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THE TEMPORARY NATURE OF NUMBER-SPACE INTERACTIONS

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ABSTRACT

It is commonly accepted that the mental representation and processing of number and of space are tightly linked. This is evident from studies showing relations between math ability and visuospatial skill. Also, math instruction and education rely strongly on visuospatial tools and strategies. The dominant explanation for these number-space interactions is that the mental representation of numbers takes the form of a mental number line with numbers positioned in ascending order according to our reading habits. A long-standing debate is whether the link between numbers and space can be considered as evidence for a spatial number representation in long-term semantic memory, or whether this spatial frame is a temporary representation that emerges in working memory (WM) during task execution. Here we give an overview of our recent work that indicates that basic number processing tasks do not operate on a long-term spatial memory representation, but on a representation constructed in serial order WM, where the elements are spatially coded as a function of their ordinal position in the memorized sequence. Implications for a new theoretical framework linking serial order WM and basic number processing are discussed.

Keywords: Numbers, space, SNARC, bisection bias, attention, working memory

INTRODUCTION

It is commonly accepted that the mental representation and processing of number and of space are tightly linked. This is evident from introspective reports, for instance of mathematicians who describe their mathematical thinking to rely strongly on visuospatial imagery (e.g. the Physics Nobel Prize winner Dirac in Farmelo, 2009, or Einstein in Hadamard, 1954). Also mathematical instruction and education build strongly on instruments that require visuospatial processing. Importantly, the spatial aspect of number processing is not only something that is specific to the more complex forms of number processing, like mathematical thinking or problem solving. It also seems to be a core property of basic number representation that is automatically engaged in very simple numerical tasks. Initial reports of the close link between number and space processing already date back to Galton (1880a, 1880b) who described individuals who, when simply thinking about numbers, reported vivid experiences of numbers organized on a mental number line. Recently, more formal experimental settings have been adopted to investigate the link between number and space. Results obtained from these studies indeed suggest a line-like representation in most people. Three main empirical phenomena led to this conclusion: the SNARC effect, number interval bisection bias and number-based attentional cueing.

Dehaene, Bossini, and Giraux (1993) observed a systematic link between number magnitude and the ease with which a left or a right response was made. Participants were asked to perform a parity judgment tasks with left or right hand responses as a function of the odd-even status of the target number. It was observed that the responses to small numbers were faster with the left hand than with the right hand and vice versa for large numbers. This observation was dubbed the SNARC effect (an acronym for spatial-numerical association of response codes) and is considered as a reflection of the mental representation of numbers taking the form of a left-to-right oriented mental number line, with small numbers on the left and large numbers on the right. Within this framework, the compatibility of the spatial position of the target number on the line and the side of the response determines the reaction times of the responses. Ever since the original report, the SNARC effect has been reproduced numerous times with a variety of stimulus types, tasks and response modalities. A systematic overview is beyond the scope of the present article but good reviews can be found elsewhere (e.g. Fias & Fischer, 2005; van Dijck, Ginsburg, Girelli, & Gevers, 2015; Wood, Willmes, Nuerk, & Fischer, 2008). A few findings are interesting to mention at this point. First, the SNARC effect occurs not only for Arabic digits but

also for number words (Fias, 2001), suggesting that it originates from the activation of a general aspect of number magnitude. Second, it is not restricted to parity judgment but also occurs in other numerical tasks (like number comparison, e.g. Gevers, Verguts, Reynvoet, Caessens, & Fias, 2006) and even in tasks that do not require any processing of the number at all, for example when the numbers serve as a background for superimposed targets of which orientation has to be judged (Fias, Lauwereyns, & Lammertyn, 2001). This latter indicates a high degree of automaticity in the spatial coding. Third, the SNARC effect does not depend on a specific response setting as it has been observed not only with manual responses but also with other effectors, such as with oculomotor responses (Fischer, Warlop, Hill, & Fias, 2004). Finally, the direction of the SNARC effect is shaped by the reading direction of the tested subjects, as the association is reversed in people who speak and read a language with a right-to-left reading direction (Zebian, 2005).

Another important phenomenon that reflects number-space associations was discovered by Zorzi, Priftis and Umiltà (2002). They found that (hemi-) neglect patients, who after right brain damage have an impairment orienting attention to the left side of space, show a remarkable and systematic bias in number interval bisection. When asked to give (without calculation) the number that is in the middle between two other numbers, they show a systematic bias towards the larger number. For example, when asked to indicate the number in the middle between 1 and 9, neglect patients tend to answer 6 or 7, rather than the correct number 5. This bias is considered to be the result of the fact that these patients have difficulties in attending the left part of the mental number line and perform the bisection task on the remaining part that is attended. Importantly, the characteristics of the error pattern in this number interval bisection task largely overlap with the characteristics of the rightward bias observed in line bisection performance, a standard task administered to measure the spatial-attentional imbalance in neglect patients. The size of the bias increases with the size of the to-be-bisected interval together with a cross-over effect (i.e. a bias in the opposite direction) for very short intervals. Moreover, also neurologically intact individuals show a bisection bias when bisecting lines (Jewell & McCourt, 2000) thereby exhibiting a bias towards the left. The same type of pseudoneglect, as this phenomenon is called, has been found in healthy individuals when bisecting number intervals (Longo & Lourenco, 2007). These biases highlight the role of spatial attention when operating on the mental number line.

The involvement of spatial attention has been further demonstrated using a variant of the Posner cueing paradigm. In this paradigm a spatial cue is presented that directs attention to the left or the right. If a target is presented at a cued location, then target detection is facilitated. Fischer et al. (2003) designed a variant of this Posner cueing paradigm using small and large numbers as attentional cues. It was found that small number cues facilitated detection of a left target and that large number cues facilitated right target detection. This phenomenon of number-based attentional cueing is less robust and reliable than the original SNARC effect and the bisection bias. It has been proven hard to replicate (Zanolie & Pecher, 2014), but this might be related to the fact that it is after all not necessary or beneficial for the task to process the number cue. Using a different but related attentional paradigm Casarotti and colleagues (2007) showed that when the task imposed explicit number processing the attentional effects became more reliable. In addition, several studies indicate that the number-based attentional cueing effect might not be as automatic and obligatory as one would expect from the mental number line idea. For example, when asked to imagine numbers on a clock-face, number cues induces attentional shifts in accordance with the position of the number on the clock (Ristic, Wright, & Kingstone, 2006). Similarly, when providing the direct instruction to associate small numbers with right and large numbers with left, the number-based attentional cueing effect reverses as well (Galfano, Rusconi, & Umiltà, 2006).

Together, these three phenomena have reinforced the view that the mental representation of numerical magnitude takes the form of a mental number line on which numbers are organized from small to large according to our reading habits (from left to right in West-European languages). It is believed that this spatial location constitutes a part of the number's semantic meaning and that spatial attentional mechanisms are engaged to move back and forth along this mental number line when performing numerical tasks. The most pronounced version of the mental number line hypothesis claims that there is a functional isomorphism between number space and physical space, in the sense that there is a common metric for the representation of number and of physical space (Hubbard, Piazza, Pinel, & Dehaene, 2005; Priftis, Zorzi, Meneghello, Marenzi, & Umiltà, 2006; Umiltà, Priftis, & Zorzi, 2009). Similarly, it is assumed that the attentional system that operates on the number line is the same system than the one that operates in physical space (Zorzi et al., 2002).

In what follows we present data that challenge this mental number line hypothesis and we present working memory (WM) as a starting point for an alternative framework. For each of the three phenomena reviewed above, we will present evidence that questions some of the hallmark assumptions of the mental number line and we will discuss empirical findings that propose order in WM rather than numerical magnitude to be the determining factor underlying these number-space interactions.

THE SNARC EFFECT: DRIVEN BY SERIAL POSITION IN WORKING MEMORY

The mental number line is being conceived of as a long-term memory representation of number magnitude. Yet, a number of observations show that the SNARC effect is more flexible than one would expect from a long-term memory representation. First, the SNARC has been shown to be range-dependent (Dehaene et al., 1993; Fias, Brysbaert, Geypens, & d'Ydewalle, 1996). The numbers 4 and 5 receive faster right-hand than left-hand responses when they are presented in the context of numbers ranging from 0 to 5. Yet, when the numbers appear in the range of numbers from 4 to 9, the numbers 4 and 5 are now responded to preferentially with the left hand compared to the right hand. In contrast to the idea that the spatial code is a part of its semantic meaning, this observation shows that the association between a number and space depends on the context in which the number appears. Second, another strong indication that the link between numbers and space is highly flexible is the fact that the association is very sensitive to visual imagery. Bächtold et al. (1998) asked participants to imagine numbers as being positioned on a ruler or on a clock face while performing a number comparison task. A normal SNARC effect was observed in the ruler condition, but a reversed SNARC effect in the clock face condition, consistent with the number positions on the clock. Third, in bilinguals the SNARC effect is flexibly depending on reading direction of the language in which the instructions are given. Shaki and Fischer (2008) found that when Russian - Hebrew bilinguals had read a Russian text (which is read from left to right) just before the SNARC effect was measured, a normal SNARC effect was observed, but after having read a Hebrew text (which is read from right to left), the SNARC effect was reversed.

While none of the above observations on itself provide definitive arguments against the mental number line being the long-term memory representation of number magnitude, they

strongly suggest that spatial coding is not necessarily inherently associated to numerical magnitude but that it is constructed during task execution. This latter idea strongly suggests a crucial role of working memory (WM) in the interactions between numbers and space. To investigate the role of WM, a few studies embedded number tasks in dual task designs. For example, Lindemann and colleagues (2008) asked participants to memorize three Arabic digits describing an ascending, descending or random sequence and measured the SNARC effect during retention using parity judgment with the digits 1, 2, 8, and 9. The SNARC effect was significantly modulated by the coding direction in WM as a significant SNARC effect was only observed in the ascending condition. The role of WM for the SNARC effect was further investigated with secondary tasks that loaded specific components of WM. Herrera, Macizo, and Semenza (2008) found that a visuospatial WM load abolished the SNARC effect in a number comparison task. Van Dijck, Gevers and Fias (2009) further extended this and investigated the SNARC effect both in number comparison and in parity judgment under visuospatial as well as verbal WM load. It was found that the parity judgment SNARC effect was abolished by a verbal WM load while in number comparison the SNARC effect disappeared under a visuospatial WM load. These results clearly confirm the necessity of having WM resources available for the SNARC effect to occur. Yet on itself, this does not explain what role is played by WM.

A plausible hypothesis is that serial position in WM rather than number magnitude is associated with space. After all, the capacity to order information is a crucial characteristic of WM (e.g. Marshuetz, 2005). Moreover, the SNARC effect has been established not only with numbers but also with other types of ordinal information, like alphabet position or days of the week (Gevers, Reynvoet, & Fias, 2003). In addition, it has been shown that number processing and WM order use common neural resources (Attout, Fias, Salmon, & Majerus, 2014; Marshuetz, Reuter-Lorenz, Smith, Jonides, & Noll, 2006). Spatial coding of serial position in WM can explain the SNARC effect, if one makes the additional assumption that WM is invoked, even during simple number tasks, to temporarily store stimuli and response as part of a task set to optimize task performance (Monsell, 2003). Then, storing numbers in WM as a function of magnitude would be a useful means to overcome the limited capacity of WM.

To test the hypothesis that the SNARC effect is driven by serial position in WM rather than by number magnitude, van Dijck and Fias (2011) designed the following experiment.

Participants had to keep a series of numbers in WM. The numbers were presented in (pseudo) random order, e.g. 5-3-8-6-2. During retention, subjects were presented with numbers in the context of a parity judgment task and to ensure WM consultation, they only had to respond if the number belonged to the WM sequence. Care was taken that over the experiment, the number's magnitude and the serial position in WM was orthogonal. In this way it was possible to disentangle the link between position in WM and space versus number magnitude and space. After the retention interval, the accuracy of the WM content was verified with the request to indicate within a couple of sequences the one of which the order of the elements corresponded to the sequence in WM. It turned out that serial position in WM determined the speed with which the left and the right responses were emitted: Numbers from the beginning of the sequence being responded to faster with the left hand than with the right hand, and numbers from the end of the sequence receiving faster right-than-left hand responses. This occurred irrespective of number magnitude which was not associated with the side of response. Next, van Dijck and Fias (2011) reasoned that, given that spatial coding of position in WM is the determinant of the SNARC effect, it should be possible to elicit SNARC effects with whatever information that is serially stored in WM. To test this hypothesis, the experiment was repeated, but rather than having to remember numbers, participants had to remember fruit and vegetable names. During retention, participants were asked to perform a fruit-vegetable classification task by giving left/ right responses. Again, an association between serial position in WM and space was observed. Interestingly, the same subjects were submitted to a classical SNARC measurement using parity judgment. Remarkably, the ordinal position effect correlated significantly with the parity judgment SNARC effect, suggesting that it is indeed the spatial coding of serial WM position that drives the SNARC effect.

These studies clearly show that it are the temporary position-space associations that drive the SNARC effect, rather than the long-term number line representation to which the SNARC effect is traditionally ascribed. Assuming that even while performing simple classification tasks on number (like parity judgment or number comparison), participants encode the numbers that are used in the experiment in WM as part of the task-set that stores stimuli and responses to facilitate efficient task execution (Monsell, 2003) and that they spontaneously make use of the inherent ordinal structure of the number system and systematically map numbers to the temporary task-set store as a function of numerical magnitude, this provides a unitary

explanation for a whole variety of SNARC phenomena that have been reported. First, the dilution of the SNARC effect under WM load (Herrera et al., 2008; van Dijck et al., 2009) naturally follows. Second, the fact that the SNARC effect has been observed when number magnitude is irrelevant for the task (e.g. phoneme monitoring, Fias et al., 1996) is a consequence of the fact that number magnitude is useful to order stimuli and responses in WM as part of the task set to optimize performance. Third, the fact that only the numbers that are currently used for the task are stored in WM explains the range-dependency of the SNARC effect (Dehaene et al., 1993; Fias et al., 1996). Fourth, since WM is subserved by verbal and by visuospatial routines (the phonological loop and the visuospatial sketch-pad), the link to space can be determined by serial position in the verbal sequence but also by position in the visual layout as when imagining numbers on a clock face (Bachtold et al., 1998). Fifth, the rapid changes of direction of the SNARC effect as a function of reading direction are compatible with the intrinsic flexibility of the WM account, although the precise nature of the impact of reading direction needs to be determined. Finally, the fact that SNARC effects also occurs with non-numerical ordinal information, like letters, days of the week, etc. (Gevers et al., 2003; Previtali, de Hevia, & Girelli, 2010; Van Opstal, Fias, Peigneux, & Verguts, 2009) does not come as a surprise as any type of ordinal structure can be used to systematically organize information in WM to overcome its capacity limits.

BISECTION BIAS IN NEGLECT: A ROLE FOR WORKING MEMORY

The bias that characterizes performance of neglect patients when bisecting physical lines and number intervals has been taken as strong evidence for the fact that number space is encoded in a way that is isomorphic to physical space and that the same systems for orienting spatial attention are operating on it (Zorzi et al., 2002). However, this reasoning is only valid if it can be shown that the bisection bias in the two tasks is correlated. By now several studies have reported that there is no correlation (e.g. Aiello et al., 2012; Ashkenazi & Henik, 2010). Of course null findings are hard to interpret. However there is one convincing study that reported a double dissociation between the biases observed in both tasks, as a function of the location of the brain lesion. Doricchi et al. (2005) found that patients with posterior lesions (suffering from neglect and hemianopia) show a bias in line bisection but not in number interval bisection, whereas patients with lesions extending more anteriorly comprising frontal areas (suffering from neglect

in the absence of hemianopia) show bias in number interval bisection but not in line bisection. These observations suggest that different cognitive mechanisms are underlying both tasks. Interestingly, these latter patients also showed a reduced visuospatial working memory (WM) span. Yet, at this point it is hard to tell what the role of WM could be. A reduced WM capacity can explain bad performance in number interval bisection in general, but by itself it does not account for a systematic bias towards larger numbers.

Whereas most cases of neglect occur after right hemisphere damage accompanied with inattention of the left side of space, we had the opportunity to test a patient with a left hemispheric lesion, that neglected the right side of physical space as reflected in her line bisection performance showing a bias to the left (van Dijck, Gevers, Lafosse, Doricchi, & Fias, 2011). Also in representational space, the performance on the patient showed inattention to the right side of representational space (like her living room, geographic maps etc; van Dijck, Gevers, Lafosse, & Fias, 2013). From the mental number line hypothesis, we expected a bias towards smaller numbers in a number interval bisection task, but that was not the case. The patient showed a systematic bias and produced numbers that were larger than the actual midpoint, thereby mimicking performance of patients with the opposite (right hemisphere) lesion site. The patient also exhibited a normal SNARC effect with smaller numbers associated with left and large number with right. This excludes an account in terms of a reversed mental number line, with small numbers on the right and large numbers on the left. Altogether, these results clearly indicate a strong dissociation between physical space and number space within the same subject.

Based on Doricchi et al. (2005) we investigated her WM capacity. The patient exhibited a normal visuospatial WM span (5 items) but a reduced verbal WM span (3 items vs 5 items in healthy controls). Again, a reduced span does not explain the systematic bias in number interval bisection. We thought that the search for position-specific problems in WM could be more revealing and decided to investigate whether the patient was more impaired with initial items of a sequence compared to items towards the end of the verbal WM sequence. That is exactly what we observed, both in recognition and production tasks. The same tasks with visuospatial WM did not reveal any performance differences across WM positions. Altogether, this single case study shows that a bias towards larger numbers in a number interval bisection task can dissociate from

the bisection bias in physical line bisection, making the hypothesis of a functional isomorphism between number and physical space hard to maintain. The results also show that the bias is associated to a positional deficit in verbal WM, thus urging one to consider serial position in WM as a potential determinant of number interval bisection bias. Again this emphasizes that the number-space association as reflected in the biased number interval bisection of neglect patients is less determined by long-term representations but has a strong temporary component. Given that we are dealing with a single case (that is atypical in the sense of her language abilities being largely unaffected despite the left hemisphere damage), one should not generalize and conclude that verbal WM performance is the driving factor behind all patients that show a number interval bisection bias. In fact, a recent multiple case study shows that indeed the number interval bisection bias is not determined by a unique underlying deficit (Storer & Demeyere, 2014). Yet, our single case study makes it worthwhile to evaluate serial position working memory performance in future studies investigating number interval bisection performance in neglect patients.

THE NUMBER-BASED ATTENTIONAL CUEING EFFECT OPERATES ON WORKING MEMORY

Given that the spatial coding of numbers may for a large part be mediated by serial position in working memory (WM), as demonstrated by the SNARC effect and the number interval bisection bias in neglect, one can also wonder to what extent the attentional cueing effect with numbers originates from the same spatial coding system. To test this, van Dijck et al. (2013) embedded the attentional cueing paradigm, as originally developed by Fischer et al. (2003) in a WM context. Participants received a sequence of random numbers, which they had to keep in WM in the order of presentation. During the retention interval they performed a dot detection task, with the appearance of a dot to be signaled with a unimanual central key press irrespective of the dot appearing on the left or on the right. Importantly, the dot detection task only had to be performed if a number cue, that was presented shortly before the dot appeared, belonged to the memorized set. In case the number cue did not belong to the set, no response had to be given. After the retention interval, the accuracy of the WM content was verified by a number of yes/no questions that asked whether one number came before the other in the memorized sequence. It was found that the speed with which a dot was detected depended on the congruency between the

position of the cue in the WM sequence and the side of the dot on the screen. Specifically, the further the cue was located in the sequence, the faster a dot on the right was detected compared to the detection of a dot on the left. No effect of digit magnitude was observed. The same pattern of results was observed with a verbal response, saying “yes” when a dot was detected, indicating that the effect does not have anything to do with the lateralization of the motor response. Together, these results suggest that number cues do not induce automatic shifts of spatial attention, but that it is the temporary organization of information at distinct serial positions in WM that drives the effect. Thus, only when serial position is actively engaged, number-based attentional cueing is to be expected.

In a follow-up study, van Dijck et al. (2014) put this hypothesis to an explicit test. In a first experiment, the importance of serial order processing in WM was minimized. This was done as follows. Participants performed the traditional version of the paradigm as developed by Fischer et al. (2003), except for the fact that subjects were occasionally requested to write down the number cue they had last seen. This latter manipulation was included to force the participants to memorize only the last item with no need to process serial order. Although it was made sure that enough participants were tested to have sufficient statistical power and indications were present that the magnitude of the number cues was effectively processed, no attentional cueing was observed. The same participants were also tested for the presence of a classic parity judgment SNARC effect. The fact that they showed a clear SNARC effect refutes the possibility that the absence of an attentional cueing effect was due to the fact that the group of participants did not show any evidence of spatial coding at all. In a subsequent experiment the WM-based paradigm of van Dijck et al. (2013) was administered again, but this time with a broader range of cue-target intervals, to make sure that the failure to find a cueing effect as a function of number magnitude was not due to the use of an inappropriate time window to give the magnitude-based cueing a fair chance to occur. Again, it was found that number cues from the beginning of the sequence induced attention shifts to the left and number cues from the end of the sequence to the right, yet, there were no signs of number magnitude to systematically impact the orientation of attention. Finally, in a third experiment, the following hypothesis was tested: If it is indeed serial position in WM that is crucial for the cueing effects to occur rather than the long-term mental number line, then there is no reason why the attentional cueing effect would be restricted to numbers and the same effects are expected to occur with other materials as well. In line with this

hypothesis, a robust attentional cueing effect with letters from the alphabet was observed, as a function of their position in WM and irrespective of the alphabetic position.

Taken together, these results clearly show that a robust attentional modulation with WM cues can be obtained when the cues are part of a sequence serially stored in WM. As in a typical number-based attentional cueing task the number cues are not task relevant, the WM account offers a parsimonious explanation why the number-based attentional cueing effect is so difficult to replicate (e.g. Zanolie & Pecher, 2014). After all in such context, numbers are not part of the task-set, and therefore not every subject will spontaneously memorize and order this information in WM. Additionally, the WM account has the potential to offer a coherent framework for earlier observations in the literature on number-based attentional cueing. For example, while mapping small numbers to the beginning and large numbers to the end of the memorized sequence may be the default association, this can be easily changed by the instructions given to the participants (e.g. the request to imagine the numbers as hours on a clock-face, Ristic et al., 2006; or to associate small numbers with a right location and large numbers with a left one, Galfano, et al., 2006). Again, whereas the mental number line account has difficulties to explain these findings, the flexible nature of WM can easily account for these observations.

DISCUSSION AND CONCLUSIONS

Based on the work reviewed above, it is clear that a long-term memory representation of number magnitude that takes the form of a mental number line is not necessarily a valid theoretical proposal to account for the temporary nature of the associations between number and space. Instead, there are clear indications that what is crucial for numbers to be linked to space is the fact that serial position in WM is coded in spatial terms.

The fact that number, spatial attention and WM are tightly interwoven might also be a reflection that they recruit overlapping brain areas. Indeed, brain imaging studies have proposed the intraparietal sulcus to be crucial for number processing (e.g. Dehaene, Piazza, Pinel, & Cohen, 2003), for spatial processing (e.g. Corbetta & Shulman, 2002) and for serial order processing in WM (Majerus et al., 2010). Of course, the fact that common brain regions are involved, might be suggestive but can by itself not be considered to be conclusive. One and the same brain region, which typically hosts millions of neurons, may support different cognitive

functions (e.g. Zorzi, Di Bono, & Fias, 2011). Hence, explicit testing for the involvement of shared neural circuitry is necessary.

Considerable progress has been made in this respect, although this work did not take the spatial coding as a starting point but rather focused on the distance effect. Interestingly, the distance effect, which is a very strong and robust characteristic of the processing of numerical magnitudes (and is often also taken as another indication of a mental number line representation; Moyer & Landauer, 1967), also characterizes performance in WM tasks that address order. When two numbers have to be compared in terms of their magnitude (which is the larger number) the ease of the comparison process depends on the distance between the two numbers, with larger distance being easier than smaller distances. Similarly, the closer two items are in WM, the more difficult it is to tell which of the two items is positioned before or after the other (e.g. Marshuetz, Smith, Jonides, DeGutis, & Chenevert, 2000). A number of fMRI studies have shown that activity in the intraparietal sulcus is modulated by numerical distance, in comparison tasks (Pinel, Dehaene, Riviere, & LeBihan, 2001) but also with other paradigms like priming and adaptation (Piazza, Pinel, Le Bihan, & Dehaene, 2007). Also for WM the distance effect has been shown to activate the intraparietal sulcus in regions similar to the ones activated with numbers (e.g. Marshuetz et al., 2006). In a recent study, Attout et al. (2014) directly compared the distance effect in number comparison and in a WM order task and were able to explicitly demonstrate the overlap in the same subjects.

Hence, in addition to the behavioral evidence reported above, also brain imaging studies strongly suggest that the neural circuitry that is used in number processing is strongly related to the processing of serial order in WM. At this point, however, it is not known which processing components are subserved by this shared neural machinery. There are a few plausible possibilities to be considered. First, it is possible that somehow numbers are used to provide the serial position code of WM. This can be done in a more or less explicit way as when using counting to keep track of items in WM (Ebenholtz, 1963). Another possibility is that it is not so much the act of counting or the number series that is important, but that it is the representational characteristics of the number-coding neural system itself that are important. Botvinick and Watanabe (2007) showed that a computational model of WM in which ordinal rank was coded with the same properties as number-selective neurons (as they have been described in the brain

of macaque monkeys; e.g. Nieder, 2005) is able to predict the details of serial position effects in WM. Second, it is also meaningful to consider the possibility that a number is not processed in isolation but always in the context of other numbers, whereby WM provides this context. By placing numbers in WM together with other numbers and by doing this in a systematic way, numbers may acquire their functional meaning. A straightforward prediction of this idea is that number processing is to a large extent context dependent. And that is exactly what has been observed with the SNARC effect, as reported above.

An important question is to what extent the configuration of the relatively basic cognitive components of serial order WM, spatial coding and attentional orienting are a determining factor of mathematical skill. Bachot et al. (2005) found that children (aged 7 to 12) with a small visuospatial WM capacity and poor performance on number concept (e.g. 12 is 9 apples more than?) and complex addition tasks ($26+63=$) also exhibited a reduced SNARC effect in a number comparison task, compared to a matched control group. However, recent evidence obtained in adults suggests the opposite relationship: smaller parity judgment SNARC effects were observed in math-proficient participants, with no mediating effect of visuospatial WM capacity (Hoffmann, Mussolin, Martin, & Schiltz, 2014). This was attributed to the fact that those proficient in math are more efficient in inhibiting the magnitude information which is irrelevant in a parity judgment task. Why it is that the two studies come to different conclusions is far from clear. Is there an initial link in childhood which later disappears? Or is there a difference between the parity judgment and the comparison SNARC effect? Additional research is needed to solve these issues and establish the link between number-space associations and mathematical skill. Given the abundant evidence that WM is of crucial importance for the number-space interactions to occur, we recommend considering serial position coding in WM as an important explanatory factor. So far, we focused on the most frequently investigated signatures of number-space interactions. Yet, there are other phenomena that express spatial-numerical associations (see for instance Fischer and Brugger (2011) or Fischer and Shaki (2014) for overviews). In the absence of empirical testing it is hard to tell whether or not serial position in WM is the determining factor in these cases as well. Investigating the generality of the serial position account is an important future step. At the same time a better description and understanding of the role of spatial processing in more complex forms of number processing, i.e. mental arithmetic and

mathematical reasoning, is an avenue for future progress. Considering serial position in WM as a contributing factor might be beneficial for this endeavour.

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