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**SPECIAL ISSUE: ORIGINAL ARTICLE****Sensory and cognitive processes of shifts of spatial attention induced by numbers: an ERPs study**Elena Salillas<sup>a</sup>, Radouane El Yagoubi<sup>a</sup> and Carlo Semenza<sup>a</sup><sup>a</sup> Department of Psychology, University of Trieste, Italy;

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## Abstract

The relationship between space and number has become a focus of intensive investigation (Hubbard et al., 2005; Walsh, 2003). The present paper aims to explore the nature of attentional shifts induced by the perception of irrelevant numbers as it was shown by Fischer and collaborators (2003). We measured the event related potentials induced by the perception of visual lateralized targets cued by numbers that differed in their magnitude. Congruent trials were defined as those where a target presented in the right visual field followed a large number and those where a target presented in the left visual field followed a small number. Numbers generate a modulation of evoked potentials on targets as soon as 80 msec. after the presentation of the target: congruency of the target determined the amplitude on perceptual P100 and cognitive P300 in both sides of presentation of the target. Although a typical distribution of the components was found, effects of congruency were distributed around anterior and centro-parietal sites. Due to the functional properties of the mentioned components, the present data suggests that, in fact, perception of numbers does affect the location of attention to external space. Moreover, the distribution of the congruency effect signals that the representational nature of numbers makes a difference with respect to the stimuli classically used in cueing studies of visual attention to location. The role of top-down control generated by numbers is discussed.

**Keywords:** attention, numbers representation, ERPs, P100, P300

## I. Introduction

There is mounting evidence that the number representation involves a spatial component (see Hubbard et al., 2005 for a review; Priftis et al., this issue). For example, the SNARC effect (Spatial Numerical Association of Response Codes; Dehaene et al., 1993) has been demonstrated using a parity judgment task (odd or even?) about a centrally presented digit. Typically, results show that large numbers (e.g., numbers 8 or 9) are responded to faster with the right hand, whereas small numbers (e.g., numbers 1 or 2) are responded to faster with the left hand. The SNARC effect is generally interpreted as reflecting the automatic activation of an internal representation of magnitude where numbers are represented along a left-to-right oriented mental number line.

More recently, Fischer et al. (2003) adapted the paradigm of Posner and Cohen (1980) to investigate the use of numbers as cues to the detection of lateralized spatial targets. In order to explore whether the representation of numbers could induce shifts of attention to the location of the subsequent target, they presented numbers centrally (1, 2, 8 or 9) followed by the target in the right visual field (RVF) or in the left visual field (LVF). The number, irrelevant to the task, was presented for 300 msec. Then, after a variable delay (Inter-Stimulus Interval) that varied from 50 to 1000 msec., the target to be detected appeared on the right or on the left. Interestingly, after perception of large numbers (8 and 9), detection was faster for targets in the RVF, whereas after small numbers (1 and 2) detection was faster for targets in the LVF. This effect appeared at ISIs from 400 msec. until 750 msec. with maximal effect occurring with ISIs of 400 and 500 msec.

These findings add important evidence to what is known about the space-numbers relationship, suggesting that the redirection of attention over an internal representation after perceiving a number influences the allocation of attention in the visual field. According to the authors, similar structures underlie attention shifts across internal representations and external

space. Analogous results have been shown in other studies (eg., Tlauka, 2002), although some variations in the paradigm (eg. timing in Keus and Schwarz, 2005) lead to a failure in reproducing the effect.

Other studies such as Gevers et al. (2006) indicate that an association between numbers and space can be detected at the response stage, but additional research is required to determine whether such an association is also present at the attentional stage when participants are initially attracted to the target stimuli. We sought to address this issue by studying the electrophysiological correlates using the paradigm of Fischer and collaborators. The ERP method offers a high temporal resolution in the range of milliseconds and precisely reflects the temporal sequence of perceptual and cognitive computations. We varied slightly Fischer's paradigm by means of a delayed detection response, where the detection response was not requested immediately after the target but following a fixed time after the target. This variation simply allowed us to capture the stimulus processing phase and to separate it from the preparation of the response. In this way, we examined possible variations in the sensorial and cognitive electrophysiological components time locked to the target, which may be dependent on the previous perception of numbers.

Several experimental studies have explored biases induced by attention on the perception of visual targets using ERPs. Different components (P100, N100 and P300) have been reported to be modulated as a function of previous cueing. One of the most important components related to spatial attention is the P100, a positive component with maximum amplitude peaking around 100 msec post-stimulus onset and typically showing an occipital scalp distribution. Stimuli presented at attended locations elicit larger P100 components than unattended locations with no change in P100 latencies or scalp distribution (Hillyard et al., 1995; Mangun, 1995; Mangun et al., 1998). Reflexive and top-down orienting produce a similar P100: Both exogenous orienting, generated by non-predictive cues (e.g., salient

sensory cue like a flash presented in the periphery) and endogenous orienting, generated by predictive cues (classically presenting an arrow in the centre) produce an amplification of the P100. This component has been also shown to be modulated by the cueing originated in representations held in working memory (e.g. Awh, et al., 2000; see Awh and Jonides, 2001 for a review). According to some authors (eg. Hillyard and Anllo-Vento, 1998; Brefczynski and DeYoe, 1999), the cueing produces a sensory amplification or gain control on subsequent stimulation at the attended location already from the engagement of extrastriate cortex. But this sensory activity can be modulated by other areas. Some neuroimaging studies suggest that parietal areas can modulate this striate activity, indicating the possibility of top-down modulation of the processing of the input to early visual areas (Fink et al., 1996; Wood et al., 2006).

A later stage of processing indexed by the P300 component has been shown to be modulated by attention (Hopfinger and Mangun, 1998, 2001; Hopfinger and West, 2006). The P300 is a high-level positive component that typically shows a Centro-Parietal scalp distribution with maximum amplitude around 300 msec. post-stimulus onset. Different temporal windows have been reported for this component though depending on task demands and experimental paradigms. A number of factors are known to influence P300 amplitude, such as the relevance or frequency of the stimulus, the amount of attention resources necessary to perform a task, working memory updating and decision making (Kok, 2001; Bashore and Van der Molen, 1991; Donchin and Coles, 1988). The modulation of the amplitude in this component is also dependent on the process measured. P300 is typically larger to attended than to unattended targets. When a probability over targets is manipulated (e.g. oddball paradigm, see Priftis this issue), the P300 is larger to infrequent than frequent stimuli (Donchin, 1981). Previous studies have shown that exogenous attention can enhance the P300 showing that the amplitude of the P300 is significantly larger for cued-location than

for uncued-location targets at short ISIs (Hopfinger and Mangun, 1998; 2001). Interestingly, the modulation of the P300 produced by endogenous attention seems to be bigger (e.g., Hopfinger and West, 2006).

With respect to the mental number line representation and the cueing paradigm used in our study, four different conditions can be constructed depending on the size of the number and the location of the target (Fischer et al., 2003). A design congruency (2) x side of presentation of the target (2) was chosen due to the moment of measurement of the ERPs: the presentation of the lateralized target. Congruent trials were thus defined as RVF and LVF targets presented after a large or a small number respectively, and incongruent trials were defined as the opposite combination of number size and target location.

Based on the review of the literature using ERP methods and on Fischer et al.'s previous results presented above, we made the following predictions. If shifts of attention across an internal representation (induced by perceiving numbers) influence the allocation of attention in the visual field, then modulations of the P100 and P300 components would be expected, showing larger amplitudes for congruent than for incongruent trials irrespective of the side of presentation of the target. A modulation of these components dependent on the congruency between the number-cue and the target location would agree with the behavioural data of Fischer et al. (2003). Importantly, due to the recording of ERPs time locked to the presentation of the target, an effect on the P100 would entail an initial sensory process induced by numbers in the processing of the target. This effect would better characterize the interaction found by Fischer et al., between the number and the spatial target, at the level of shifts of spatial attention induced by numbers. The modulation of P300 amplitude by congruency would signal an impact of number representation on higher (spatial) cognitive processes undertaken when detecting a lateralized target. Since P300 is related to the elaboration of the stimulus, and reveals the behavioural relevance computation of the cued

location (Hopfinger and Mangun, 1998, 2001), a modulation of the P300 would imply an influence of the number-spatial representation on conditioning higher processes related with the computation of the relevance of a spatial location. In other words, the location activated by the relative size of the number would have been tagged as being more relevant than other locations.

## **II. Methods**

### **II.1. Participants**

After giving informed consent, 12 Italian students (mean age = 23; range = 20-29; 5 males) were tested individually in a single session that lasted for about 30 minutes. All of them were right-handed, neurologically normal and had normal or corrected-to-normal vision.

### **II.2. Stimulus presentation and procedure**

Participants were comfortably seated at 90 cm. from a computer monitor and were asked to fixate the centre during the whole the experiment. They completed 240 trials in a simple detection task. Each trial started with a central dot flanked by two peripheral (left and right) empty black square-outline boxes (size  $2.54^\circ$ ) presented for 500 msec., and then the fixation point was replaced by the cue. The cue consisted of one out of white digits (1, 2, 8 or 9; visual angle  $1.9^\circ$ ) which was centrally presented for 300 msec. After a fix delay (ISI) of 450 msec., the target was presented for 700 msec. The target consisted of a white circle ( $1.9^\circ$ ), which was presented with equal probability within one of the two peripheral boxes on 67% of all trials (visual angle of presentation  $1.88^\circ$ ). In the remaining trials (33%), a target was not presented (catch trials), they were constituted to prevent anticipatory responses. ERPs time-locked to the appearance of the target were registered. Differing from Fischer et al. (2003) experiment, a delayed response was required to avoid that the electrophysiological response to



the target being obscured by the preparation of the response. After the target, a question mark was presented in the centre of the screen for 1000 msec. In delayed detection task, participants were instructed to respond as quickly as possible when the question mark appeared by pressing a button with the right hand only if a target, irrespective of its location, had appeared before. The participants were instructed that the digits did not predict target location. The set of 240 trials was divided in two blocks of 120 trials each, with an equal number of trials (40) by condition (large-number/RVF (congruent); small-number/LVF (congruent); large-number/LVF (incongruent); small-number/RVF (incongruent); large-number/catch; small-number/catch). Trials were randomized for each participant within each block. Each block lasted approximately 8 min and a short rest period was provided between blocks. To familiarize participants with the task, the experiment started with a practice session consisting of 10 trials.

### II.3. Data acquisition and analysis

Continuous EEG was recorded from 28 scalp electrodes mounted on a elastic cap (Electrocap) and located at standard left and right hemisphere positions over frontal, central, parietal, occipital and temporal areas (International 10 / 20 System, at Fz, FCz, Cz, CPz, Pz, Oz, Fp1, Fp2, F3, F4, C3, C4, P3, P4, O1, O2, F7, F8, T3, T4, Ft7, Ft8, Fc3, Fc4, Cp3, Cp4, Tp7, Tp8). These recording sites plus an electrode placed over the right mastoid were referenced to the left mastoid electrode. The data were recorded continuously throughout the task by SynAmps amplifier and software NeuroScan 4.3. Each electrode was re-referenced off-line to the algebraic average of the left and right mastoids. Impedances of these electrodes never exceeded 5 k $\Omega$ . The horizontal electro-oculogram (HEOG) was recorded from a bipolar montage with electrodes placed 1 cm. to the left and right of the external canthi; the vertical (VEOG) was recorded from a bipolar montage with electrodes placed beneath and above the eye, to detect blinks and vertical eye movements. EOG activity was subtracted from EEG

epochs using a regression method in the time domain (Semlitsch et al., 1986). Epochs from 100 msec. before and 600 msec. after the presentation of the target were extracted from the EEG. The EEG and EOG were amplified by a Synamp's amplifier and filtered with a band pass of 0.01-30 Hz, and digitized at 500 Hz. Epochs were excluded from averaging if they contained amplitudes outside the range  $\pm 150 \mu\text{V}$  at any EEG site. ERPs were extracted by averaging trials separately for subjects, electrodes and experimental conditions.

The averages were then baseline corrected, with the 100 msec. pre-stimulus period serving as baseline. ERP averages were analysed by computing the mean amplitude in selected latency windows relative to a 100 msec. baseline. ANOVAs were used for all statistical tests and were carried out with the Greenhouse-Geisser correction for sphericity departures (Geisser and Greenhouse, 1959). ANOVAs were conducted separately for midline and lateral electrodes. ANOVAs for midline electrodes used a repeated-measures design taking as factors congruent/incongruent, side of presentation of the target (Left Visual Field (LVF) / Right Visual Field (RVF)), Localization (2 Regions Of Interest [ROIs] or Area; Anterior and Posterior) and electrodes (3 for each ROI with Anterior including: Fz, FCz, Cz, and Posterior including: CPz, Pz and Oz). ANOVAs for lateral electrodes also used a repeated-measures design with congruency (congruent/incongruent), side of presentation of the target (Left Visual Field (LVF) / Right Visual Field (RVF)), hemispheres (Left vs. Right), Localization (3 Regions Of Interest [ROIs] or Area; Anterior, Centro-Parietal, and Occipito-Temporal), and electrodes (3 for each ROI with Left Anterior including: F7, F3, FC3; Left Centro-Parietal: CP3, C3, P3; Left Occipito-Temporal: T3, TP7, O1; Right Anterior: F8, F4; FC4; Right Centro-Parietal: CP4, C4, P4 and Right Occipito-Temporal: T4, TP8, O2). The electrodes Fp1, Fp2, Ft7, Ft8 were excluded from the analysis in order to obtain ROI including the same number of electrodes.

### III. Results

#### Behavioural data

Average reaction times for the go-response of the twelve participants were determined with a 2 x 2 ANOVA including two levels of congruency (congruent vs. incongruent) and two levels of side of presentation of the target (LVF/RVF) as factors. Due to the delayed characteristic of the response, no significant main effects or interactions were found.

[congruency:  $F(1,11)=1.3$ ; ns; side:  $F(1,11)=0.03$ ; ns; side x congruency:  $F(1,11)=2.6$ ; ns].

The difference between congruent and incongruent was 2 msec. in the RVF and -17 msec. in the LVF.

#### ERP data.

The traces presented in Figure 1 show the grand average potentials with congruent and incongruent trials superimposed recorded at Cz (central midline electrode). Visual inspection seems to reveal two positive differences, larger for congruent than for incongruent trials. The first difference was an early positivity with bigger amplitudes distributed around the occipital sites and peaking at 114 msec. (according to peak detection). Based on its latency and global distribution, this first positivity can be identified as the P100 component. The second positivity was distributed around the Centro-Parietal sites and peaking at 314 msec. Based on its latency and global distribution, this second positivity can be identified as the P300 component. With respect to the catch trials, visual inspection shows clearly that these two components (P100 and P300) were not elicited when a target was not presented (see Figures 2 and 3)<sup>1</sup>. In order to examine these congruency effects in further detail, two latency ranges of main interest were selected, both from visual inspection of the ERP traces and from comparison with previous results available in the literature: the 80-130 msec. interval, to test the P100 component and 200-400 msec. to test the P300 component (see Hillyard and Anllo

Vento, 1998 for a review; Duncan-Johnson and Donchin, 1982 or Donchin, 1981 for the P300).

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(Insert Figure 1 about here)

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### **P100 (80-130 msec.)**

The first latency range between 80 and 130 msec. showed a significant main effect of congruency both in midline [ $F(1,11)=11.34$ ;  $MSe=11.34$ ;  $p<.001$ ] and lateral [ $F(1,11)=7.99$ ;  $MSe=16.37$ ;  $p<.05$ ] electrodes: congruent trials elicited a larger positivity compared to incongruent trials, with no interaction by side. In the midline electrodes a significant triple interaction congruency X ROI X electrode was found [ $F(2,22)=12.92$ ;  $MSe=0.43$ ;  $p<.001$ ]. Post Hoc analyses showed that the difference between congruent and incongruent trials was significant in all midline electrodes except in Oz. Moreover, congruency interacted by ROI in the lateral electrodes [ $F(2,22)=5.94$ ;  $MSe=3.76$ ;  $p<.05$ ], reflecting that the congruency effect was localized only at the Centro-Parietal [ $F(1,11)= 13.68$ ;  $MSe=6.75$ ;  $p<0.005$ ] and Anterior areas [ $F(1,11)=5.16$ ;  $MSe=12.51$ ;  $p<0.05$ ].

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(Insert Figures 2 and 3 about here)

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### **P300 (200-400 msec.)**

This second latency range showed again a main effect of congruency both in midline [ $F(1,11)=16.38$ ;  $MSe=3.9$ ;  $p<.005$ ] and lateral [ $F(1,11)=7.26$ ;  $MSe=9.1$ ;  $p<.05$ ] electrodes: congruent trials elicited larger positivities than incongruent trials. Once again, congruency did not interact by side. Midlines electrodes showed also a triple interaction between congruency, ROI and electrodes [ $F(2,22)=7.57$ ;  $MSe=2.3$ ;  $p<.005$ ]: as in previous latency range, Post Hoc

analysis revealed that the effect of congruency was present in all midline electrodes except in Oz. Moreover, significant interaction between congruency and ROI [ $F(2,22)=4.73$ ;  $MSe=4.73$ ;  $p<.05$ ] was found in lateral electrodes, reflecting that the congruency effect was mainly distributed around the Anterior [ $F(1,11)=11.42$ ;  $MSe=2.88$ ;  $p=0.006$ ] and Centro-Parietal sites [ $F(1,11)=9.57$ ;  $MSe=5.38$ ;  $p<.01$ ] but not in Occipito-Temporal areas ( $F<1$ ).

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(Insert Table 1 about here)

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#### IV. Discussion

The ERP results from this experiment are consistent with the behavioural data of Fischer and collaborators (2003) and add new important information: First, as revealed by the modulation of the P100 sensory processes seem to be modulated by the congruency between number-cue and the target location. These early congruency effects begin as early as 80 msec. after the presentation of the target. Second, not only sensory processes but also later cognitive processes are modulated by the congruency between number size and location of the target, as revealed by the modulation of the P300. Third, maximal amplitude differences of the congruency effects are located in Anterior and Centro-Parietal areas (for P100 and P300)

The sensory P100 component has been shown to be enhanced when a target is presented at an attended location, which has been previously cued by an external cue. The effects of congruency in this component are typically distributed in occipital sites and the generators of the P100 have been identified in the extrastriate cortex (Hillyard and Anllo-Vento, 1998; Mangun et al., 1997). The cueing generates an amplification of the signal (i.e. P100 bigger amplitude) when a target appears at the cued location. Some studies have explored the bias of selective attention to location generated by representational stimuli (e.g.

Awh et al., 2000; Nobre et al., 2004), but these studies always entail that a previously presented visual stimulus is held in memory. By contrast, in our study, the shifts of spatial attention generated by numbers were purely representational and there is no explicit spatial stimulation, as the number was presented centrally. Modulation of the P100 (larger positivities for congruent than incongruent trials) provides neural evidence that a centrally presented number-cue can also influence the mechanism of attention to external locations. However, and although the P100 component had a tendency to have larger amplitudes in occipital sites, the effects of congruency were not located in occipital areas (see Table 1). Therefore, the stage of processing indexed by the modulation of the early-P1 could receive input from different generators with external and internal representational spatial cues acting through different mechanisms. This process points to the presence of more widely distributed networks in congruency effects when representations with spatial characteristics like numbers are taken as cues (which may be due to the close relation between parietal cortex and number representation). On the basis of our results, we may speculate that perceiving number cues implies an intermediate spatial representation (generated in the intraparietal cortex) that has a direct effect on the amplitude of the P100. Different fMRI studies have suggested the possibility that parietal areas can exert attentional control over the neural transformations occurring in striate cortex (Fink et al., 1996; Wood et al., 2006), demonstrating top-down modulation of early processes of selective attention. We believe that this top-down mechanism could also explain the distribution of the congruency effect in our experiment.

Not only sensory processes are influenced by congruency: the two congruency conditions differed in their cognitive requirements, as evidenced by the fact that P300 component is modulated by the cue-target congruency. P300 increases in amplitude in congruent trials. This result differs from Mangun and Hillyard (1991) which showed smaller amplitude for valid trials. The difference between their study and ours has to do with the

manipulation of the probability of the target. In their study, Mangun and Hillyard presented invalid targets with a lower probability of appearance, which triggered a larger P300. In our study congruent and incongruent trials are equally probable. Thus P300 is an index of validity and not of detection of infrequent stimuli. Our results are rather consistent with those of studies where the degree of endogenous attention to the location of the target increases gradually the amplitude of the P300 (Mangun and Hillyard, 1990). Exogenous (at short ISIs) and endogenous attention can modulate the amplitude of the P300 depending on the cueing condition (Hopfinger and Magnun, 1998, 2001; Hopfinger and West, 2006). This P300 effect is explained in terms of the increase of relevance of the cued location. Endogenous factors have also been described in terms of attention allocation, retrieval and maintenance of a representation in working memory (Kok, 2001; Bashore and Van der Molen, 1991; Johnson, et al., 2007); factors that increase P300 amplitude. We believe that the larger P300 amplitude found for congruent trial signals that a trace of the relevance of a location may have been hold in working memory (Donchin, 1981). In our view, the perception of the digit could activate the spatial representation of the number. Then its position in the mental number line is held in working memory determining the relevance of a certain location in external space. In support to this interpretation, a previous study of neglect patients has shown that right brain damage to prefrontal spatial working memory structures is the main source of pathological rightward deviation observed (Doricchi et al., 2005).

One last comment concerns the degree of control in the orienting effect that comes into play within the present paradigm. Also from this perspective, the present study suggests an endogenous, top-down nature of attention orienting generated by central numbers. According to the timing conditions and the predictive characteristics of the target that have been used in the previous literature no modulation of the P100 and P300 should be found (Hopfinger and Mangum, 2001; Hopfinger and Ries, 2005). Only endogenous orienting

would increase the amplitude of the P100 and P300 at the ISI used in the present study (equal to a SOA of 750 msec.). This observation perfectly fits with the point raised by Ristic, Wright and Kingstone (2006). The orienting effect for central digits in this paradigm emerges slowly, suggesting that top-down endogenous processes may be mediating this effect. The authors give behavioural evidence of a flexible representation of the mental number line, which can be controlled endogenously.

Overall, the course of the components described in this paper better specifies the processes taking place in the paradigm proposed by Fischer et al., (2003). Although the digits are irrelevant for the task<sup>2</sup>, participants activate a spatial representation (left to right “mental number line”). The relative magnitude of the number, small or large, generates an orienting of attention on this representation towards the left or the right visual field, respectively. More precisely, P100 modulation indicates that this shift of spatial attention cues external spatial representation and is able to amplify the sensory input of the target when it coincides with the cued location. A second process implies that this spatial representation is held in spatial working memory and modifies the relative relevance of the two hemifields, as signalled by the modulation of the P300.

The present data must be taken as another index of the close link between number representation and space representation (Walsh, 2003, Dehaene et al., 2003). They extend and clearly establish that the perception of irrelevant digits activates the semantic representation of numbers and has an effect on spatial attention to subsequent spatial stimuli. Moreover, these data increase our understanding of the mechanisms behind spatial cueing generated by pure representations and provides a baseline in neurophysiologic terms for this paradigm. Whether changes in the instructions related to the kind of representation required for retention in memory would change the present pattern of ERPs is an open question.



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**REFERENCES**

- AWH E, ANLLO-VENTO L and HILLYARD SA. The role of spatial selective attention in working memory for locations: evidence from event-related potentials. *Journal of Cognitive Neuroscience*, 12: 840-847, 2000.
- AWH E and JONIDES J. Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, 5(3): 119-126, 2001.
- BASHORE TR and VAN DER MOLEN M. Discovery of P300: Attribute. *Biological Psychology*, 32: 155-171, 1991.
- BREFCZYNSKI JA and DE YOUE EA. A physiological correlate of the 'spotlight' of visual attention. *Nature Neuroscience*, 2 (4): 370-374, 1999.
- COHEN KADOSH RC, LEVIN M, BRODSKY W and HENIK A. Mental representation: Domain Specific or Task Specific? *Cortex*, this issue, 2007.
- DEHAENE S, BOSSINI P and GIRAUX P. The mental representation of parity and number magnitude. *Journal of Experimental Psychology. General.*, 122: 371-396, 1993.
- DEHAENE S, PIAZZA M, PINEL P and COHEN L. Three parietal circuits for number processing. *Cognitive Neuropsychology*, 20: 487-506, 2003.
- DONCHIN E. Surprise!... Surprise? *Psychophysiology*, 18: 493-513, 1981.
- DONCHIN E and COLES MGH. Is the P300 component a manifestation of context updating? *Behavioral and Brain Sciences*, 11: 357-374, 1988.
- DUNCAN-JOHNSON CC and DONCHIN E. The P300 component of the event-related brain potential as an index of information processing. *Biological Psychology*, 14(1-2): 1-52, 1982.
- DORICCHI F, GUARIGLIA P, GASPARINI M and TOMAIUOLO F. Dissociation between physical and mental number line bisection in right hemisphere brain damage. *Nature Neuroscience*, 8 (12): 1663-1665, 2005.

FINK GR, HALLIGAN PW, MARSHALL JC, FRITH CD, FRACKOWIAK RSJ and DOLAN RJ. Where in the brain does visual attention select the forest and the trees? *Nature*, 382: 626-628, 1996.

FISCHER M, CASTEL AD, DODD MD and PRATT J. Perceiving numbers causes spatial shifts of attention. *Nature Neuroscience*, 6: 555-556, 2003.

GEISSER S and GREENHOUSE S. On methods in the analysis of profile data. *Psychometrika*, 24: 95-112, 1959.

GEVERS W, RATINCKX E, DE BAENE and FIAS W. Further evidence that the SNARC effect is processed along a dual-route architecture. *Experimental Psychology*, 53(1): 58-68, 2006

HEINZE HJ, MANGUN GR, BURCHERT W, HINRICHS H, SCHOLZ M, MÜNTE TF, GOES A, SCHERG M, JOHANNES S, HUNDESHAGEN H, GAZZANIGA MS and HILLYARD SA. Combined spatial and temporal imaging of brain activity during visual selective attention in humans. *Nature*, 372: 543-546, 1994.

HILLYARD SA and ANLLO-VENTO L. Event related potentials in the study of visual selective attention. *Proceedings of the Natural Academy of Sciences. USA*, 95: 781-787, 1998.

HILLYARD SA, MANGUN GR, WOLDORFF MG and LUCK SJ. Neural Systems Mediating Selective Attention. In Gazzaniga, MS (Ed). *The Cognitive Neurosciences*. MIT Press, Cambridge, MA, 665-681, 1995.

HOPFINGER JB and MANGUN GR. Reflexive attention modulates processing of visual stimuli in human extrastriate cortex. *Psychological Science*, 9: 441-447, 1998.

HOPFINGER JB and MANGUN GR. Tracking the influence of reflexive attention on sensory and cognitive processing. *Cognitive, Affective and Behavioral Neuroscience*, 1: 56-65, 2001.

HOPFINGER JB and RIES AJ. Automatic versus contingent mechanisms of sensory-driven neural biasing and reflexive attention. *Journal of Cognitive Neuroscience*, 17: 1341-1352, 2005.

HOPFINGER JB and WEST VM. Interactions between endogenous and exogenous attention on cortical visual processing. *Neuroimage*, 31: 774-789, 2006.

HUBBARD EM, PIAZZA M, PINEL P and DEHAENE S. Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience*, 6: 435-448, 2005.

JOHNSON MR, MITCHELL KJ, RAYE CL, D'ESPOSITO M and JOHNSON MK. A brief thought can modulate activity in extrastriate visual areas: Top-down effects of refreshing just-seen visual stimuli. *NeuroImage*, 37(1):290-299, 2007.

COHEN KADOSH RC, LEVIN M, BRODSKY W and HENIK A. Mental representation: Domain Specific or Task Specific? *Cortex*, this issue, 2007.

KEUS IM and SCHWARZ W. Searching for the functional locus of the SNARC effect: Evidence for a response-related origin. *Memory and Cognition*, 33 (4): 681-695, 2005.

KOK A. On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*, 38: 557-577, 2001.

MANGUN GR, HOPFINGER J, KUSSMAUL CL, FLETCHER E and HEINZE HJ. Covariations in ERP and PET measures of spatial selective attention in human extrastriate visual cortex. *Human Brain Mapping*, 5: 273-279, 1997.

MANGUN GR, HOPFINGER JB and HEINZE HJ. Integrating electrophysiology and neuroimaging in the study of human cognition. *Behavior Research Methods, Instruments and Computers*, 30: 118-130, 1998.

MANGUN GR. Neural mechanisms of visual selective attention. *Psychophysiology*, 32: 4-18, 1995.

MANGUN GR and HILLYARD SA. Modulations of sensory-evoked brain potentials indicate changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychology: Human Perception and Performance*, 17: 1057-1074, 1991.

MANGUN GR and HILLYARD SA. Allocation of visual attention to spatial locations: Tradeoff functions for event-related brain potentials and detection performance. *Perception & Psychophysics*, 47: 532-550, 1990.

NOBRE AC, COULL JT, MAQUET P, FRITH CD, VANDERBERGHE R and MESULAM MM. Orienting attention to locations in perceptual versus mental representations. *Journal of Cognitive Neuroscience*, 16(3): 363-373, 2004.

POSNER MI and COHEN Y. Orienting of attention. *Quarterly Journal of Experimental Psychology*, 32: 3-25, 1980.

RISTIC J, WRIGHT A and KINGSTONE A. The number line effect reflects top-down control. *Psychonomic Bulletin and Review*, 13(5): 862-868, 2006.

TLAUKA M. The processing of numbers in choice-reaction tasks. *Australian Journal of Psychology*, 5: 94-98, 2002.

WALSH V. A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends in Cognitive Sciences*, 7: 483-488, 2003.

WOOD G, NUERK HC and WILLMES K. Neural representations of two digit numbers: A parametric fMRI study. *NeuroImage*, 29: 358-367, 2006.

Table 1. Mean amplitudes and standard deviations of the ROI x congruency interaction for the P100 and P300 components.

ROI	P100		P300	
	Incongruent	Congruent	Incongruent	Congruent
Anterior	-1.54 (0.45)	-0.82 (0.36)	3.74 (0.37)	4.31 (0.39)
Centro-Parietal	-1.57 (0.38)	-0.83 (0.42)	6.16 (0.77)	6.82 (0.76)
Occipito-Temporal	-0.61 (0.25)	-0.51 (0.23)	3.63 (0.67)	3.61 (0.59)

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### Figure captions

Figure 1. Illustration of the variations in brain electrical activity time-locked to the left target (left panel) and right target (right panel) when large number (solid line) or small number (dashed line) were presented in cue. Each trace represents an average of electrophysiological data from Cz electrode and recorded from 12 participants.

Figure 2. Illustration of the variations in brain electrical activity time-locked to the left target (black trace) and catch (blue trace) when large number (solid line) or small number (dashed line) were presented in cue. Each trace represents an average of electrophysiological data recorded from 12 participants. While EEG was recorded from 28 electrodes, only the most representative clusters of electrodes (24 electrodes) were analysed using ANOVAs, and selected traces from 12 electrodes are presented.

Figure 3. Illustration of the variations in brain electrical activity time-locked to the right target (black trace) and catch (blue trace) when large number (solid line) or small number (dashed line) were presented in cue.

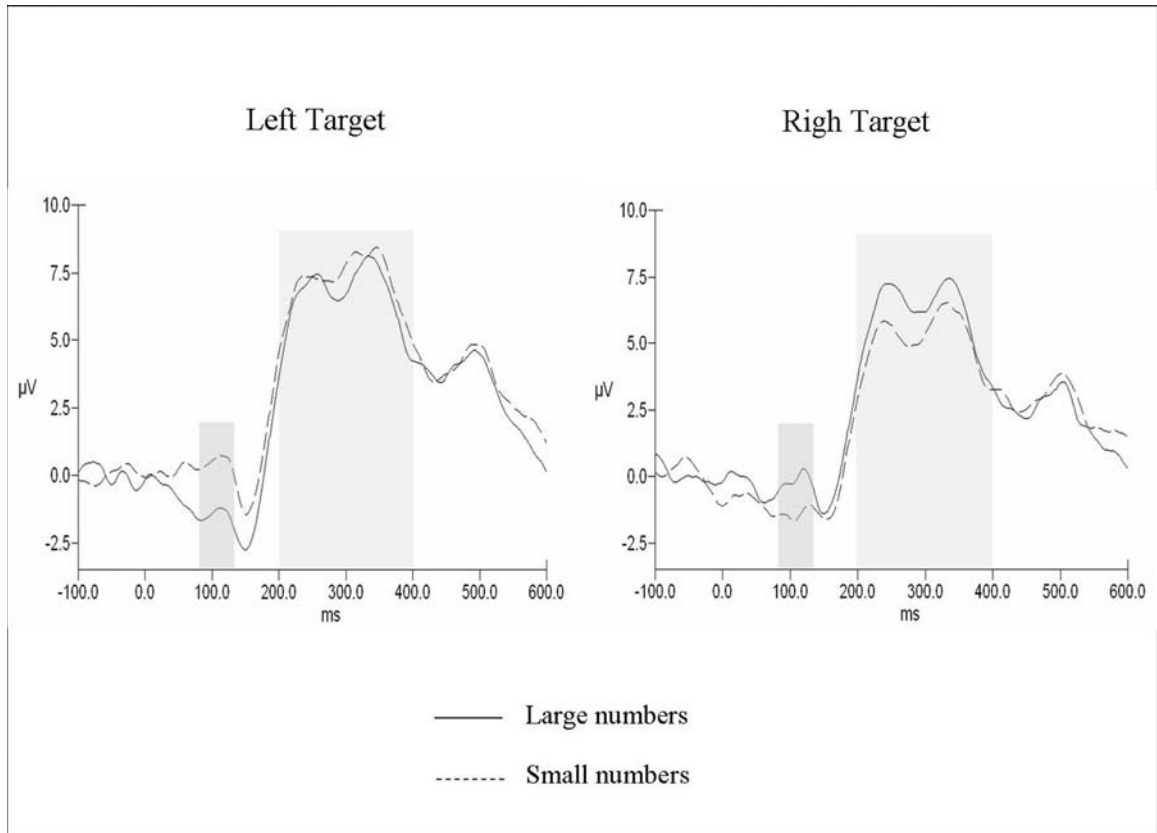
## FOOTNOTES

<sup>1</sup> A separate analysis was made for catch trials comparing large and small numbers. This was made in order to identify possible differences between numbers not due to the experimental manipulation. Results showed no significant differences in both latency bands.

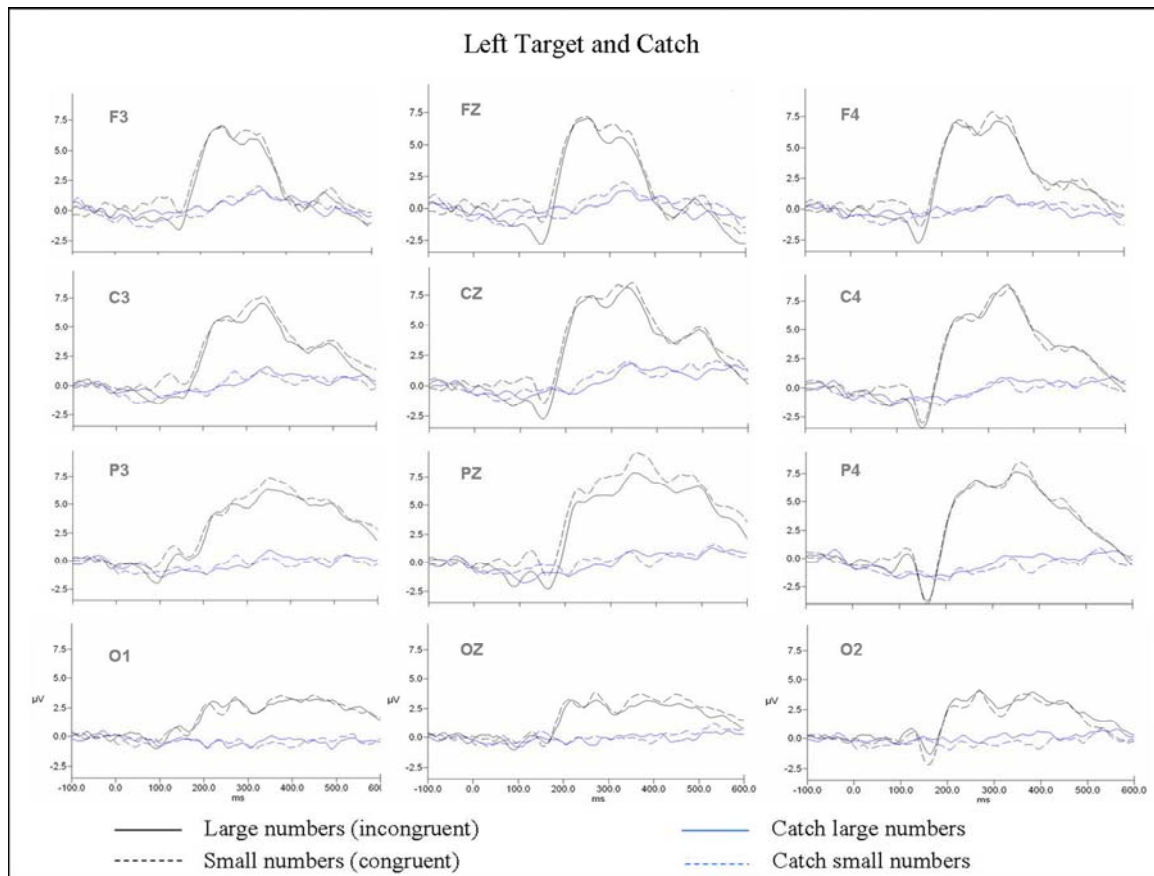
<sup>2</sup> Note that the task is indirect, which according to Cohen Kadosh et al., (this issue) allows a clear access to mental representation.

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