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Larger, smaller, odd or even? Task-specific effects of optokinetic stimulation on the mental number space

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Previous studies have shown that number processing can induce spatial biases in perception and action and can trigger the orienting of visuospatial attention. Few studies, however, have investigated how spatial processing and visuospatial attention influences number processing. In the present study, we used the optokinetic stimulation (OKS) technique to trigger eye movements and thus overt orienting of visuospatial attention. Participants were asked to stare at OKS, while performing parity judgements (Experiment 1) or number comparison (Experiment 2), two numerical tasks that differ in terms of demands on magnitude processing. Numerical stimuli were acoustically presented, and participants responded orally. We examined the effects of OKS direction (leftward or rightward) on number processing. The results showed that rightward OKS abolished the classic number size effect (i.e., faster reaction times for small than large numbers) in the comparison task, whereas the parity task was unaffected by OKS direction. The effect of OKS highlights a link between visuospatial orienting and processing of number magnitude that is complementary to the more established link between numerical and visuospatial processing. We suggest that the bidirectional link between numbers and space is embodied in the mechanisms subserving sensorimotor transformations for the control of eye movements and spatial attention.

Keywords: Embodied cognition; Magnitude processing; Number processing; Number–space associations.

A large amount of evidence exists in favour of the view that the way humans process and represent numbers is strongly linked to motor actions (Andres, Olivier, & Badets, 2008; Fischer & Lindemann, 2014; Walsh, 2003). Behavioural and neuroimaging studies have provided compelling evidence that the representation of numerical magnitude is tightly linked to the processing of spatial information (e.g., Hubbard, Piazza, Pinel, & Dehaene, 2005; Zorzi, Priftis, & Umiltà, 2002), suggesting that number

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processing and sensorimotor processes share overlapping neural mechanisms (Knops, Thirion, Hubbard, Michel, & Dehaene, 2009). Numerous studies have shown effects of number processing on spatially encoded responses; for example, when participants are asked to classify numbers, they are typically faster in responding to smaller numbers with left-sided responses, whereas they are faster in responding to larger numbers with right-sided responses (the Spatial–Numerical Association of Response Codes (SNARC) effect; Dehaene, Bossini, & Giraux, 1993; see Wood, Willmes, Nuerk, & Fischer, 2008, for a review). This relation between numbers and space is independent of the effector used (e.g., hands: Dehaene et al., 1993; fingers of the same hand: Priftis, Zorzi, Meneghello, Marenzi, & Umiltà, 2006; feet: Schwarz & Müller, 2006; saccades: Fischer, Warlop, Hill, & Fias, 2004; Schwarz & Keus, 2004) and it has a key neural correlate in the human posterior parietal cortex (Cutini, Scarpa, Scatturin, Dell'Acqua, & Zorzi, 2014). The classic explanation of the SNARC effect is based on the notion of an analogue, left-to-right oriented mental number line (MNL; Restle, 1970), with relatively small numbers on the left and relatively large numbers on the right (Dehaene et al., 1993). The direction of the MNL was shown to be embodied in cultural experiences, such as the direction of reading and writing habits (Dehaene et al., 1993; Shaki & Fischer, 2008; Shaki, Fischer, & Petrusic, 2009), or finger counting habits (Fischer & Brugger, 2011; see also Wasner, Moeller, Fischer, & Nuerk, 2014), which might shape, during lifespan, the numerical representation along with neural mechanisms involved in sensorimotor processes that subserve visuospatial attention.

Primary evidence that the orienting of spatial attention might be the crucial factor relating numbers and space comes from studies on patients with left neglect (LN), a neuropsychological syndrome characterised by the failure to detect, orient to, or report stimuli in the contralesional side of space (Halligan, Fink, Marshall, & Vallar, 2003). Importantly, several studies have shown the difficulties of LN patients in explicitly accessing larger magnitudes on the MNL (Masson, Pesenti, & Dormal, 2013; Priftis et al., 2006; Van Dijck, Gevers, Lafosse, & Fias, 2012; Vuilleumier, Ortigue, & Brugger, 2004; Zorzi, Priftis, Meneghello, Marenzi, & Umiltà, 2006; Zorzi et al., 2002, 2012; see Umiltà, Priftis, & Zorzi, 2009, for a review). LN patients' impairment in processing numerical magnitude might be explained by their difficulty in orienting spatial attention towards the left in the imaginal space, and thus in exploring the *left part* of the number space (Zorzi et al., 2002, 2012; but see Aiello et al., 2012, for a contrasting view).

Evidence for a link between number processing and spatial attention has also been reported in studies on healthy participants. The main finding is that number processing facilitates the visual processing of targets located in the left or right side of space according to numerical magnitude in a cued detection paradigm (Fischer, Castel, Dodd, & Pratt, 2003; also see Dodd, Van der Stigchel, Adil Leghari, Fung, & Kingstone, 2008; Galfano, Rusconi, & Umiltà, 2006; for electrophysiological evidence, see Ranzini, Dehaene, Piazza, & Hubbard, 2009; Schuller, Hoffmann, & Schiltz, 2014) or temporal order judgement (Casarotti, Michielin, Zorzi, & Umiltà, 2007). Other studies have reported that number processing induces spatial biases in both healthy participants (e.g., de Hevia, Girelli, & Vallar, 2006; Fischer, 2001; Nicholls, Loftus, & Gevers, 2008) and brain-damaged patients (e.g., Bonato, Priftis, Marenzi, & Zorzi, 2008; Loftus, Nicholls, Mattingley, & Bradshaw, 2008a).

Besides the influence of number processing on spatial attention, a key question for better understanding the mechanisms underlying number processing is whether the latter is influenced by spatial attention. In this respect, it is crucial that the evidence from studies on neglect patients (for reviews, see Umiltà et al., 2009; Zorzi et al., 2012) is complemented by studies where orienting of spatial attention is explicitly manipulated during number processing tasks. Only a few studies have tackled this issue. Effects on number processing have been observed following manipulations of visuospatial processing (and presumably spatial attention orienting) based on lateralised spatial cues (Kramer, Stoianov, Umiltà, & Zorzi, 2011; Stoianov, Kramer, Umiltà, & Zorzi, 2008), gaze cues (Grade, Lefèvre, & Pesenti, 2013) or prism adaptation (LN patients: Rossetti et al., 2004; healthy participants: Loftus, Nicholls, Mattingley, & Bradshaw, 2008b). For instance, Stoianov et al. (2008) observed that lateralised irrelevant spatial cues can influence the participants' response in numerical tasks when they temporally overlap with the processing of numerical stimuli. Specifically, participants' responses were faster in the cue-target compatible condition (i.e., left cue and small digit or right cue and large digit) than in the cue-target incompatible condition (i.e., left cue and large digit or right cue and small digit). This effect was named spationumerical interaction between perception and semantics (SNIPS). Importantly, this effect provides evidence that space–number interactions occur well before the response selection stage (also see Kramer et al., 2011). Nevertheless, the effects of spatial cueing paradigms, as the SNIPS effect, can be attributed either to exogenous shifts of attention triggered by the visuospatial cue or to spatial priming arising from the automatic spatial coding of the visual cue, without the possibility to disentangle between these two alternative explanations (Stoianov et al., 2008). The influence of visuospatial attention orienting on number processing is also suggested by studies that investigated the direction of eye movements after number processing, based on the widely accepted view that attention orienting is embedded in the planning and execution of gaze shifts (Casarotti, Lisi, Umiltà, & Zorzi, 2012; Moore, Armstrong, & Fallah, 2003; Rizzolatti, Riggio, Dascola, & Umiltà, 1987). For instance, Loetscher, Bockisch, Nicholls, and Brugger (2010) observed that eye movement direction during a random digit generation task predicted the next digit said by the participant: more specifically, leftward (or downward) gaze shifts predicted digits smaller than the previous one, whereas rightward (or upward) gaze shifts predicted larger digits. These findings fit well with those of neuroimaging studies showing overlapping neural circuits for number processing and saccades (Knops et al., 2009; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). Finally, interference with number processing tasks has been reported following the delivery of transcranial magnetic stimulation (TMS) on the parietal (Göbel, Calabria, Farnè, & Rossetti, 2006) and frontal (Rusconi, Bueti, Walsh, & Butterworth, 2011) nodes of the dorsal attention network (Corbetta & Shulman, 2002).

One visuo-motor technique that can be used to modulate visuospatial attention orienting is the optokinetic stimulation (OKS). OKS consists of a full-field visual stimulus (either random dots or vertical black and white stripes) moving coherently towards a specific direction. In accordance with the premotor theory of attention (Casarotti et al., 2012; Rizzolatti et al., 1987), OKS triggers visuospatial attention shifts by inducing the optokinetic nystagmus (OKN), an oculomotor reflex consisting of two different alternating phases: first, the eyes follow the moving pattern trying to stabilise the image on the retina (slow eye movement phase); second, when the eyes reach a certain distance from the initial gaze position, they snap back with a fast saccadic movement in the opposite direction (fast movement phase)—(Figure 1b; see Kerkhoff, 2003, for a review). Spatial attention is mainly oriented towards the direction of the OKS, as testified by clinical studies showing that leftward OKS ameliorated visuospatial attention deficits in LN patients (e.g., Kerkhoff, Keller, Ritter, & Marquardt, 2006; Pizzamiglio, Frasca, Guariglia, Incoccia, & Antonucci, 1990). Importantly, recent studies on LN patients have shown that number processing can be influenced by OKS-like stimulation in the horizontal plane (Priftis, Pitteri, Meneghello, Umiltà, & Zorzi, 2012; Salillas, Granà, Juncadella, Rico, & Semenza, 2009). In particular, Priftis et al. (2012) used moving vertical black-and-white stripes that elicited OKN, whereas Salillas et al. (2009) used coherent dot motion and a central fixation point that prevented the triggering of eye movements (i.e., OKN was not elicited). Both studies observed an improvement of the typical number processing biases shown by LN patients following leftward motion stimulation.

The aim of the present study was to investigate the effects of exogenous spatial attention orienting on number processing in healthy participants by means of OKS. In Experiment 1, participants were required to perform a parity judgement task during leftward and rightward OKS; in Experiment 2, participants were required to perform a number comparison task during leftward and rightward OKS. We investigated the OKS effects on these two tasks because they imply different processing demands in terms of magnitude information. Indeed, while number comparison requires explicit access to magnitude information, in the parity judgement task the numerical magnitude is task irrelevant and the access to magnitude information is therefore implicit. Dissociation between explicit and implicit access to numerical magnitude has been observed in LN patients (Priftis et al., 2006) and most recently in the direct comparison between parity judgement and number comparison tasks (Zorzi et al., 2012). Moreover, dissociation between the two tasks has also been observed in healthy participants as a function of the type of concurrent working memory load (verbal vs. visuospatial; Herrera, Macizo, & Semenza, 2008; Van Dijck, Gevers, & Fias, 2009), possibly reflecting the use of different spatial representations during number comparison and parity judgement tasks.

In both experiments, we used different OKS conditions (static, leftward, rightward) to investigate their effect on numerical magnitude (<5 = small; >5 = large). Following Stoianov et al. (2008), responses to the numerical tasks were vocal and non-spatial to ensure that they were not

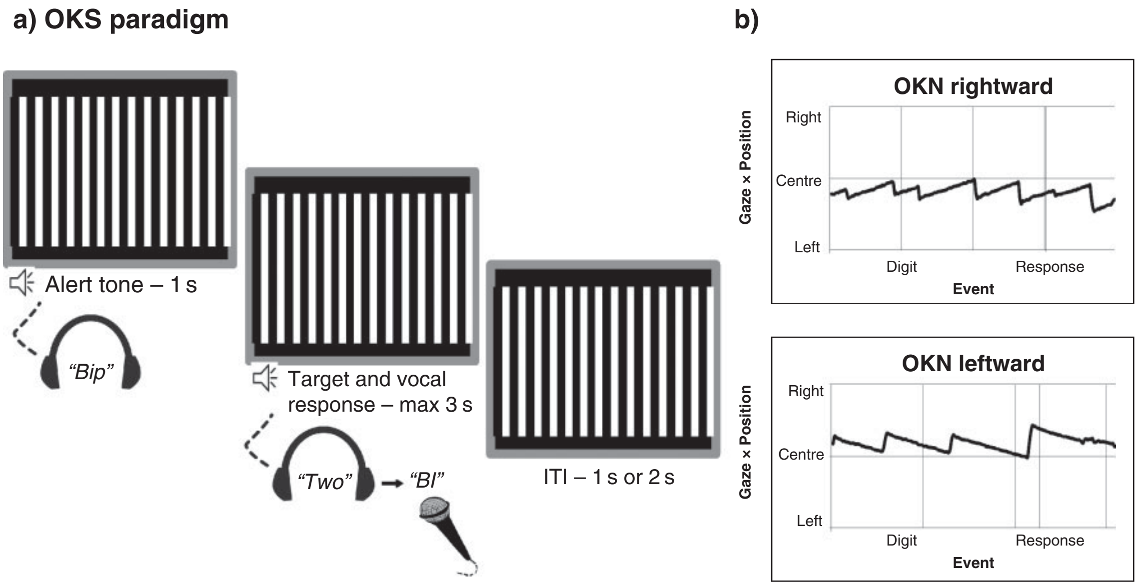

Figure 1. (a) Schematic representation of the experimental procedure. After a brief alert tone, a one-digit number (range 1–9, excluding "5") was presented acoustically via stereo headphones. Participants responded using two meaningless verbal labels ("BI" or "BO") to indicate the digit's parity (odd vs. even; Experiment 1) or magnitude (smaller vs. larger than 5; Experiment 2). Vocal RTs were collected using a microphone connected to a voice-key. OKS, or the static condition, was concurrently presented visually during all trials. (b) Time points of eye position traces showing OKN during rightward and leftward OKS. This graphical representation was displayed in real time on a second screen for online monitoring of the OKN by the experimenter.

contaminated by the SNARC effect. Accordingly, we investigated whether the orienting of visuospatial attention through OKS would affect number processing, yielding an interaction between Direction of OKS and Numerical Magnitude. Specifically, we hypothesised faster responses for smaller magnitudes during leftward OKS and for larger magnitudes during rightward OKS as compared to the performance in the baseline condition (i.e., static condition). Importantly, we also predicted that OKS should be more effective in the number comparison task than in the parity judgement task, because the former is more heavily reliant on visuospatial mechanisms (Herrera et al., 2008; Van Dijck et al., 2009; Zorzi et al., 2012).

MATERIALS AND METHODS

Stimuli and procedure of Experiments 1 and 2 were identical, except for the task (Experiment 1: parity judgement task; Experiment 2: number comparison task).

Participants

Twenty-four (8 males; 20 right-handers; age: *M* = 25 years, *SD* = 2.5) participants took part in Experiment 1, and twenty-four (8 males; 24 right-handers; age: *M* = 24.6 years, *SD* = 4.6) participants took part in Experiment 2. All volunteers had no history of neurological disorders, were Italian native speakers, and had normal or corrected to normal vision. All participants gave their informed consent prior to take part in the experiment according to the Declaration of Helsinki standards. The study was approved by the local Ethical Committee.

Apparatus and stimuli

The experiment was carried out in a quiet and dimly lit room. Participants sat centrally in front of the screen at a distance of approximately 40 cm. E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA) was used to run the numerical task and the OKS on two different personal computers. Eye movements were recorded at 60 hz with a Tobii T120 screen-based eyetracker (Tobii Technology, Sweden), which was also used to present OKS bars through its embedded 17-inch TFT monitor.

OKS consisted of white vertical stripes (width: 1 cm, height: 18 cm) presented against a black background and moving leftward or rightward on the horizontal plane at a constant speed of 8.4 cm/s. The inter-stripe distance was 1 cm. The moving bars covered the full monitor width and 2/3 of the monitor height. The bars did not move in the static (control) OKS condition. The numerical stimuli were single-digit number words (range: 1–9, excluding 5) presented acoustically as synthetic speech through stereo headphones (PHILIPS SHP2000).

Procedure

The structure of the trials is illustrated in Figure 1a. The tasks consisted in judging the parity (Experiment 1) or the magnitude (Experiment 2) of acoustically presented digits by verbally responding "BI" or "BO". Note that the use of two syllables with the same initial consonant as verbal response labels prevents any confound in the reaction times (RTs) related to triggering of the voice-key. In Experiment 1, participants used the two response labels to say whether the target digit was odd or even, whereas in Experiment 2 they used the same labels to say whether the target digit was smaller or larger than the fixed reference ("5"). Digits were presented through stereo headphones while participants observed OKS in three separate conditions: static, leftward and rightward.

The static OKS (control) condition was always performed as first and consisted of a set of 112 trials, divided in 4 blocks of equal duration. Leftward and rightward OKS were then presented in separate blocks, consisting of 224 trials divided in 8 blocks (4 blocks in leftward OKS condition and 4 blocks in rightward OKS condition). The motion direction was counterbalanced between blocks. The order of OKS direction (i.e., leftward first vs. rightward first) and the assignment of verbal response labels (i.e., the parings between "BI" or "BO" and the parity or magnitude information) were counterbalanced across participants. Digits were presented pseudo-randomly: in order to control for effects related to the order of presentation, each digit followed each other for the same number of trials. RTs for the vocal response were analysed as a function of OKS condition (static, leftward, rightward) and numerical magnitude (<5 = small; >5 = large). Each condition (OKS Direction × Numerical Magnitude) consisted of 56 trials.

At the beginning of each block (except for the static OKS condition), prior to the beginning of the numerical task, participants were presented with the leftward or rightward OKS. Eye movements were recorded and the current gaze position was plotted in real time on a supplementary screen (not visible to the participant) to control for the presence of the OKN in the leftward and rightward OKS conditions. The graphical representation of the participant's eye movements allowed the experimenter to monitor online the beginning of OKN and its persistence throughout each block (Figure 1b). After each block, participants were asked to take a break, for a minimum of 1 min (and as long as needed), to rest and recover from the OKS after-effect. Prior to the next block, the experimenter asked the participants to confirm the absence of the after-effect.

RESULTS

Mean RTs were calculated for each participant and condition and analysed with a repeated-measures ANOVA with the following within-subject factors: Direction of OKS (static, leftward, rightward), Number Magnitude (small, large).

The percentage of errors was very low (Experiment 1: 1.7% for static OKS, 2.9% for leftward OKS, 3.1% for rightward OKS; Experiment 2: 1.0% for static OKS, 1.5% for leftward OKS, 1.9% for rightward OKS). Accordingly, all analyses focused on RTs for correct responses. Trials where no response was detected (i.e., the voice-key was not triggered) were excluded from the analyses (Experiment 1: 0.5% for static OKS, 0.3% for leftward OKS, 0.2% for rightward OKS; Experiment 2: 0.8% for static OKS, 0.2% for leftward OKS, 0.1% for rightward OKS). We also excluded trials in which participants' gaze wandered outside the area of the display covered by the OKS stimulus for more than two time points: this led to the exclusion of 1.2% of static OKS trials, 2.1% of leftward OKS trials and 2.3% of rightward OKS trials in Experiment 1; 14.0% of static OKS trials, 0.2% of leftward OKS trials and 0.03% of rightward OKS trials in Experiment 2. Finally, RTs were trimmed with cut-off set at 2.5 *SD* from the mean, computed separately for each participant and OKS conditions (Experiment 1: 2.4% for static OKS, 2.2% for leftward OKS, 2.6% for rightward OKS; Experiment 2: 2.5% for static OKS, 2.2% for leftward OKS, 2.5% for rightward OKS). Overall, in Experiment 1 we excluded 5.7% of trials from the static OKS, 7.3% of trials in the leftward OKS and 8.1% of trials in the rightward OKS. In Experiment 2 we excluded 17.6% of trials from the static OKS, 4.2% of trials in the leftward OKS and 4.46% of trials in the rightward OKS.

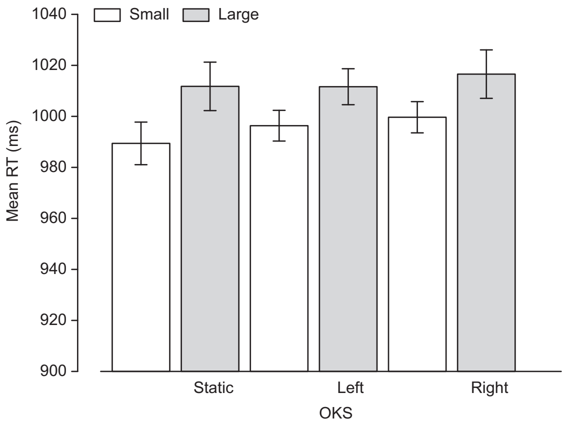

Figure 2. Results of Experiment 1, in which participants had to judge whether the presented number was odd or even. The OKS manipulation did not affect performance. Small numbers were classified faster than large numbers (number size effect). Error bars show within-subjects standard errors of the mean (*SEM*; Cousineau, 2005).

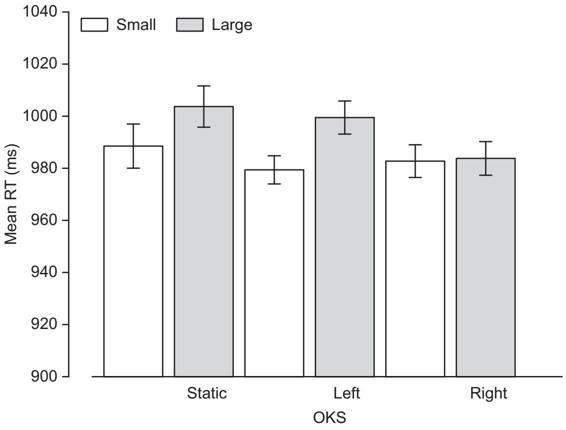

Figure 3. Results of Experiment 2, in which participants were asked to judge whether the presented number was smaller or larger than the fixed reference "5". The number size effect (faster responses to small than to large numbers) was abolished during rightward OKS. Error bars indicate within-subjects *SEM* (Cousineau, 2005).

Experiment 1: parity judgement task

Mean RTs for each condition are represented in Figure 2. The ANOVA revealed only a main effect of number magnitude, $F(1, 23) = 8.52$, $MSE = 1{,}397.56$, $p = .008$, $\eta_p^2 = .27$, indicating the typical pattern with faster RTs for small (M = 995 ms, $SEM = 28$) than large number magnitudes (M = 1,013 ms, $SEM = 28$). The main effect of Direction of OKS, $F(2, 46) = .22$, $MSE = 3{,}160.39$, $p = .8$, $\eta_p^2 = .01$, and its interaction with Numerical Magnitude, $F\ (2, 46) = .26$, $MSE = 624.91$, $p = .77$, $\eta_p^2 = .01$, were not significant.[1]

Experiment 2: number comparison task

Mean RTs for each condition are represented in Figure 3. The ANOVA revealed a main effect of number magnitude, $F(1, 23) = 6.45$, $MSE = 817.33$, $p = .018$, $\eta_p^2 = .22$, highlighting the same pattern found in Experiment 1, with faster RTs for small (M = 995 ms, $SEM = 28$) than large number magnitudes (M = 1,013 ms, $SEM = 28$). The main effect of Direction of OKS was not significant, $F(2, 46) = .72$, $MSE = 2{,}740.76$, $p = .49$, $\eta_p^2 = .03$; however, we found a significant interaction between Direction of OKS and Numerical Magnitude, $F(2, 46) = 4.32$, $MSE = 271.49$, $p = .019$, $\eta_p^2 = .16$: the comparison between small and large numbers within each OKS condition was significant in the static OKS condition, $t(23) = 3.7$, $p = .001$, in the leftward OKS condition, $t(23) = 2.49$, $p = .02$, but not in the rightward OKS, $t(23) = .15$, $p = .88$ (all t-tests were two-tailed).[2]

To further explore the interaction between Direction of OKS and Numerical Magnitude, we computed differences in RTs (dRTs) for rightward OKS minus leftward OKS for each number. In this way, positive dRTs indicate an advantage—in terms of faster RTs—during leftward OKS as compared to rightward OKS (Figure 4). Then, we computed for each participant the regression slope on dRTs with numerical magnitude as predictor, and entered these coefficients in a one-sample t-test. The asymmetry in RTs between leftward and rightward OKS was modulated by numerical magnitude, $t(23) = 2.96$, $p < .01$ (two-tailed), as revealed by a significant mean negative

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[1] To investigate the possible interaction between parity status and OKS direction, we conducted an additional repeated-measures ANOVA including Direction of OKS (static, leftward, rightward) and Number Parity (odd, even) as within-subject factors. Neither the main effects, nor the interaction were significant (all $ps > .3$).

[2] We conducted an additional repeated-measures ANOVA including Direction of OKS (static, leftward, rightward) and Numerical Distance (close: 3–4, 6–7; far: 1–2, 8–9) as within-subject factors to assess the presence of the classic distance effect (i.e., slower responses for digits close to the reference than far ones) and its possible interaction with OKS direction. The distance effect was significant, $F(1, 23) = 87.48$, $MSE = 1{,}162.25$, $p < .0001$, $\eta_p^2 = 0.79$ (close: M = 1,017 ms, $SEM = 22$; far: M = 964 ms, $SEM = 24$), but there was no interaction with OKS direction, $F(2, 46) = 0.65$, $MSE = 443.95$, $p = .52$, $\eta_p^2 = 0.03$. The main effect of OKS was not significant either, $F(2, 46) = 0.75$, $MSE = 2{,}680.27$, $p = .48$, $\eta_p^2 = 0.03$.

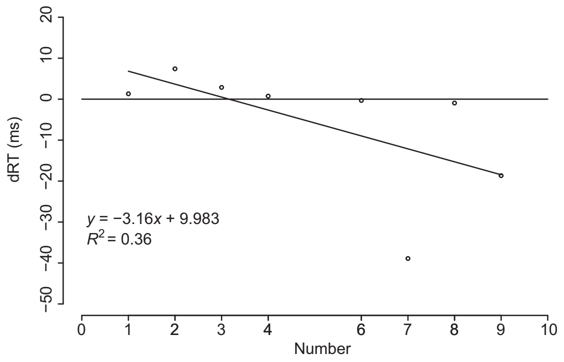

Figure 4. Differences in RTs (dRTs) for rightward OKS minus leftward OKS for each number are plotted. Negative dRTs indicate faster response during rightward OKS.

slope (mean $\beta = -3.16$, $SEM = 1.07$): decreasing dRTs as a function of numerical magnitude revealed a relative increasing advantage in answering to large numbers during rightward OKS as compared to leftward OKS.

DISCUSSION

In the present study we investigated the effect of OKS on numerical magnitude processing. Participants performed a parity judgement task (Experiment 1) or a number comparison task (Experiment 2) during OKS moving leftward or rightward and inducing OKN, or while observing static bars (control condition). We found the effects of OKS direction on the participants' performance in number processing but this was contingent on the type of task: rightward OKS abolished the classic number size effect (i.e., faster RTs for small than large numbers) in the comparison task but not in the parity task. Importantly, our choice to collect vocal responses with meaningless labels ("BI" or "BO") allowed to avoid confounds that might arise either with a manual response or with a spatial configuration of response keys in the physical space, ultimately suggesting that the observed effect might arise at an earlier—semantic—stage (see also Stoianov et al., 2008).

As noted in the Introduction section, the OKN elicited by OKS produces shifts of spatial attention coherent with the direction of the slow eye movements phase (e.g., Pizzamiglio et al., 1990; see Kerkhoff & Schenk, 2012, for review). We therefore suggest that OKS shifted spatial attention in the number space in a way consistent with the left-to-right orientation of the MNL. This result is consistent with the studies on LN patients that reported the effect of OKS on mental number bisection (Priftis et al., 2012), as well as the effect of coherent dot motion on number comparison (Salillas et al., 2009). It is worth noting that the manipulation of motion direction employed by Salillas et al. had no effects on the performance of healthy participants. Given that the numerical task was identical in Salillas et al.'s study and in ours, it appears that the presence of eye movements might be a crucial factor for influencing number comparison. As noted in the Introduction section, eye movements were prevented in the paradigm of Salillas et al., whereas the presence of OKN during the numerical task was a pre-requisite in our study. Thus, the comparison of the two studies suggest that, in healthy participants, (1) perceived direction of motion does not influence number processing and (2) though coherent dot motion may induce covert shifts of attention, only the overt shifts of attention triggered during OKN influences number processing.

The abolishment of the classic number size effect induced by OKS in number comparison was asymmetrical, being observed only during rightward OKS. This asymmetry is in line with the observation of a previous study that used a different technique to deploy visuospatial attention, that is, prismatic adaptation (Loftus et al., 2008b). Loftus and colleagues observed significant effects of prismatic adaptation on mental number interval bisection in healthy participants only following leftward prism adaptation, which induce rightward shifts of visuospatial attention, but not following exposure to rightward shifting or neutral prisms. Interestingly, this effect is opposite to what observed with LN patients, for which leftward shift of visuospatial attention is associated to amelioration of LN signs (e.g., Pizzamiglio et al., 1990; Rossetti et al., 1998): for instance, in the specific context of number processing, leftward OKS (Priftis et al., 2012) or adaptation to right prisms (Rossetti et al., 2004) were shown to ameliorate LN patients' biases in mental number interval bisection. The selective sensitivity to rightward shift of visuospatial attention in healthy participants, and to leftward one in LN patients, might originate from hemispheric asymmetries in visuospatial attention. Indeed, several models of visuospatial attention are in line with the view that the right side of space is overrepresented in the brain, with the right hemisphere playing a critical role in the spatial balancing of attention (e.g., Mesulam, 1981). This might explain why in healthy conditions only a rightward deployment of attention modulates performance on spatial-related tasks (e.g., numerical tasks), while the opposite is observed when the right hemisphere is damaged as in the case of LN patients.

The dissociation between the effect of OKS on number comparison and parity judgements, despite the use of the same stimuli and response modality, mirrors the recent findings of Zorzi et al. (2012) on LN patients. LN patients showed an atypical performance pattern in number comparison (i.e., a stronger SNARC effect, particularly for larger numbers, and an asymmetrical distance effect), whereas performance in parity judgement was typical (including a regular SNARC effect) and did not differ from that of control patients. This dissociation was interpreted in terms of the different demands of the two tasks on processing magnitude information. Indeed, a dissociation between explicit and implicit processing of numerical magnitude was first reported by Priftis et al. (2006), who found that LN patients were impaired in the mental number interval bisection task (explicit task) but showed a regular SNARC effect in parity judgements (implicit task). In LN patients, the difficulty in explicitly processing numerical magnitude is likely to reflect the impaired orienting of attention in number space. Nevertheless, dissociation between number comparison and parity judgement tasks has also been reported in healthy participants under dual task as a function of the type of working memory load (Herrera et al., 2008; Van Dijck et al., 2009). Specifically, the SNARC effect in parity judgement was abolished under verbal load (i.e., when the concurrent task required to remember a list of words) but not under visuospatial load (i.e., when the concurrent task required to remember a list of spatial locations; Van Dijck et al., 2009), while the converse was found for number comparison (Herrera et al., 2008; Van Dijck et al., 2009). This was interpreted in terms of reliance on visuospatial vs. verbal-spatial coding of numbers in the two tasks (Van Dijck et al., 2009). The selective effect of OKS on number comparison is not only compatible with this view, but it also highlights the role of attentional mechanisms in mediating number–space interactions, in line with the findings on LN patients. Overall, our findings confirm that number comparison (and hence the explicit processing of magnitude information) is more reliant on visuospatial mechanisms than parity judgement.

Finally, it should be highlighted that the observed effect of OKS on number processing in the number comparison task is coherent with previous findings showing that during random number generation participants' eyes tend to shift to the right for ascending number sequences and to the left for descending sequences (Loetscher, Bockisch, & Brugger, 2008); some authors argued that these gaze shifts may play a major role in the redeployment of attention in visual space after number processing (e.g., Blini, Cattaneo, & Vallar, 2013). However, while previous studies have revealed that number processing influences gaze shifts, in the present study we showed that eye movements can influence number processing. The present findings support the view of a primary role of gaze direction in shifting visuospatial attention (i.e., premotor theory of spatial attention; see Casarotti et al., 2012) that, as a consequence, can affect number processing. Correlational studies (e.g., neuroimaging studies: Knops et al., 2009) and studies reporting shifts of spatial attention following the processing of number magnitudes (e.g., Fischer et al., 2003; Ranzini et al., 2009; Schuller et al., 2014) provide interesting information about the cognitive and neural architecture of the numerical (and spatial) domain but do not allow to disentangle between a functional role of spatial attention and eye movements in number processing or a mere epiphenomenal effect. In the present study, instead, we report evidence supporting the first view, showing that a manipulation of spatial attention through eye movements can modulate performance in a numerical task.

The present study highlights the importance of embodied accounts of numerical cognition. Visuospatial attention orienting is a mechanism that is strongly embedded in gaze shifts and body movements during everyday activities, such as reaching locations or grasping objects. Crucially, action–number interactions extend the causal role of attention in number processing to action (Badets & Pesenti, 2010; Ranzini et al., 2012), thereby confirming the reliance of number processing on sensorimotor experience (Fischer & Lindemann, 2014). Indeed, many effects linking numbers to space have underlined the contribution of visuospatial attention in paradigms where attention was not directly investigated or manipulated. For instance, Gianelli, Ranzini, Marzocchi, Rettore, Micheli, and Borghi (2012) observed that, when required to grasp and freely change the location of an object while performing a magnitude comparison task, participants tended to place the object further towards the left if they were concurrently processing small numbers, while the opposite was observed during the processing of larger numbers. This result implies the contribution of attention orienting mechanisms in both number processing and reaching (for modulations of number processing in reaching movements, see also Ganor-Stern & Goldman, 2014). Moreover, Loetscher, Schwarz, Schubiger, and Brugger (2008) reported that healthy participants, when asked to randomly generate numbers, produced smaller numbers while moving the head leftwards, and larger numbers while moving the head rightwards along the transversal/yaw axis. The finding of Loetscher et al. was interpreted in the light of an asymmetrical hemispheric activation, induced by the lateral head turning, that triggered a shift in visuospatial attention counteracting the tendency to randomly generate small numbers within a given interval (i.e., pseudoneglect for number space; Loetscher & Brugger, 2007). More recently, Shaki and Fischer (2014) observed that turn selection during walking influenced the magnitude of randomly generated numbers, thereby providing compelling evidence of the link between magnitude processing and action execution in everyday life. Importantly, a similar pattern of results was also found for passive whole-body motion induced by a vestibular bottom-up manipulation that does not require any action or intention to move (Hartmann, Grabherr, & Mast, 2012, Experiment 1), suggesting that a purely sensorial—i.e., vestibular—stimulation could be sufficient to modulate performance during random number generation (but see Ferrè, Vagnoni, & Haggard, 2013, for a contrasting result using galvanic vestibular stimulation). Hartmann et al. (2012, Experiment 2; Hartmann, Farkas, & Mast, 2012) also found that leftward passive motion of the whole-body affected participants' RTs in an auditory SNARC paradigm (Hartmann, Grabherr, et al., 2012, Hartmann, Farkas, et al., 2012). We acknowledge that the vestibular stimulation procedure is linked to a shift in covert spatial attention, as demonstrated in previous studies (e.g., Figliozzi, Guariglia, Silvetti, Siegler, & Doricchi, 2005). Future studies should shed light and better define the relative contribution of each perceptual sense (visual, auditory, tactile), in addition to motor aspects, as to better understand the sensory and motor basis of numerical cognition.

In conclusion, while it is clear that both sensory and motor processes are strongly involved in some aspects of numerical cognition, our findings highlight that numerical processing is deeply embodied in neural circuits for eye movements and sensorimotor transformations that support visuospatial attention.

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