Psychological Research
DOI 10.1007/s00426-015-0741-2

ORIGINAL ARTICLE

Voluntary eye movements direct attention on the mental number space

Mariagrazia Ranzini[1] · **Matteo Lisi**[2] · **Marco Zorzi**[3,4]

Received: 14 July 2015 / Accepted: 17 December 2015

Abstract Growing evidence suggests that orienting visual attention in space can influence the processing of numerical magnitude, with leftward orienting speeding up the processing of small numbers relative to larger ones and the converse for rightward orienting. The manipulation of eye movements is a convenient way to direct visuospatial attention, but several aspects of the complex relationship between eye movements, attention orienting and number processing remain unexplored. In a previous study, we observed that inducing involuntary, reflexive eye movements by means of optokinetic stimulation affected number processing only when numerical magnitude was task relevant (i.e., during magnitude comparison, but not during parity judgment; Ranzini et al., in J Cogn Psychol 27, 459–470, (2015). Here, we investigated whether processing of task-irrelevant numerical magnitude can be modulated by voluntary eye movements, and whether the type of eye movements (smooth pursuit vs. saccades) would influence this interaction. Participants tracked with their gaze a dot while listening to a digit. The numerical task was to indicate whether the digit was odd or even through non-spatial, verbal responses. The dot could move leftward or rightward either continuously, allowing tracking by smooth pursuit eye movements, or in discrete steps across a series of adjacent locations, triggering a sequence of saccades. Both smooth pursuit and saccadic eye movements similarly affected number processing and modulated response times for large numbers as a function of direction of motion. These findings suggest that voluntary eye movements redirect attention in mental number space and highlight that eye movements should play a key factor in the investigation of number–space interactions.

Introduction

The way humans process numerical magnitude is closely linked to the processing of spatial information. One classic demonstration comes from studies where participants are required to indicate with a spatially lateralized response, such as left or right hand, whether a digit is odd or even (parity judgment task). Even if the task does not explicitly require to process the magnitude of the digit, participants typically show faster left-sided responses to small numbers and faster right-sided responses to large numbers when compared to the opposite paring between number magnitude and response side (i.e., the SNARC effect; Dehaene, Bossini, & Giraux, 1993). Since the discovery of the SNARC effect numerous studies have been conducted to investigate the cognitive and neural mechanisms underlying the link between number and space. It has been proposed that numerical magnitudes are mentally represented along a continuum, a *mental number line* (Restle, 1970; Zorzi, Priftis, & Umiltà, 2002). Numerical magnitude would be spatially ordered on this mental line in a way that is strongly influenced by cultural habits such as reading/writing direction, that is from left to right in Western societies (e.g., Dehaene et al., 1993; Göbel, Shaki, &

✉ Marco Zorzi
marco.zorzi@unipd.it

[1] Centre de Recherche Cognition & Neurosciences (CRCN), Université Libre de Bruxelles (ULB), Brussels, Belgium

[2] Laboratoire Psychologie de la Perception, Université Paris Descartes & CNRS (UMR 8242), Paris, France

[3] Department of General Psychology and Center for Cognitive Neuroscience, University of Padova, Via Venezia 8, 35131 Padua, Italy

[4] IRCCS San Camillo Hospital Foundation, Lido-Venice, Italy

Fischer, 2011; Shaki, Fischer, & Petrusic, 2009). The hypothesis that number–space interactions like the SNARC effect tap an intrinsic property of the mental representation of numbers is still debated (e.g., Gevers et al., 2010) but it has been recently supported by neuropsychological (Zorzi, Bonato, Treccani, Scalambrin, Marenzi, & Priftis, 2012) and neuroimaging studies (Cutini, Scarpa, Scatturin, Dell'Acqua, & Zorzi, 2012). A corollary to this hypothesis is that number processing involves orienting of spatial attention in the *number space* (Hubbard, Piazza, Pinel, & Dehaene, 2005; Umiltà, Priftis, & Zorzi, 2009; Zorzi et al., 2002).

Numerous studies on healthy adults support the latter hypothesis. The first evidence showing that processing numerical magnitudes induces shifts of attention was provided by Fischer, Castel, Dodd and Pratt (2003) by means of a simple detection task. Participants performed detection of a peripheral target that followed a non-predictive digit presented at fixation. Reaction times were faster for left-sided targets when cued by a small digit with respect to a large digit, whereas right-sided targets showed the opposite pattern. This suggested that the numerical cue triggered stimulus-driven, reflexive shifts of attention (see also: Dodd, Van der Stigchel, Leghari, Fung, & Kingstone, 2008; but see: Ristic, Wright, & Kingstone, 2006; Galfano, Rusconi, & Umiltà, 2006; Bonato, Priftis, Marenzi, & Zorzi, 2009 for contrasting results). Evidence that numerical stimuli induce reflexive shifts of attention was also provided at the neurophysiological level (e.g., Ranzini, Dehaene, Piazza, & Hubbard, 2009). Finally, other studies adopting different paradigms have substantiated the view that numerical magnitudes can trigger reflexive orienting of attention (e.g., Blini, Cattaneo, & Vallar, 2013; Casarotti, Michielin, Zorzi, & Umiltà, 2007; Di Luca, Pesenti, Vallar, & Girelli, 2013; Fischer, 2001; Masson & Pesenti, 2014; Nicholls, Loftus, & Gevers, 2008; Bonato, Priftis, Marenzi, & Zorzi, 2008).

Crucially, the influence of numerical magnitude on spatial attention extends to the execution of eye movements. In the study of Fischer, Warlop, Hill and Fias (2004), participants performed parity judgments but had to respond with leftwards or rightwards saccadic eye movements rather than key presses. The SNARC effect extended to this type of response modality, as participants were faster in initiating a leftward eye movement for small compared to large digits, and they were faster in initiating a rightward eye movement for large compared to small digits (see also Schwarz, & Keus, 2004). Loetscher, Bockisch and Brugger (2008) analyzed participants free gaze shifts during number bisection (i.e., indicating the mid-number within a pair: e.g., the mid-number for the pair 1-9 is 5). They found that the horizontal eye position shifted toward the left when the number pairs were presented in descending order (9 and 1), and it shifted toward the right when the number pairs were presented in ascending order (1 and 9). In another study, Loetscher, Bockisch, Nicholls and Brugger (2010) observed that eye position predicted the upcoming number that the participant would produce during a random digit generation task. Specifically, leftwards and downwards shifts in eye position preceded the upcoming generation of a smaller digit as compared to the previous one. Ruiz Fernández, Rahona, Hervás, Vázquez and Ulrich (2011) analyzed the position on the screen of the first gaze fixation following the presentation of a number and observed that the probability of fixating firstly to the left decreased as a function of increasing numerical magnitude (also see Myachykov, Ellis, Cangelosi, & Fischer, 2016, for evidence of spontaneous oculomotor drift elicited by numerical stimuli). The interplay between numerical magnitude, attention orienting and eye movements suggests that the representation of numerical magnitude might be embedded in the same sensorimotor mechanisms involved in attention and eye movements (Hubbard et al., 2005). Functional imaging studies corroborate this idea by describing overlapping cortical regions in the parietal lobes involved in both numerical tasks and saccades (Knops, Thirion, Hubbard, Michel, & Dehaene, 2009; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002).

Though the effect of number processing on the orienting of attention and eye movements suggests that the representation of number magnitude might be embodied in sensorimotor transformations, support for the hypothesis that spatial attention is a core mechanism for number processing requires evidence for a causal link. Neuropsychological studies have shown that deficits in orienting attention and in processing numerical magnitude can co-occur in patients with neglect (see Umiltà, et al., 2009 for a review). Neglect consists in the inability to detect or orient to stimuli in the hemifield contralateral to the lesioned (usually right) hemisphere (Halligan, Fink, Marshall, & Vallar, 2003). It has been reported that neglect patients can show impairment in the explicit processing of smaller numerical magnitudes within a given range (e.g., Zorzi et al., 2002, 2012), suggesting that they are impaired in orienting attention to the left of the mental number space (for alternative views, see Aiello et al., 2012; van Dijck, Gevers, Lafosse, & Fias, 2012). More recently, studies on healthy individuals have investigated whether manipulating the orienting of attention in visual space influences the processing of numerical magnitude (e.g., Stoianov, Kramer, Umiltà, & Zorzi, 2008; Ranzini et al., 2015). For instance, it has been shown that during the execution of a numerical task (parity judgment or magnitude comparison) a spatial cue directing attention leftward induced slower responses to large digits relative to smaller ones, while a cue directing attention rightward had the opposite effect (Stoianov et al., 2008; Kramer, Stoianov, Umiltà, & Zorzi, 2011; see also Grade, Lefèvre, & Pesenti, 2013).

Given the tight relationship between eye movements and spatial attention (as more formally suggested by the premotor theory of attention; Rizzolatti, Riggio, Dascola, & Umiltà, 1987; see Casarotti, Lisi, Umiltà, & Zorzi, 2012, for an updated and computationally explicit version), an efficient way to induce and control for the orienting of visuospatial attention consists of manipulating eye movements. We have recently investigated whether inducing involuntary, reflexive eye movements through optokinetic stimulation (OKS) could affect the processing of numerical magnitude (Ranzini et al., 2015). OKS is a technique commonly used for the rehabilitation of visuospatial attentional deficits (Pizzamiglio, Frasca, Guariglia, Incoccia, & Antonucci, 1990; Pizzamiglio et al., 1992); it consists in presenting a high contrast, whole-field pattern that continuously moves in a given direction. Observing such moving display triggers a pattern of automatic eye movements known as optokinetic nystagmus. More specifically, nystagmus consists of an alternation of smooth pursuit in the direction of the pattern movement, and compensatory saccades in the opposite direction. In the study of Ranzini et al., participants were required to stare at OKS while performing parity judgment (Experiment 1) or magnitude comparison (Experiment 2). OKS affected number processing during magnitude comparison: in particular, the classic number size effect (i.e., faster response times for small numbers relative to larger ones) was not present during rightward OKS, thereby suggesting a facilitation (compared to leftward OKS) for processing larger numbers. In contrast, OKS did not affect parity judgment, in line with previous findings dissociating between parity judgment and magnitude comparison (e.g., Priftis, Zorzi, Meneghello, Marenzi, & Umiltà, 2006; Zorzi et al., 2012). More generally, these findings are consistent with the hypothesis that spatial attention is particularly engaged by the explicit (e.g., magnitude comparison, number bisection) rather than the implicit (e.g., parity judgment) processing of magnitude information (Zorzi et al., 2012).

Though the study of Ranzini et al. (2015) provides a clear demonstration that the overt orienting of attention induced by OKS affects the explicit processing of magnitude (also see Priftis, Pitteri, Meneghello, Umiltà, & Zorzi, 2012, for related findings on neglect patients), the OKS procedure itself suffers from one important shortcoming. As noted before, nystagmus consists of an alternation of smooth pursuit in the direction of the pattern movement and compensatory saccades in the opposite direction. It is therefore conceivable that the coexistence of two phases with opposite spatial directions may somehow dilute the overall strength of attention and in particular its spillover into the representational space of number magnitude. Moreover, nystagmus is an oculomotor reflex, which implies that attention orienting is involuntary. For these two reasons, in the present study we assessed whether a manipulation of overt attention that should be stronger than the one obtained through OKS would affect a parity judgment task, in which magnitude processing is only implicit. To do this, we investigated the effect of voluntary eye movements, executed by participants as part of the task demands, on the processing of number magnitude. Participants performed parity judgments, using non-spatial verbal responses, while tracking with their gaze a dot that moved on the screen, leftwards or rightwards along the horizontal axis. We expected to observe a modulation of response times in the numerical task as a function of numerical magnitude and oculomotor movement direction, with leftward eye movements facilitating large numbers relative to small numbers and rightward movements yielding the opposite pattern. Additionally, we controlled for the different effects of smooth pursuit and saccadic eye movements. Accordingly, we made the dot either move continuously, inducing a smooth pursuit movement (pursuit condition), or move through a series of discrete jumps to consecutive locations, thus triggering a series of saccades (saccade condition). Experimental evidence suggests that pursuit and saccades orient attention in a similar way (Krauzlis & Miles, 1996; Krauzlis, Zivotofsky, & Miles, 1999; Adler, Bala, & Krauzlis, 2002). Therefore, we expected to observe number–space interactions in both conditions of oculomotor movement. However, we acknowledge that this manipulation has never been tested previously in the context of number–space interactions: if pursuit and saccades have different impact on number–space interaction, differently from what expected, this would be an important finding with implication for future experiments and theoretical models of number processing and attention.

Finally, though this was not a main aim of the study, we also analyzed eye movements (pursuit gain, and the amplitude and peak velocity of saccades) to assess the possible effects of numerical magnitude.

Materials and methods

Participants

Sixteen participants (12 females; 15 right-handers; age: *M* = 27 years, SD = 4.5) took part in the experiment. All volunteers had normal or corrected to normal vision, they gave their informed consent prior to take part in the experiment, and they received a small monetary reimbursement for their participation. The study was approved by the local Ethics Committee (Department of General Psychology, University of Padova) and performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

Apparatus, stimuli, and procedure

Participants sat centrally in front of the screen at a distance of approximately 60 cm. EPrime 2.0 software (Psychology Software Tools, Pittsburgh, PA) was used to run the experiment. Eye movements were recorded at 120 Hz with a Tobii T120 screen-based eyetracker (Tobii Technology, Sweden), which was also used to present the visual stimuli through its embedded 17-in. TFT monitor (refresh rate 60 Hz). In each trial, the visual target consisted in a black dot [radius ≈ 0.3 degree of visual angle (°)] presented against a gray background. The dot moved leftward or rightward, in two different ways: either continuously, allowing tracking by smooth pursuit eye movements (pursuit condition), or it jumped across a series of adjacent locations, triggering a sequence of saccades (saccade condition). The dot could move leftward or rightward, starting from the screen center or from one of two lateral positions, at 9.8° on the left or right of the screen center. Different starting points were used to counterbalance the starting position of the eye movement, as well as the gaze position with respect to the body midline. Direction of motion (leftward, rightward) and type of movement (pursuit, saccade) conditions were presented in random order. Conditions where the dot started to move from the center or from the periphery were presented in two different counterbalanced blocks. Participants were required to maintain their gaze on the dot as it moved. In the pursuit condition, the dot appeared at the starting position, and immediately started moving horizontally at about 4.5°/s (corresponding to a displacement of 2 pixels each frame, every 16.6 ms). In the saccade condition, the dot could occupy a maximum number of nine consecutive equidistant locations (about 2° from one location to the next one) on the left or on the right of the screen center. The timing of the jumps was set to make the dot travel over the same total distance in the same time as in the pursuit conditions (i.e., the overall speed was the same). Binocular gaze position was recorded at 120 Hz and analyzed offline. While tracking the dot, participants listened to a target digit presented through stereo headphones (PHILIPS SHP2000) as synthetic speech. Target digits were digits 2–3, belonging to the small digit condition, and digits 8–9, belonging to the large digit condition. The digits were acoustically presented after 880 or 1080 ms from the presentation of the moving dot. The delay between the dot and digit onsets varied to avoid habituation effects, and it was not taken into consideration in the analyses. The numerical task was to indicate whether the digit was odd or even through a vocal response that was collected by a microphone. The microphone was connected to a PST serial response box that detected voice onset. For each trial, the response time corresponded to the latency of the vocal response from the onset of the numerical stimulus. Participants responded “BI” or “BO” for odd or even digits, and the experimenter encoded the response out of the sight of the participant. Response mapping (“BI”-odd and “BO”-even, or vice versa) was counterbalanced within the participants group. As in previous studies (e.g., Ranzini et al., 2015; Stoianov et al., 2008), we used a verbal response modality to avoid any response-related effect that might be induced by lateralized, spatially defined responses such as key presses. The syllables “BI” and “BO” were used as vocal responses because they have the same initial consonant, thereby avoiding any confound related to the triggering of the voice key. For each trial, the dot continued moving on the screen until the response was detected or a response deadline of 3800 ms was passed. Each digit (2, 3, 8, 9) × direction of motion (leftward, rightward) × type of movement (pursuit, saccade) condition included ten trials, for a total of 160 trials for each of the two blocks (dot starting from the center or from the periphery). Thus, the whole experiment consisted of 320 experimental trials, which were preceded by 16 practice trials. The experiment was carried out in a quiet and dimly lit room, and it lasted about 50 mins. The structure of a trial is illustrated in Fig. 1.

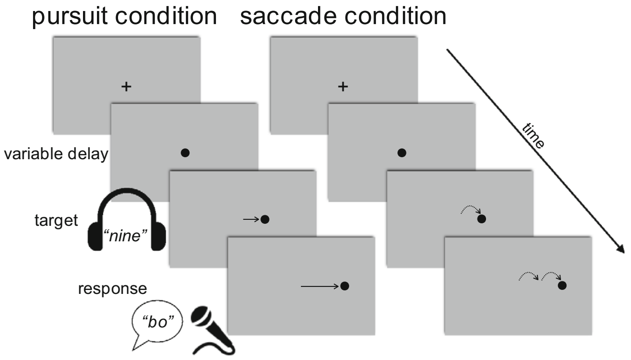

Fig. 1 Illustration of the trial structure in the pursuit (*left side*) or saccade (*right side*) condition. Each trial started with a fixation cross lasting 1 s, followed by the presentation of the moving *dot*. The *dot* started to move (*rightward* in this example) and participants tracked its movement with their gaze. After a variable delay, a digit was acoustically presented and participants performed a parity judgment while continuing tracking the *dot*. Parity responses were vocal and non-spatial to avoid any response-related effect

Results

Participants made few errors ($M = 1.6$ %, range between participants: 0–4 %). Trials with incorrect responses were therefore discarded and all analyses focused on response times (RTs). Trials in which the dot had crossed the screen center or disappeared before the participant’s response were excluded from analysis. Gaze position was then analyzed offline for each trial to ensure that participants accurately tracked the dot. A graphical illustration of gaze position along

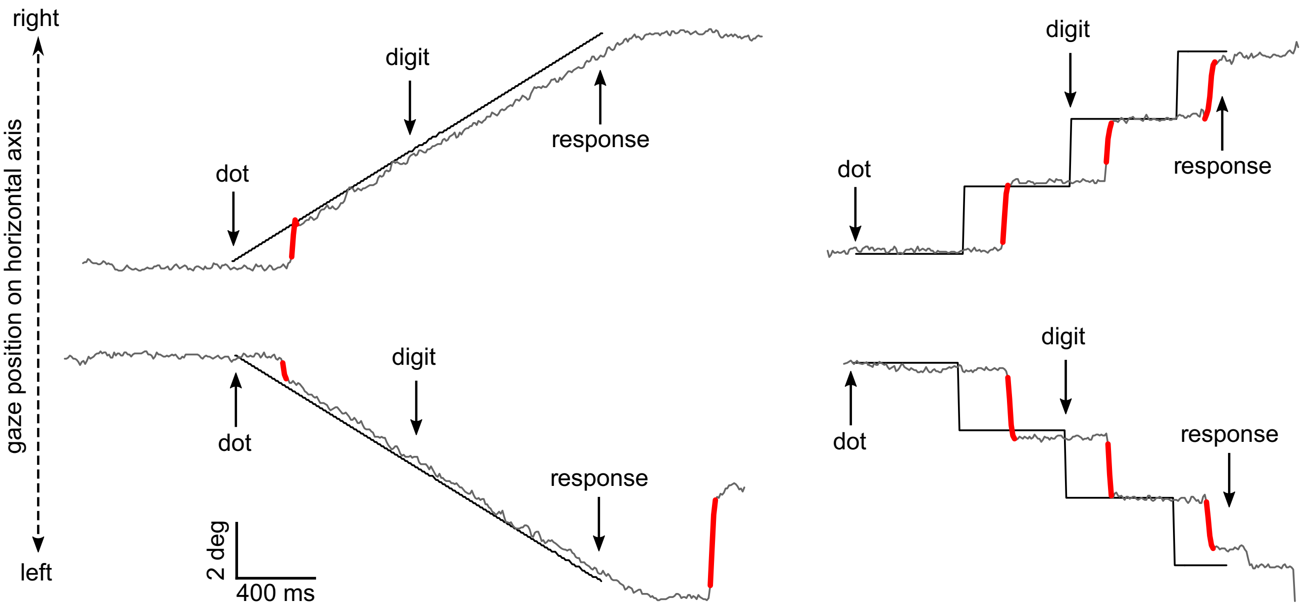

Fig. 2 Examples of horizontal gaze position traces of one participant during single trials belonging to the different experimental conditions (pursuit conditions, on the *left*; saccade conditions, on the *right*). For *each panel*, the *black line* indicates *dot position* and the *gray line* indicates *horizontal gaze position*, with the saccades (as detected by the algorithm) highlighted in *red*. *Vertical arrows* indicate points in time corresponding to the occurrence of the *dot*, the digit and the response of the participant (color figure online)

the horizontal axis in the different conditions is provided in Fig. 2. For each trial, we computed the mean and standard deviation of the difference between gaze and dot positions (both horizontal and vertical) at each time point in the interval between target onset and the participant's response. For each participant and movement type condition, trials in which one of these measures exceeded 2.5 standard deviations from the mean of all trials were classified as incorrect (i.e., inappropriate eye movements) and were discharged from subsequent analyses. These criteria led to the exclusion of 8 % (between participants range: 4–15 %) of the trials (4 % for the pursuit condition, range between participants: 1–8 %; 4 % for the saccade condition, range between participants: 2–7 %).

Reaction times analyses

Mean RTs were analyzed with a repeated measures ANOVA with the following within-subjects factors: number magnitude (small, large), direction of motion (leftward, rightward) and type of movement (pursuit, saccade).[1] The analysis revealed a significant main effect of number magnitude, $F(1,15) = 4.90$, $p = 0.04$, $\eta_p^2 = 0.25$, indexing the classic finding of slower responses for large ($M = 783$ ms, SEM $= 18$ ms) than for small numbers ($M = 771$ ms, SEM $= 19$ ms) (number size effect; Moyer & Landauer, 1967), and showing that task-irrelevant numerical magnitude was processed during parity judgment (Dehaene et al., 1993). The main effect of movement type was also significant, $F(1,15) = 7.10$, $p = 0.02$, $\eta_p^2 = 0.32$, indicating that responses were on average slower in the condition with discrete target motion and saccadic tracking (pursuit: $M = 769$ ms, SEM $= 20$ ms; saccade: $M = 786$ ms, SEM $= 18$ ms). This effect might indicate a higher cost, in terms of attentional resources, of planning and executing saccades as compared to pursuit eye movement, resulting in a modulation of response times in the concurrent numerical task. Importantly, the crucial interaction between number magnitude and direction of motion was significant, $F(1,15) = 5.71$, $p = 0.03$, $\eta_p^2 = 0.28$ (see Fig. 3). Planned comparisons (paired, two-tailed *t* tests) revealed a significant difference between trials with small versus large number magnitude when the direction of motion was leftward [$t(15) = 3.50$, $p = 0.003$] but not when it was rightward [$t(15) = 0.49$, $p = 0.63$]. Furthermore, we found that while small numbers required the same time to be processed independently from the direction of motion [$t(15) = 0.79$, $p = 0.44$], large numbers were indeed processed faster when the motion was rightward as compared to leftward [$t(15) = 2.66$, $p = 0.02$]. Importantly, the type of

---

[1] In a preliminary analysis we also included the starting position of the dot target (central, peripheral) as within-subjects factor. Starting position did not yield a significant main effect, and it did not enter in any significant interaction with number magnitude (all $p > 0.05$). Conversely, the critical interaction between number magnitude and movement direction was unaffected [$F(1,15) = 5.916$, $p = 0.028$]. Therefore, we collapsed trials from the two conditions and excluded this factor from the analysis.

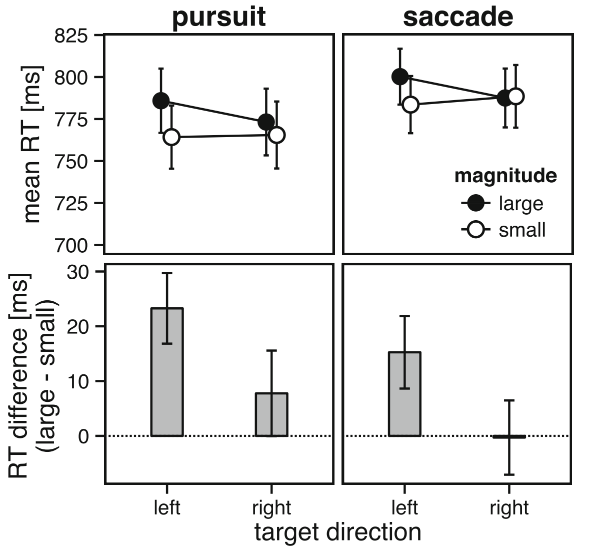

Fig. 3 Mean response times as a function of *dot* motion direction and number magnitude (*top panels*). *Error bar*s represent bootstrapped within-subjects SEM. *Lower panels* represent within-subject differences in reaction times between large and small number magnitudes, with *error bars* representing bootstrapped SEM

movement did not interact with number magnitude, $F(1,15) = 2.98, p = 0.10$, and also the three way interaction between type of movement, direction of motion and number magnitude was not significant, $F(1,15) = 0.00$, $p = 0.99$. No other main effects or interactions were significant [motion direction: $F(1,15) = 2.37$, $p = 0.14$, motion direction by type of movement: $F(1,15) = 0.04$, $p = 0.84$]. Overall, these results suggest that the effect of eye movements, whether pursuit or saccade, modulated the processing of large numbers as a function of the direction of motion.

Eye movements analyses

We analyzed eye movements to investigate whether number processing had a detectable effect on oculomotor planning and execution. In our paradigm, the number was presented after the initiation of the eye movement, so it was not possible to analyze the latency of eye movements as a function of numerical magnitude. Instead, we focused on the speed of the pursuit, and on the amplitude and peak velocity of saccades. As a first step in our analysis we detected within each trial saccades' onsets and offsets using an algorithm based on two-dimensional eye velocity (Engbert & Mergenthaler, 2006). Next, for trials in the pursuit condition, we removed parts of the recording that were identified as saccades, and calculated the average speed of the eye in the temporal interval between the onset of the number and the participants' response. We analyzed pursuit gain (the ratio between gaze and dot speeds) as a function of movement direction (left vs. right) and numerical magnitude (small vs. large). We found only a significant, although small, main effect of numerical magnitude, $F(1,15) = 4.59$, $p = 0.049$, which revealed that pursuit gain was, on average, higher in trials where small numbers were presented (average gain = 0.85, bootstrapped SE across participants = 0.018) than in trials with large numbers (average gain = 0.82, bootstrapped SE across participants = 0.016). This indicated that pursuit was slightly faster during the processing of smaller numbers than during the processing of larger ones, and it is in line with the hypothesis that both pursuit and number processing tap into shared attentional resources (cf., main effect of movement type on response times). We found no evidence for an effect of movement direction, $F(1,15) = 0.20$, $p = 0.66$, or an interaction between movement direction and numerical magnitude, $F(1,15) = 0.002$, $p = 0.97$. For both the pursuit and the saccade conditions, we repeated the same analysis on saccade amplitude, and on saccade peak velocity (more precisely we analyzed the peak velocity or amplitude average across all the saccades that occurred in the temporal window between number onset and response; on average 1.75 saccades occurred in this time window) but found no significant effect (all $p > 0.1$). However, we would like to note that the parameters of the saccades that can be recovered from recordings at relatively low sampling frequency, as it is here (120 Hz), have limited accuracy, and therefore we cannot exclude an effect of number processing on saccade planning on the basis of the current results.

Discussion

In the present study, we examined whether the voluntary execution of eye movements, and therefore the voluntary orienting of visuospatial attention, would affect number processing in a task in which the access to numerical magnitude is only implicit (i.e., magnitude is task irrelevant). Participants performed a parity judgment task while tracking a moving dot with their gaze. The dot could move leftward or rightward, either continuously (pursuit condition) or by jumping to consecutive locations (saccade condition). Basing on previous findings (e.g., Stoianov et al., 2008) we predicted that number processing would be affected by the concurrent shifts of attention in the direction of the moving dot, thereby yielding an interaction between numerical magnitude and direction of motion in the analysis of parity response times. Indeed, we observed that in both pursuit and saccade conditions large digits were processed slower when the dot was moving leftward than rightward, thereby abolishing the number size effect during rightward eye movements. This finding supports the idea that numbers are mentally represented on a spatial continuum that can be conceived as a mental line (Restle, 1970), and that spatial attention operates along this continuum (Hubbard et al., 2005; Zorzi et al., 2002, 2012).

It is worth noting that the expected modulation of parity response times was reliable for large numbers but not for small numbers. We suspect that the null effect for small numbers might reflect a floor effect. While rightward eye movements might have speeded up the processing of large numbers and slowed down the processing of small numbers (thereby abolishing the magnitude effect), leftward eye movements might have slowed down large numbers but failed in speeding up small numbers. In other words, it is possible that response times for small numbers, which were overall faster than for large numbers, clustered around a lower limit that prevented the emergence of a reliable modulation.

Slower response times for large digits in the leftward than in the rightward dot condition mirror the results obtained by Stoianov et al. (2008). In their Experiment 2, participants performed parity judgment on centrally presented digits using non-spatial vocal responses. A left- or right-sided irrelevant visual cue preceded or followed the number target (forward and backward conditions, respectively). An interaction between cue side and numerical magnitude was found in the backward condition, where the cue followed the target. This effect, named spatio-numerical interaction between perception and semantics (SNIPS) in the follow-up study of Kramer et al. (2011), was explained in terms of temporal overlap between the processing of spatial and numerical information: given that number processing is slower than the processing of an exogenous spatial cue, only the backward condition generated this overlap. This explanation holds for the current results: since the dot started to move well before the presentation of the digit and continued until response, it is conceivable that attention orienting was continuously activated, thereby fostering the overlap between number and spatial processing. Interestingly, Kramer et al. (2011) also showed by means of a “no-cue” control condition that the SNIPS effect is inhibitory, with spatially incongruent cues interfering with number processing, and symmetric, acting both for small and for large numbers. We note that designing a proper “neutral” condition to distinguish between facilitation and interference is often difficult (also see Kramer et al., 2011, for discussion); in the context of our experimental paradigm, removing the concurrent task of tracking the moving dot to obtain a “no-movement” condition would dramatically change task demands and make any comparison with the experimental conditions hardly tenable. Nevertheless, in light of the strong similarity between the current results and those of Stoianov et al. (2008), we suggest that our manipulation of eye movements indeed produced an instance of SNIPS effect.

More generally, the present study complements the existing literature on the effects of visuospatial attention on the processing of numerical magnitude, by showing that not only reflexive shifts of attention (e.g., Grade et al., 2013; Kramer et al., 2011; Stoianov et al., 2008; Ranzini et al., 2015) but also voluntary orienting can affect number processing. Note that we use the term *voluntary* instead of *endogenous* in the context of the present study because ocular movements were voluntary but not completely endogenous since they were triggered by an external stimulus (i.e., the moving dot). It is well established that involuntary/reflexive attention and voluntary attention belong to two functionally distinct systems: the former is triggered by sensory events like peripheral visual cues, whereas the latter is controlled by the individual’s goals and expectations (Posner, 1980; Berger, Henik, & Rafal, 2005; Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000). Voluntary and involuntary attention have also different time courses (e.g., Nakayama & Mackeben, 1989) that can be characterized in terms of fast and transient allocation or slower but sustained allocation, respectively. At the cortical level, a fronto-parietal attentional network for the control of spatial attention has been described, with distinct (though interconnected) areas subserving voluntary and reflexive orienting mechanisms (Corbetta & Shulman, 2002; Corbetta, Patel, & Shulman, 2008; Posner & Petersen, 1990). The present study shows that the voluntary deployment of attention triggered by eye movements was strong enough to impact number processing during parity judgment. In contrast, the OKS manipulation used by Ranzini et al. (2015, Experiment 1) failed to produce any effect on parity judgment and it was effective only when the task required explicit processing of numerical magnitude (i.e., number comparison). Concerning the nature of number processing, these results also suggest that besides the plurality of mechanisms at play during parity judgment and magnitude comparison (e.g., Gevers et al., 2010; Herrera, Macizo, & Semenza, 2008; van Dijck, Gevers, & Fias, 2009; van Dijck et al., 2012; Zorzi et al., 2012), both tasks tap on visuospatial attentional mechanisms, even though to different extents.

A second important finding of this study is that the effects of eye movements on number processing were independent of the type of eye movement. This finding is in line with the recent view that ascribes a similar functional organization to pursuit and saccade systems (Krauzlis,2004). Pursuit has been traditionally regarded as a relatively automatic behavior, driven by visual motion signals and controlled by a simple circuit connecting visual areas in the cortex to the pursuit-related motor region in the cerebellum (Lisberger, Morris, & Tychsen, 1987). More recent studies have questioned this view, showing for example that pursuit involves an extended network of cortical and subcortical areas, many of which are also associated with saccade execution, such as the superior colliculus (Basso, Krauzlis, & Wurtz, 2000), a subregion of the frontal eye field (Tanaka & Lisbgerger, 2001, 2002), and the lateral intraparietal area (Bremmer, Distler, & Hoffman, 1997). These same areas are recruited during covert attention shifts and during saccadic eye movements (Corbetta et al., 1998; Moore, Armstrong, & Fallah, 2003). Is it thus likely that the same attentional system is recruited during the planning of either pursuit or saccades (Krauzlis & Miles, 1996; Krauzlis et al., 1999; Adler et al., 2002), with similar effects on the processing of numerical magnitude.

Finally, this study highlights the importance to take into account eye movements in the investigation of number–space interactions and more in general in the investigation of how human minds represent spatial aspects of concrete and abstract knowledge. In has been demonstrated that eye movements can move among different spatial locations in a visual scene as well as they can move in an imagined representation of a scene in absence of visual stimuli (Spivey & Geng, 2001), thus suggesting that visual and mental representations share common spatial coordinates. This is in line with the hypothesis that the visual and the mental number space can be considered as homeomorphic (Zorzi et al., 2002, 2012). Importantly, the use of eye movements in cognitive research can also provide important information concerning how the human mind operates with mental representations of numbers (Hartmann, 2015). For instance, eye movements have been shown to disclose spatial biases during arithmetic operations (Hartmann, Mast, & Fischer, 2015; Hartmann, Mast, & Fischer, 2015; Yu, Liu, Li, Cui, & Zhou, 2015), and to reveal the nature of the organization of thinking that brings to the solution of complex mathematical expressions (Schneider, Maruyama, Dehaene, & Sigman, 2012), and finally they have been shown to be responsible for the outcome of problem solving (Grant & Spivey, 2003).

In conclusion, the present study is in line with action-based theories of cognition claiming that human knowledge is embodied into perception–action systems (e.g., Barsalou, 1999). In the context of number processing, evidence supporting embodied and grounded cognition theories has been provided by studies showing number–action interactions (e.g., Badets & Pesenti, 2010; Ranzini, Lugli, Anelli, Carbone, Nicoletti, & Borghi, 2011), as well as by studies showing that number–space interactions depend on action-based cultural experiences, such as the direction of reading and writing (e.g., Göbel et al., 2011) or of finger counting (Fischer & Brugger, 2011). Our findings show that eye movements, which are responsible for the deployment of visuospatial attention, influence number processing and can unveil the spatial nature of the mental representation of numbers.

Acknowledgments This study was supported by University of Padova Strategic Grant “NEURAT” to M.Z.

References

Adler, S.A., Bala, J., & Krauzlis, R.J. (2002). Primacy of spatial information in guiding target selection for pursuit and saccades. *Journal of Vision,* 2, 627–644.

Aiello, M., Jacquin-Courtois, S., Merola, S., Ottaviani, T., Tomaiuolo, F., Bueti, D., … Doricchi, F. (2012). No inherent left and right side in human ‘mental number line’: Evidence from right brain damage. *Brain, 135*, 2492–2505.

Badets, A., & Pesenti, M. (2010). Creating number semantics through finger movement perception. *Cognition, 115*(1), 46–53.

Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences, 22*, 577–609.

Basso, M. A., Krauzlis, R. J., & Wurtz, R. H. (2000). Activation and inactivation of rostral superior colliculus neurons during smooth-pursuit eye movements in monkeys. *Journal of Neurophysiology, 84*, 892–908.

Berger, A., Henik, A., & Rafal, R. (2005). Competition between endogenous and exogenous orienting of visual attention. *Journal of Experimental Psychology: General, 134*, 207–221.

Blini, E., Cattaneo, Z., & Vallar, G. (2013). Different effects of numerical magnitude on visual and proprioceptive reference frames. *Frontiers in Psychology, 4*, 190.

Bonato, M., Priftis, K., Marenzi, R., & Zorzi, M. (2008). Modulation of hemispatial neglect by directional and numerical cues in the line bisection task. *Neuropsychologia, 46*, 426–433.

Bonato, M., Priftis, K., Marenzi, R., & Zorzi, M. (2009). Normal and impaired reflexive orienting of attention following central non-predictive cues. *Journal of Cognitive Neuroscience, 21*, 745–759.

Bremmer, F., Distler, C., & Hoffmann, K. P. (1997). Eye position effects in monkey cortex. II. Pursuit- and fixation-related activity in posterior parietal areas LIP and 7A. *Jouranl of Neurophysiology, 77*, 962–977.

Casarotti, M., Lisi, M., Umiltà, C., & Zorzi, M. (2012). Paying attention through eye movements: A computational investigation of the premotor theory of spatial attention. *Journal of Cognitive Neuroscience, 24*, 1519–1531.

Casarotti, M., Michielin, M., Zorzi, M., & Umiltà, C. (2007). Temporal order judgment reveals how number magnitude affects visuospatial attention. *Cognition, 102*(1), 101–117.

Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., … Shulman, G. L. (1998). A common network of functional areas for attention and eye movements. *Neuron, 21*, 761–773.

Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience, 3*, 292–297.

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: From environment to theory of mind. *Neuron, 58*, 306–324.

Corbetta, M., & Shulman, G. L. (2002). Control of goal directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3*, 201–215.

Cutini, S., Scarpa, F., Scatturin, P., Dell’Acqua, R., & Zorzi, M. (2014). Number-space interactions in the human parietal cortex: Enlightening the SNARC effect with functional near-infrared spectroscopy. Cerebral Cortex, 24(2), 444-451.

Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General, 122*, 371–396.

Di Luca, S., Pesenti, M., Vallar, G., & Girelli, L. (2013). Numbers reorient visuo-spatial attention during cancellation tasks. *Experimental Brain Research, 225*, 549–557.

Dodd, M. D., Van der Stigchel, S., Adil Leghari, M., Fung, G., & Kingstone, A. (2008). Attentional SNARC: There's something special about numbers (let us count the ways). *Cognition, 108*, 810–818.

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 7192–7197.

Fischer, M. H. (2001). Number processing induces spatial performance biases. *Neurology, 57*, 822–826.

Fischer, M. H., & Brugger, P. (2011). When digits help digits: Spatial–numerical associations point to finger counting as prime example of embodied cognition. *Frontiers in Psychology, 2*, 260.

Fischer, M. H., Castel, A. D., Dodd, M. D., & Pratt, J. (2003). Perceiving numbers causes spatial shifts of attention. *Nature Neuroscience, 6*, 555–556.

Fischer, M. H., Warlop, N., Hill, R. L., & Fias, W. (2004). Oculomotor bias induced by number perception. *Experimental Psychology, 51*, 91–97.

Galfano, G., Rusconi, E., & Umiltà, C. (2006). Number magnitude orients attention, but not against one's will. *Psychonomic Bulletin & Review, 13*, 869–874.

Gevers, W., Santens, S., Dhooge, E., Chen, Q., Van den Bossche, L., Fias, W., & Verguts, T. (2010). Verbal–spatial and visuospatial coding of number–space interactions. *Journal of Experimental Psychology: General, 139*, 180–190.

Göbel, S. M., Shaki, S., & Fischer, M. H. (2011). The cultural number line: A review of cultural and linguistic influences on the development of number processing. *Journal of Cross-Cultural Psychology, 42*, 543–565.

Grade, S., Lefèvre, N., & Pesenti, M. (2013). Influence of gaze observation on random number generation. *Experimental Psychology, 60*, 122–130.

Grant, E. R., & Spivey, M. J. (2003). Eye movements and problem solving guiding attention guides thought. *Psychological Science, 14*, 462–466.

Halligan, P. W., Fink, G. R., Marshall, J. C., & Vallar, G. (2003). Spatial cognition: Evidence from visual neglect. *Trends in Cognitive Sciences, 7*, 125–133.

Hartmann, M. (2015). Numbers in the eye of the beholder: What do eye movements reveal about numerical cognition? *Cognitive Processing, 1*, 245–248.

Hartmann, M., Mast, F. W., & Fischer, M. H. (2015). Spatial biases during mental arithmetic: Evidence from eye movements on a blank screen. *Frontiers in Psychology, 6*, 12.

Hartmann, M., Mast, F. W., & Fischer, M. H. (2015). Counting is a spatial process: Evidence from eye movements. *Psychological Research*. doi:10.1007/s00426-015-0722-5

Herrera, A., Macizo, P., & Semenza, C. (2008). The role of working memory in the association between number magnitude and space. *Acta Psychologica, 128*, 225–237.

Hubbard, E. M., Piazza, M., Pinel, P., & Dehaene, S. (2005). Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience, 6*, 435–448.

Kincade, J. M., Abrams, R. A., Astafiev, S. V., Shulman, G. L., & Corbetta, M. (2005). An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *The Journal of Neuroscience, 25*, 4593–4604.

Knops, A., Thirion, B., Hubbard, E. M., Michel, V., & Dehaene, S. (2009). Recruitment of an area involved in eye movements during mental arithmetic. *Science, 324*, 1583–1585.

Kramer, P., Stoianov, I., Umiltà, C., & Zorzi, M. (2011). Interactions between perceptual and numerical space. *Psychonomic Bulletin & Review, 18*, 722–728.

Krauzlis, R. J. (2004). Recasting the smooth pursuit eye movement system. *Journal of Neurophysiology, 91*(2), 591–603. doi:10.1152/jn.00801.2003.

Krauzlis, R. J., & Miles, F. A. (1996). Release of fixation for pursuit and saccades in humans: Evidence for shared inputs acting on different neural substrates. *Journal of Neurophysiology, 76*, 2822–2833.

Krauzlis, R. J., Zivotofsky, A. Z., & Miles, F. A. (1999). Target selection for pursuit and saccadic eye movements in humans. *Journal of Cognitive Neuroscience, 11*, 641–649.

Lisberger, S. G., Morris, E. J., & Tychsen, L. (1987). Visual motion processing and sensory-motor integration for smooth pursuit eye movements. *Annual Review of Neuroscience, 10*, 97–129.

Loetscher, T., Bockisch, C. J., & Brugger, P. (2008). Looking for the answer: The mind's eye in number space. *Neuroscience, 151*, 725–729.

Loetscher, T., Bockisch, C. J., Nicholls, M. E. R., & Brugger, P. (2010). Eye position predicts what number you have in mind. *Current Biology, 20*, R264–R265.

Masson, N., & Pesenti, M. (2014). Attentional bias induced by solving simple and complex addition and subtraction problems. Quarterly Journal of Experimental Psychology, 67 (8), 1514-1526.

Moore, T., Armstrong, K. M., & Fallah, M. (2003). Visuomotor origins of covert spatial attention. *Neuron, 40*, 671–683.

Moyer, R. S., & Landauer, T. K. (1967). Time required for judgements of numerical inequality. *Nature, 215*, 1519–1520.

Myachykov, A., Ellis, R., Cangelosi, A., & Fischer, M. H. (2016). Ocular drift along the mental number line. *Psychological Research*. doi:10.1007/s00426-015-0731-4

Nakayama, K., & Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research, 29*, 1631–1647.

Nicholls, M. E. R., Loftus, A. M., & Gevers, W. (2008). Look, no hands: A perceptual task shows that number magnitude induces shifts of attention. *Psychonomic Bulletin & Review, 15*, 413–418.

Pizzamiglio, L., Antonucci, G., Guariglia, C., Judica, A., Montenero, P., Razzano, C., & Zoccolotti, P. (1992). Cognitive rehabilitation of the hemineglect disorders in chronic patients with unilateral right brain damage. *Journal of Clinical and Experimental Neuropsychology, 14*, 901–923.

Pizzamiglio, L., Frasca, R., Guariglia, C., Incoccia, C., & Antonucci, G. (1990). Effect of optokinetic stimulation in patients with visual neglect. *Cortex, 26*, 535–541.

Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology, 32*, 2–25.

Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Reviews in Neuroscience, 13*, 25–42.

Priftis, K., Zorzi, M., Meneghello, F., Marenzi, R., & Umiltà, C. (2006). Explicit versus implicit processing of representational space in neglect: Dissociations in accessing the mental number line. *Journal of Cognitive Neuroscience, 18*, 680–688.

Prifts, K., Pitteri, M., Meneghello, F., Umiltà, C., & Zorzi, M. (2012). Optokinetic stimulation modulates neglect for the number space: Evidence from mental number interval bisection. *Frontiers in Human Neuroscience, 6*, 23.

Ranzini, M., Dehaene, S., Piazza, M., & Hubbard, E. M. (2009). Neural mechanisms of attentional shifts due to irrelevant spatial and numerical cues. *Neuropsychologia, 47*, 2615–2624.

Ranzini, M., Lisi, M., Blini, E. A., Pitteri, M., Treccani, B., Priftis, K., & Zorzi, M. (2015). Larger, smaller, odd or even? Task-specific effects of optokinetic stimulation on the mental number space. *Journal of Cognitive Psychology,* 27(4), 459–470.

Ranzini, M., Lugli, L., Anelli, F., Carbone, R., Nicoletti, R., & Borghi, A. M. (2011). Graspable objects shape number processing. *Frontiers in Human Neuroscience, 5*, 147.

Restle, F. (1970). Speed of adding and comparing numbers. *Journal of Experimental Psychology, 83*, 274–278.

Ristic, J., Wright, A., & Kingstone, A. (2006). The number line reflects top-down control. *Psychonomic Bulletin & Review, 13*(5), 862–868.

Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia, 25*(1), 31–40.

Ruiz Fernández, S., Rahona, J. J., Hervás, G., Vázquez, G., & Ulrich, R. (2011). Number magnitude determines gaze direction: Spatial–numerical association in a free-choice task. *Cortex, 5*, 617–620.

Schneider, E., Maruyama, M., Dehaene, S., & Sigman, M. (2012). Eye gaze reveals a fast, parallel extraction of the syntax of arithmetic formulas. *Cognition, 125*, 475–490.

Schwarz, W., & Keus, I. (2004). Moving the eyes along the mental number line: Comparing SNARC effects with manual and saccadic responses. *Perception and Psychophysics*, *66*, 651-664.

Shaki, S., Fischer, M. H., & Petrusic, W. M. (2009). Reading habits of both words and numbers contribute to the SNARC effect. *Psychonomic Bulletin & Review, 16*, 328–331.

Simon, O., Mangin, J.-F., Cohen, L., Le Bihan, D. D., & Dehaene, S. (2002). Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron, 33*, 475–487.

Spivey, M. J., & Geng, J. J. (2001). Oculomotor mechanisms activated by imagery and memory: Eye movements to absent objects. *Psychological Research, 65*(235), 241.

Stoianov, I., Kramer, P., Umiltà, C., & Zorzi, M. (2008). Visuospatial priming of the mental number line. *Cognition, 106*, 770–779.

Tanaka, M., & Lisberger, S. G. (2001). Regulation of the gain of visually guided smooth-pursuit eye movements by frontal cortex. *Nature, 409*, 191–194.

Tanaka, M., & Lisberger, S. G. (2002). Role of arcuate frontal cortex of monkeys in smooth pursuit eye movements. I. Basic response properties to retinal image motion and position. *Journal of Neurophysiology, 87*, 2684–2699.

Ulrich, R., & Miller, J. (1994). Effects of truncation on reaction time analysis. *Journal of Experimental Psychology: General, 123*, 34–80.

Umiltà, C., Priftis, K., & Zorzi, M. (2009). The spatial representation of numbers: Evidence from neglect and pseudoneglect. *Experimental Brain Research, 192*, 561–569.

Van Dijck, J.-P., Gevers, W., & Fias, W. (2009). Numbers are associated with different types of spatial information depending on the task. *Cognition, 113*, 248–253.

Van Dijck, J.-P., Gevers, W., Lafosse, C., & Fias, W. (2012). The heterogeneous nature of number–space interactions. *Frontiers in Human Neuroscience, 5*, 182.

Yu, X., Liu, J., Li, D., Cui, J., & Zhou, X. (2015). Dynamic mental number line in simple arithmetic. *Psychological Research*. doi:10.1007/s00426-015-0730-5.

Zorzi, M., Bonato, M., Treccani, B., Scalambrin, G., Marenzi, R., & Priftis, K. (2012). Neglect impairs explicit processing of the mental number line. *Frontiers in Human Neuroscience, 6*, 125.

Zorzi, M., Priftis, K., & Umiltà, C. (2002). Brain damage: Neglect disrupts the mental number line. *Nature, 417*, 138–139.