for either a numerical or neutral cue. No suprathreshold voxels were found in the contrasts done for low number cue and high number cue, either.

DISCUSSION

In this study, we investigated the neural correlates of the SNARC effect by recording brain responses during target detection tasks with low- and high-magnitude numbers presented on the left or right side of the visual field. The right-side/left-side presentation of the target numbers required participants to respond with the right or left hand. Thus, in some trials, the side of presentation was congruent with the localization of the number representations on the MNL. In the other trials, the side of presentation and MNL-localization were incongruent.

When comparing RTs obtained from congruent and incongruent conditions, we observed the SNARC effect evoked by the manipulation of the side where the target digit was displayed. The fMRI results indicated that responses to congruent and incongruent targets were found mainly in several sensory-motor regions as well as in parietal areas linked to numerical processing. Surprisingly, the contrast between the congruent and non-numerical targets did not reveal any activation cluster, while the same contrast performed for incongruent stimuli showed stronger activation clusters in only the occipital and parietal regions which are known to be the neural basis for number processing. Likewise, that contrast did not show an evident activation in the

areas related to cognitive conflict, which is manifested as the SNARC effect.

Targets with low-magnitude numbers evoked activation in several regions located in the right and left hemisphere with a small disproportion of activation clusters for the right side, while targets with high-magnitude numbers caused activation in the left hemisphere. The much greater lateralization obtained both for low and high numbers would confirm that numbers activate areas in the hemispheres that are contralateral to the spatial localization of the numbers on the MNL - and not to the spatial localization of the number stimuli on the screen (a hand performing a motor reaction to the number). This would confirm the effector hypothesis. Here, however, we showed bilateral activation patterns. It should be emphasized that motor activations were obtained for all small numbers (congruent and incongruent ones) and for all high numbers (calculated for all "8" and "9" trials, independently of their congruency). A probable explanation for this bilateral pattern is that the presentation of the number and the perception of its magnitude evoke the activation in the hemisphere contralateral to the locus of number on MNL – and, simultaneously, in the hemisphere contralateral to the hand pressing the reaction key (= the visual field of number presentation). Future studies, using a larger sample size, are necessary to verify this assumption. We observed a clear asymmetry in activation only in the additional contrasts between incongruent and congruent conditions (and in the opposite contrast congruent > incongruent), calculated distinctly for low and for high numbers. Importantly, these activation clusters were found in the hemisphere contralateral to the hand, which reacted to number on the screen and not to the position of the number on the MNL. This lateralized activation in motor regions, which was obtained in all these contrasts, may confirm the engagement of response selection process - but generally, in the case of subjects' reaction to numbers both congruent and incongruent. Thus, this pattern of results does not enable us to determine the functional locus of the examined effect.

The SNARC effect and the number magnitude effect at the behavioral level

When studying the neural correlates of the SNARC effect, we primarily had to ensure that the stimuli used in the experiment evoked significant differences between the RTs and/or PCs, calculated for congruent *vs.* incongruent trials. In other words, we had to ensure that the SNARC effect was demonstrated in the behavioral data. Although no effect was found in the PCs, a clear SNARC effect was visible in the prolonged RTs - in trials with incongruent positions of numbers on the screen. However, an inspection of the interaction between a number's magnitude and the side on which it was presented revealed that this effect mainly resulted from the difference between responses to congruent *vs.* incongruent high-magnitude numbers; while in the case of low numbers, the SNARC effect did not occur. This can be explained on the basis of another effect revealed in the RTs. Participants' reactions were generally faster for lower than for higher numbers. This means that, independently of congruence, the processing of "1" and "2" was quicker than for "8" and "9".

Low-magnitude numbers guide our attention – as demonstrated by attentional bias, which is also called pseudoneglect – toward the left side of the MNL in the numerical intervals bisection task (Göbel et al., 2006; Longo and Lourenco, 2007; Longo et al., 2012). An advantage of low-magnitude numbers has also been demonstrated in a study of the temporal perception of digits (Schwarz and Eiselt, 2009), which was interpreted as the effect of faster processing of smaller numbers. Cai and Li (2015) have also revealed that targets preceded by small numbers had shorter RTs, while Gut and Staniszewski, (2016) have shown faster and more correct retrieval of small numbers from short-term memory. The faster RT associated with low-magnitude numbers could be described as an effect of both the greater ease and automatic nature of processing smaller numbers and our familiarity with and more frequent use of them. This finding is also consistent with results of studies using the random number generation task: individuals produce small numbers more frequently than high ones (Rath, 1966; Boland and Hutchinson, 2000; Loetscher and Brugger, 2007). The magnitude effect can be interpreted as the result of low numbers being learned earlier and being processed more frequently (Loetscher and Brugger, 2007) or in relation to the size effect (Buckley and Gillman, 1974; Gevers et al., 2006), which refers to the greater difficulty in comparing high-magnitude numbers as opposed to low-magnitude numbers.

Interestingly, in the context of the number magnitude effect, the differences between RTs to low and high numbers - calculated separately for congruent and incongruent trials - suggest that faster responses to low numbers are shown only in the case of incongruent targets. There was no significant difference between RTs for low *vs.* high numbers, when they were presented on the congruent side. However, it must be stressed that the two mean RTs obtained in the congruent condition were as short as the RTs for low incongruent numbers.

Accordingly, we can conclude that the RTs for low incongruent numbers were comparatively as fast as all RTs revealed in the congruent condition.

The effect of the side of presentation and the type of target on reaction time

At the behavioral level, significant effects were also observed in RTs for the side of target presentation and for the type of stimulus. Participants reacted faster to the target (both number and neutral symbol) when it was presented on the right side; the reaction was also accelerated for small numbers in comparison to high numbers and neutral symbols. The latter result may be a manifestation of the specificity of low numbers as stimuli, which drives our attention more effectively than do neutral symbols.

The right-side predominance is likely also the origin of the SNARC effect occurring primarily for high-magnitude numbers (as reported above). This effect, which in fact for indicates an advantage of right-hand responses, may be related to the right-handedness of participants - more so, since it was observed not only for numbers but also for symbols. This side-related effect may also be in line with the functional brain lateralization of number processing in the task performed in the present study. However, taking into consideration the type and congruence of stimuli, together with the side of presentation, several additional interaction effects were found. First, it seems that in the case of congruent numbers (low on the left and high on the right), the right-side domination disappears and an equally fast reaction to each congruent number occurs. Meanwhile, in the case of incongruent targets, the side matters. Thus, the side effect was pronounced particularly in the incongruent trials. Moreover, participants reacted faster for all small numbers in general, both congruent and incongruent; and in this specific experimental task, incongruent low-magnitude numbers meant small numbers presented on the right. This probably determined the right-side bias in RT. We can see the same effect in the interaction between number magnitude and the side of presentation: in the case of high number trials, a faster reaction was observed for right-side presentations (= to congruent stimuli), while – in the case of low number trials – the side did not matter. This implies that in the case of high-magnitude numbers, the MNL representations have significantly more impact on RT during the processing of incongruent localizations of digits. Yet, in the case of low-magnitude numbers, the greater automaticity in their processing reduces the influence of the spatial-numerical association on RT.

Are there neural correlates of conflict evoked by incongruent position of digits in the stimulus?

We examined the neural correlates of the conflict evoked by incongruent trials. The question was whether the localization of activation revealed for incongruent trials would be relevant to those reported in studies using other types of tasks to generate cognitive conflict, i.e., the areas linked to executive attention (Fan et al., 2002; Gut et al., 2012). In previous studies, its neuronal underpinnings have been localized mainly in the anterior cingulate cortex (ACC), which is responsible for conflict resolution, as well as in the dorsolateral prefrontal cortex, which is engaged in conflict monitoring and inhibiting incorrect responses (Bush et al., 2000; MacDonald et al., 2000; Botvinick et al., 2001; Fan et al., 2003; Fan et al., 2005). Here, however, we did not find any suprathreshold clusters within these regions, neither in the case of incongruent trials nor in the case of contrasts involving the incongruent condition.

Several neuroimaging studies (Bench et al., 1993, Peterson et al., 1999; Adleman et al., 2002) have shown activation in the inferior and/or superior parietal areas evoked by conflict. Others have shown activation in the prefrontal regions (including the ACC) together with the parietal areas (Hazeltine et al., 2000; Kaufmann et al., 2005). These findings concerning parietal activation appear to be more consistent with our results, since – during the trials with incongruent numbers (and, partially, in the contrast incongruent > neutral targets) – activation was observed in the postcentral gyrus as well as in the inferior and superior parietal lobules. More precisely, when we estimated the contrasts incongruent *vs.* neutral, we found a suprathreshold cluster in the left parietal region covering the angular gyrus. On the one hand, this localization of activation is not linked to executive attention, but rather to verbal number processing (Dehaene et al., 2003). Yet, Cutini and coworkers (2012), on the other hand, used fNIRS and found that activation of this region is strongly modulated by the SNARC effect. Moreover, significant activation in this cortical region has not been revealed in the contrast congruent > neutral trials. This is probably an additional manifestation of the role played by those areas in the SNARC effect processing.

These parietal activations were also accompanied by frontal activations, localized in the SMA and precentral gyrus. This, (together with the extended activity revealed in the cerebellum) is a strong manifestation of motor control involvement during responses to numbers, yet it was revealed during the processing of both congruent and incongruent stimuli. Thus, this could not be a sign of the response selection stage as the locus of the SNARC effect. Instead, it was probably

an indication of a motor reaction to the number according to the task instruction. Separate analyses for each of the four experimental conditions (low congruent, high congruent, low incongruent, and high incongruent numbers) might shed some light on this issue (see an extensive discussion concerning the magnitude effect below). Activation in the premotor cortex may also be the manifestation of an inhibitory process involved in the SNARC effect. For example, an rTMS study on neural correlates of the Simon effect (Praamstra et al., 1999) showed that stimulation over the dorsal premotor cortex enhanced the effect, due to its role in the inhibitory control of automatic response activation in the case of incongruent stimuli.

To discuss the fMRI results, we aimed to focus on the localization of suprathreshold clusters, and their likely hemispheric lateralization. First, the localization of regions activated during the experimental task allowed us to point out the cognitive processes involved in the manifestation of the SNARC effect. It also permitted us to compare them with the results of several ERP studies on perceptual and motor processing involvement in spatial-numerical association (Keus et al., 2005; Gevers et al., 2006; Szucs and Soltesz 2007; Salillas et al., 2008; Ranzini et al., 2009; Gut et al., 2012), as well as previous fMRI (Weis et al., 2015) and fNIRS (Cutini et al., 2012) data. Second, it made it possible to answer the question about the cognitive conflict – which is a foundation of the SNARC effect – and at what stage of processing it occurs. Specifically, does this effect result from a conflict between the localization of a digit within the visual field (= required side of response) and the localization of its representation on the MNL? If this conjecture is true, then activation in the motor areas involved in response preparation linked to conflict should always be mainly present in the hemisphere contralateral to the number's position on the MNL (e.g., mainly in the left hemisphere for "8" presented on the screen, independently of the side of its presentation). This assumption seems to be relevant to the effector hypothesis (Nicholls et al., 2008, Müller and Schwarz, 2007), which describes the SNARC effect in the context of spatio-anatomical mapping (and the relation between spatially represented sides of the body and number magnitude). According to the hypothesis, for example, low numbers are represented in the brain's right hemisphere, which is dominant for left-hand movements (congruent with the locus of these magnitudes on the MNL), and this is why the left hand reacts faster to small numbers – both processes (number magnitude processing and motor preparation) are activated in the same hemisphere. The same is true for high-magnitude numbers and the left hemisphere. Moreover, this would confirm that number magnitude

processing automatically evokes motor preparation with an effector that is contralateral to the location of the number on the MNL, not to the location of the number on the screen. Thus, this response preparation in one-half of the trials would be in conflict with the side of motor reaction required by the side of presentation. Yet, one serious limitation of our experimental task was the fact that the presentation of targets obviously elicited the movement preparation process regarding the hand required to react in the hemisphere, which was contralateral to that hand. For example, a number (e.g., "9" displayed on the left side) would evoke activation within the left hemisphere (according to the right side of the MNL) while – at the same time – the task instruction required a reaction with the left hand (because "9" was displayed on the left side), which is controlled by the right hemisphere. This type of stimulus emerges in conflict and the manifestation of the SNARC effect – which was visible in our results as prolonged RT, but also evoked the bilateral brain activation. This means that the presentation of a digit also evokes a response in the regions controlling the hand performing the response, which is the typical activation pattern linked to every kind of sensory-motor task requiring motor responses to stimuli. For example, the brain activation for each number presented on the right side, independently of its number magnitude, would be found mainly in the left hemisphere, because the right side of presentation would require a right-hand response. It is well documented that the execution of motor actions is mainly controlled by the regions in the contralateral hemisphere and in the ipsilateral cerebellum, at least in right-handers, and in the case of movements of their right hand (Gut et al., 2007; Grabowska et al., 2012). In the current study, all participants were right-handed. Thus, reviewing the localization and (a)symmetry of observed activity patterns allowed us to address the question of whether these indicate merely right or left hand use in response to a stimulus, or whether it is feasible to uncover something more than just the neural correlates of hand movement control. Namely, we were focused on processes involved in reactions to numbers that were independent of the hand responding to them. All trials (except for cue-only trials) required motor responses that evoked the sensory-motor activation mainly contralateral to the hand. This comprised nothing more than the sensory-motor control of button-pressing registered for each target (also for neutral). However, in the current procedure, some stimuli required reaction using the hand that was in conflict with the hand congruent with the spatial representation of the presented number magnitude on the MNL. In other words, for example, the presentation of "8" in the left visual field required, according to instruc-

tion, the left-hand reaction. Yet, the neuronal motor control of the left effector was incongruent with the motor control of the right effector, which was placed on the same side as the locus of "8" on the MNL (= on the right). This is why we were interested in the brain activation patterns related to incongruence as well as to number magnitude (low and high).

Actually, in terms of the involvement of motor processing, the activation patterns observed when responding to low (and high) number targets did not seem to confirm that the response selection during task performance is related to the side of number localization on the MNL. The activation maps shown for all numerical stimuli (both low and high as well as both congruent and incongruent stimuli) were rather bilateral. This makes it difficult to indicate an unquestionable relationship between the side of localization of the number on MNL and the side of the required motor response (a probable cause of bilateral activation patterns is discussed above). We have observed this result pattern both in trials with low numbers (independently of congruence) and in trials with high numbers. However, this conclusion has not been confirmed in the results of additional analysis, when considering such contrasts as incongruent low > congruent low, as well as incongruent high > congruent high and their opposites. This suggests that both the incongruence and congruence of the displayed number evoke nothing more than preparation for the motor reaction (in the hemisphere contralateral to the hand) that is required by the task instruction. Thus, brain asymmetry in the motor regions observed for the contrasts indicates involvement of the hemisphere contralateral to the side of number localization on the screen, both when this number is incongruent and congruent. Therefore, in the case of all low number trials, we recorded bilateral activation (in such areas as the SMA, insula, superior and inferior parietal lobules, middle and superior temporal gyri, and in both cerebellar hemispheres). Yet, in the case of incongruent trials with low numbers, compared with congruent low numbers (and in the case of opposite comparison), activation was found in the sensory-motor regions of the left (right) hemisphere. We showed similar activation patterns for high numbers when comparing incongruent > congruent (and congruent > incongruent) trials. Specifically, for all high magnitude numbers, we obtained the bilateral activation clusters localized mainly in the SMA, insula, superior parietal lobule, basal ganglia, and cerebellum. Yet, the contrast incongruent > congruent and congruent > incongruent, which was performed for high numbers revealed activation clusters in the contralateral sensory-motor regions, as well as in the ipsilateral cerebellum. It is worth emphasizing, however, that an important addi-

tional result concerning motor cortex involvement has been demonstrated in ROIs analysis. The comparison of activation of the left and right areas showed more individual cases of clearly lateralized motor neuronal responses in the congruent condition than in the incongruent condition. This means that – in the case of incongruent trials – we confirm a more bilateral pattern of responses, while in the congruent trials – this has not been manifested.

Importantly, some EEG data from the literature (Raś et al., 2019) has indicated that even the task of number processing, with no requirement of a motor response, may evoke the changes recorded in readiness potential (RP), which has been referred mainly to motor response preparation (Libet et al., 1983). The authors revealed that this has been consequently observed not only during decision making concerning the real motor response (such as simply finger movement), but even during decisions concerning mental numerical operation, that required no actual body movement. Yet, it must be stressed that the authors used a different task than ours (a mental addition of three-digit numbers) and that no real motor reaction by the participants was required, in this experimental task.

To summarize, the distribution of activation obtained as the main effect of number magnitude (low or high) clearly indicates the engagement of the areas responsible for motor control, as well as for number processing control, during the task in response to numbers (in general, this is true independently of their congruence). However, it should be emphasized that there was no strong brain lateralization linked to the number value in the main effect of magnitude. Meanwhile – in the contrasts between congruent and incongruent trials analyzed for low and high numbers, respectively – the activation of motor regions was consequently observed in the hemisphere contralateral to the side of number presentation (= contralateral to the side of motor response). Bilateral patterns obtained as the main effect of the low (as well as the high) number targets are the result of mean activation from the congruent and incongruent conditions. This represents a net effect of both left- and right-lateralized activity responses, since a left- or right- motor response was required during the congruent and incongruent trials. These patterns are thus hardly informative, in the context of the study's aim. These suggestions can be made based on the activation localization presented in Table III – indicating that, in all contrasts calculated for a particular number magnitude, the only significant activation has been shown in the motor areas responsible for the motor control of the reacting hand. Thus, it may be concluded that the digit targets evoked heightened activity within the motor areas relevant not to the locus

of the number representation on the MNL, but rather to the responding hand. Since that lateralized pattern was not seen only in the incongruent > congruent contrast, it cannot be implied that this is a likely manifestation of a response selection process involved in the reaction to incongruent numbers linked to the SNARC effect. Therefore, on the basis of these fMRI data, it could not be undoubtedly said that the SNARC effect obtained in our behavioral data is clearly reflected in the neuro-imaging results. Future studies are necessary – using a larger (and also more heterogenous; see Cipora et al., 2019), sample as well as more strict control and manipulation of factors (as side of response, side of presentation) to avoid such methodological limitations.

The significant effect obtained for number magnitude and congruency, as well as for some contrasts (e.g., incongruent low > congruent low and incongruent high > congruent high numbers), is a probable manifestation of a preparation for motor response with no activation patterns that are typical for cognitive conflict. This may also call into question the cognitive conflict involved in the SNARC effect. The behavioral marker of number incongruence is a greater latency in reaction to, for example, low numbers displayed on the right side. Yet, in the fMRI results there is an activation that mainly shows evidence of motor processing. Moreover, this was observed in both the congruent and incongruent conditions. This means that there is no strong evidence of cognitive conflict, or that it has nothing to do with the mechanism of conflict typically observed in studies on, for example, executive attention. Given the fact that this is also not particularly clear in the main effect of the congruence calculated for fMRI data – as well as the fact that several contrasts are insignificant – all conclusions must be quite carefully drafted. Likewise, the bilateral pattern of activation observed in the congruent and incongruent conditions did not lead to an undoubted conclusion that, during incongruent number presentation, both motor cortices are engaged – contralateral to side of presentation and contralateral to the MNL locus. Yet, additional analysis, based on ROIs, seems to suggest that it is so. This result may not be emergent, but the distribution of the incidences of left or right hemisphere domination (a similar number of these showed strong left and right motor cortex dominance) in the congruent condition seems consistent with the recent critical results obtained by Cipora et al. (2019). The authors used the uniform analysis of 18 existing (published and unpublished) data sets, which revealed a clear SNARC effect at the group level, to explore this effect at the level of individual participants. Surprisingly, their results revealed that the SNARC effect observed at the group level comes from less than half of the participants, who showed the ef-

fect in their individual responses. These results question the idea that some group-level phenomena reflect cognition effects that are present in the majority of the population. This could be the cause of the results observed in our study: despite obtaining the SNARC effect at the group level in behavioral responses, the neuronal markers of this effect were difficult to demonstrate due to individual differences. Cipora and colleagues (2019) did not just show that the proportions of participants revealing a reliable SNARC effect/reversed effect/no effect differed between the particular studies, confidence level, and analysis method (psychometric or bootstrapping) chosen. Primarily, they showed that the SNARC effect is often manifested in the individual results of a minority, or even just small subgroups, of participants. In their interpretation, the authors referred to the importance of the RT's mean and variability; the task reliability; the number of stimuli repetitions; and the homogeneity of the participant sample (in terms of age, education, etc.). They indicated task parameters (number of trials, their timing) and the individual cognitive strategies of participants as significant factors affecting the SNARC effect (or its absence) reported in the literature at the group level.

In the current study, the number targets evoked responses from several cortical and subcortical regions including the frontal, parietal, temporal, and occipital cortices, as well as the thalamus and basal ganglia. A number of brain regions, as reported in the literature, constitute the neuronal system involved in numerical information processing; their activity has been observed in our study as well. The activation within the anterior frontal regions, found in the current experiment, is consistent with previous findings from studies on number processing. Yet, it must be emphasized, that these studies used other types of numerical material and that their tasks were different from those used in our experiment. Tasks included, for example, a number n-back task (Knops et al., 2006), a number comparison task (Pinel et al., 2001), or calculation (Simon et al., 2004; Arsalidou and Taylor, 2011). The same qualification concerns the results of TMS studies using, for example, oral parity judgment, counting, or magnitude comparison (reviewed in Sandrini and Rusconi, 2009). In one study on the SNARC effect (Rusconi et al., 2011), using TMS stimulation over the frontal cortex and two types of task, the authors showed that rTMS stimulation, performed over FEF and IFG in the right hemisphere, eliminated the SNARC effect. More precisely, stimulation over the right FEF resulted in the elimination of the SNARC effect only for low-magnitude numbers. Importantly, this interference was observed only during the magnitude comparison task and not in the case of parity judgment. The authors concluded that,

during number magnitude processing (when it is relevant to the task), the right IFG is responsible for orienting the whole MNL representation, while the right FEF is responsible only for its left part (where low numbers are represented). Despite the same direction of lateralization for the low magnitude incongruent numbers showed in our study, they are unfortunately not consistent with Rusconi and coworkers' results, because we observed the same direction of asymmetry in the case of high numbers; lateralization was found in completely different brain regions; and they used two tasks, which differ from that used in our study.

There were also many activation clusters in the insular region, which we observed during all experimental conditions using numerical targets. The involvement of the insula in numerical processing has been corroborated in several tasks, for example, in multiplication (Prado et al., 2013) and arithmetic problem solving (Houde et al., 2010) – but not during number detection tasks. Activation in this structure, especially that recorded in the left hemisphere, may be related to motor control regarding the verbal processing of displayed stimuli (Ackermann and Riecker, 2004; Oh et al., 2014), both numerical and non-numerical. A more probable explanation may be found in results showing the role of the insula in the decision-making process (Lamichhane et al., 2016). However, it is quite unlikely to treat the task used in the current study as difficult, in the context of decision-making.

Furthermore, we obtained clearly significant activation clusters in the parietal cortex, both in congruent and incongruent condition and for both low and high numbers. These were localized in the superior and inferior parietal lobules. These cortical pinpoints are in line with reports from fMRI and TMS studies on number processing. Yet, in these studies, a wide range of various tasks were used, such as estimation of numerosity (Piazza et al., 2006), counting (Dehaene et al., 2003), digit naming (Zago et al., 2001), number comparison (Sandrini and Rusconi, 2009), or calculation (Dehaene et al., 2004; Arsalidou and Taylor, 2011), but also the simple detection of numbers, when number magnitude is not explicitly processed (Eger et al., 2003). Parietal activation may also suggest attentional engagement in the performance of the task used in our experiment (Simon et al., 2004). Dealing with numbers and space involves a common neural basis (Hubbard et al., 2005). Here, on the other hand, we did not obtain any significant activation clusters as a result of numerical cue presentation. The limited fNIRS data from previous studies indicate that activation within the intraparietal sulcus is modulated by the SNARC effect as well as by the numerical distance effect (as mentioned above).

The insufficient simultaneous manipulation and control of such factors as side of presentation; side of motor response and number localization on MNL is a methodological limitation of the experimental procedure. Consequently, it is quite problematic to distinguish the motor preparation and motor execution and to determine their role in the SNARC effect explanation. Moreover, the activation pattern revealed for the incongruent (conflict) trials did not manifest the engagement of any brain regions that we know to be linked to conflict detection and resolution. Finally, the overly strong homogeneity of the sample and the very long interval inter trials (Cipora et al., 2019) may be serious limitations of this study. In the experimental procedures addressed by fMRI scanning, it is difficult to use intervals as short as those typical in, for example, behavioral or EEG experiments. This means that the ITIs used in our experiment could also influence the neuroimaging results.

CONCLUSIONS

It could be concluded that the SNARC effect revealed in this experiment, at the behavioral level and in terms of RTs, is not definitely manifested in the activation patterns, suggesting that the process of preparation for motor response or even for motor response execution is relevant to the side of the number's position on the MNL. Our results have mainly revealed the manifestation of motor execution relevant to the side of the digit presentation/the hand reacting to it. The bilateral and widely distributed activations obtained during participants' response to target numbers (both congruent and incongruent) did not allow us to undoubtedly confirm a hypothesis of the response selection phase as the locus of the SNARC effect. A comparison of the activation elicited by low incongruent *vs.* low congruent numbers and low congruent *vs.* low incongruent numbers as well as the same comparison calculated for high numbers showed that the only significant activation clusters were revealed in the brain areas that are responsible for pointing out the locus of the digit on the screen. These activation areas were not contralateral to the locus of the number on MNL, but they were contralateral to the side of stimulus presentation (and the hand pressing the response key). Yet, the ROI analyses performed for primary motor region, for the congruent and incongruent conditions revealed a higher incidence of less-lateralized responses in the incongruent condition. This may suggest a tendency, at least in some subjects, for a more bilateral response in the incongruent condition within the hand region of the motor cortex. Nevertheless, it may be conclud-

ed that the overall pattern of results suggests that the target stimulus evoked activity was primarily determined by the control of the hand's reaction to the digit, since we obtained this motor activation pattern not just in the contrast performed for incongruent trials, but also for the congruent condition. Finally, the fact that the SNARC effect acquired at the behavioral level was not robustly reflected in the fMRI results is likely an effect of individual differences. This is postulated in the recent literature, as a possible reason for the incompatibility between group-level and individual-level cognitive effects.

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