cortex 83 (2016) 271–279

Available online at www.sciencedirect.com

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Research report

Early blindness alters the spatial organization of verbal working memory

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ARTICLE INFO

Article history:
Received 6 June 2016
Reviewed 12 July 2016
Revised 6 August 2016
Accepted 11 August 2016
Action editor Asaf Gilboa
Published online 26 August 2016

Keywords:
Working memory
Space
Blindness
Ordinal position effect
Analogical mind

ABSTRACT

Several studies suggest that serial order in working memory (WM) is grounded on space. For a list of ordered items held in WM, items at the beginning of the list are associated with the left side of space and items at the end of the list with the right side. This suggests that maintaining items in verbal WM is performed in strong analogy to writing these items down on a physical whiteboard for later consultation (The Mental Whiteboard Hypothesis). What drives this spatial mapping of ordered series in WM remains poorly understood. In the present study we tested whether visual experience is instrumental in establishing the link between serial order in WM and spatial processing. We tested early blind (EB), late blind (LB) and sighted individuals in an auditory WM task. Replicating previous studies, left-key responses were faster for early items in the list whereas later items facilitated right-key responses in the sighted group. The same effect was observed in LB individuals. In contrast, EB participants did not show any association between space and serial position in WM. These results suggest that early visual experience plays a critical role in linking ordered items in WM and spatial representations. The analogical spatial structure of WM may depend in part on the actual experience of using spatially organized devices (e.g., notes, whiteboards) to offload WM. These practices are largely precluded to EB individuals, who instead rely to mnemonic devices that are less spatially organized (e.g., recordings, vocal notes). The way we habitually organize information in the external world may bias the way we organize information in our WM.

1. Introduction

The ability to maintain ordered items in verbal working memory (WM) is crucial in many aspects of our everyday life, from remembering a phone number to understanding complex sentences. Several studies suggest that this cognitive ability is grounded in space (Ginsburg, van Dijck, Previtali, Fias, & Gevers, 2014; van Dijck & Fias, 2011; van Dijck, Abrahamse, Majerus, & Fias, 2013). When people are asked to hold a sequence of items (e.g., words, numbers) in verbal WM they spontaneously associate items at the beginning of the list with the left side of space, and items at the end of the

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http://dx.doi.org/10.1016/j.cortex.2016.08.007

list with the right side (van Dijck & Fias, 2011; van Dijck et al., 2013). Therefore, sequences in WM appear to be represented in a spatial medium (Jaynes, 1976; Oberauer, 2009) and item retrieval is performed through spatial-attentional mechanisms analogous to the mechanisms that allow to allocate attention on physical objects in the real world (Abrahamse, van Dijck, Majerus, & Fias, 2014; Rinaldi, Brugger, Bockisch, Bertolini, & Girelli, 2015). What drives the spatial mapping of ordered series in WM remains however poorly understood.

For instance, it is still an open question whether experiential factors can determine, or at least shape, the spatial structure of verbal WM. That is, although a general predisposition to rely on spatial-attentional mechanisms to organize mental representations may be innate, as suggested by studies with non-human primates (Adachi, 2014; Drucker & Brannon, 2014), the way we use space to organize memory loads may also be shaped by our sensorimotor and cultural experience. Indeed, some degree of experiential relativity should be expected if we consider the spatial structure of WM in the context of how space is used to scaffold other cognitive domains (Casasanto & Bottini, 2014b; Casasanto, 2011).

Not only verbal WM, but several other cognitive domains seems to be spatially organized, including numbers (Dehaene, Bossini, & Giraux, 1993), time (Casasanto & Boroditsky, 2008; Santiago, Lupiáñez, Pérez, & Funes, 2007), valence (Casasanto, 2009), pitch (Rusconi, Kwan, Giordano, Umiltà, & Butterworth, 2006), episodic memory (Miles, Nind, & Macrae, 2010), levels of conceptual construal (Slepian, Masicampo, & Ambady, 2015), orthography (Caramazza & Hillis, 1990), coherence (von Hecker, Hahn & Rollings, 2016) similarity (Casasanto, 2008), etc. Yet, the organizational details of these *cognitive maps* (Tolman, 1948) may vary across individuals (according to experiential factors, such as culture or sensorimotor experience), and also across cognitive domains.

For example, both time and numbers are mapped on a lateral mental line. Along the mental number line (MNL), lower digits are associated with the left side of space and higher digits with the right side (Dehaene et al., 1993). The same arrangement occurs for past and future events, respectively (mental time line – MTL; Santiago et al., 2007). A classic test of this assumption consists in classification tasks with response codes that are either congruent or incongruent with the MTL/MNL. For instance, in what it is called the Spatial Numerical Association of Response Code (SNARC) effect (Dehaene et al., 1993), participants are faster in classifying lower digits with a left response key and higher digits with a right response key. Yet, several other paradigms has been developed to test these cognitive maps, and evidence for their psychological reality comes from the disruption of these mental lines in neglect patients (Saj, Fuhrman, Vuilleumier, & Boroditsky, 2013) to their spontaneous use in eye movement (Loetscher, Bockisch, Nicholls, & Brugger, 2010) and co-speech gestures (Casasanto & Jasmin, 2012). Interestingly, the direction, orientation and reference frame of these mental lines varies on the basis of cultural and sensorimotor experience (Casasanto & Bottini, 2014b), and different cognitive maps seem to be modulated by different experiential factors. More precisely, the spatial organization of different cognitive domains seems to vary in analogy with behaviors that are specifically relevant for each given cognitive domain.

For instance, the spatial mapping of time seems to be tightly linked with our experience of reading and writing (Casasanto & Bottini, 2014a). Events unfold rightward along the MTL in people who habitually read from left to right, and leftward in people who read from right to left (e.g., Israeli Hebrew-speakers; Fuhrman & Boroditsky, 2010; Ouellet, Santiago, Israeli, & Gabay, 2010). Consistently, a training experiment demonstrated a causal role for reading experience in determining the direction of spatial-temporal associations. Exposing people who usually read from left to right to mirror-reversed orthography reversed the direction of their MTLs (Casasanto & Bottini, 2014a). Reading seems to constitute a relevant experiential source to establish the connection between space and time: during reading earlier time points become implicitly associated with one side of space and later time points with the other side (Casasanto & Bottini, 2014b; Fuhrman & Boroditsky, 2010).

Interestingly, orthographical experience seems to be less important in establishing and modulating the MNL. The correlations between reading experience and MNL direction across cultures is less tight compared to the MTL (Rinaldi, Di Luca, Henik, & Girelli, 2016; Shaki & Gevers, 2011), and early attempts to change the direction of the MNL by mirror reading did not succeed (Dehaene et al., 1993). Consistently, a direct comparison of the effect of mirror-reading training on the two cognitive maps showed greater modulation for the MTL compared to the MNL (with the latter being unaffected by mirror reading training; Pitt & Casasanto, 2016). On the contrary, the MNL seems to be more associated with anatomical space, precisely the hands and correlated behavior. Indeed crossing hands reduces (Crollen, Dormal, Seron, Lepore, & Collignon, 2013), nullify (Wood, Nuerk, & Willmes, 2006) or even reverses (Müller & Schwarz, 2007) the SNARC effect, suggesting that the relationship between number and space is based both onto an anatomical and an external frame of reference, although the external usually dominates (Müller & Schwarz, 2007). Consistently with the spatio-anatomical component of the MNL, hand-related behaviors, such as finger-counting or finger-tapping training, modulate the direction of spatial-numerical associations whereas reading direction does not (Pitt & Casasanto, 2016).

In keeping with this picture, visual experience seems to have a different impact on the organization of temporal and numerical cognitive maps (Bottini, Crepaldi, Casasanto, Crollen, & Collignon, 2015; Crollen et al., 2013). For instance, it has been shown that crossing hands only slightly reduced the SNARC effect in sighted people whereas it reversed it in early blinds (EBs), suggesting a prevalent anatomical space-number mapping in the EB whereas sighted people rely more on an external coordinate system to map numbers onto space (Crollen et al., 2013). On the other hand, the MTL is grounded onto external coordinates both in sighted and blind (Bottini et al., 2015). This organization is coherent with the perceptual and behavioral basis of the MTL: reading experience. In reading braille text (which is conventionally written from left to right) the hand moves rightward across the page following the direction of the orthography. Thus blind people have reading experience that is similar to visual reading in the aspects that are believed to be relevant for establishing a MTL: Later timepoints are associated with rightward positions in external space, independently of the hand used to read (i.e., hand-specific spationanatomical aspects are not relevant for space-time mapping).

In this study we tested the role of visual experience in establishing the spatial mapping of verbal WM. According to evidence outlined above, whether or not visual experience should have an impact on the spatial structure of WM may depend on the analogical-behavioral basis of this mapping. Does the spatial organization of verbal WM have an analog in the physical-behavioral world? A suggestion may come from what has been called the Mental Whiteboard Hypothesis (Abrahamse et al., 2014), according to which the maintenance of ordered series in WM is performed in strong analogy to writing these items down on a physical whiteboard for later consultation. Here, we hypothesize that the analogical spatial structure of WM may depend in part from the actual experience of using spatially organized devices such as notes, whiteboards, etc. to offload WM in the everyday life. These practices are largely precluded to blind individuals, who instead rely to mnemonic devices that are less spatially organized (e.g., recordings, vocal notes). If this is the case, blind individuals may show a reduced spatialization of verbal WM.

We tested sighted, EB and LB participants in a WM task in which they had to memorize a series of items while classifying these items using two keys located in front of them on the left and the right side of space. If the spatial organization of verbal WM emerges independently from our everyday experience of externalizing WM loads in a spatially-organized way, an Ordinal Position Effect (from here, OPE) is predicted in both sighted and blind: Items at the beginning of the list should be categorized faster with the left key, whereas later items should facilitate right-key responses. Alternatively, if the access to spatially organized devices for relieving WM load provides the analogical basis for a spatially organized WM, blind participants (who have limited access to these devices) should show a reduced OPE effect. In our experiments participants accomplished the task both with parallel and crossed hands. This manipulation was introduced to test whether the OPE effect is grounded in external or anatomical spatial coordinates, both in sighted and blind. Additionally, we tested both early and late blind (LB) in order to determine whether the impact of blindness emerges only when vision is lost early in life or even when it is lost later on.

2. Method

2.1. Participants

Forty-four participants completed the experiment in exchange for payment. 14 early blind (EB; people in this group lost sight at birth or before 3 years of age, do not have visual memories and never used vision functionally), 15 late blind (LB; people in this group lost sight as adults or after 3 years of age, have visual memories and relied on vision functionally), and 15 sighted controls. All participants were Italian native speakers and were blindfolded during the tasks. The three groups did not statistically differ in terms of age (all p-values > .05). Participants in both blind groups were totally blind or had only rudimentary sensitivity for brightness differences. In all cases, blindness was attributed to peripheral deficits with no additional neurological problems. The ethical committee of the University of Trento approved this study and all participants were naive with respect to the purpose of the experiment.

2.2. Materials and procedure

Participants were asked to remember and classify orally presented Italian words referring either to fruits or vegetables. Fruits were: 'kiwi' (kiwi), 'mela' (apple), 'mora' (blackberry), 'pesca' (peach), 'uva' (grape). Vegetables were: 'aglio' (garlic), 'porro' (leek), 'rapa' (turnip), 'verza' (savoy cabbage), 'zucca' (pumpkin). All stimuli lasted 650 ms, had identical auditory properties (44,100 Hz, 16 bits, stereo), and were played through loudspeakers placed in front of the participant.

The experiment consisted of 32 blocks. Each block was divided in three different phases: an encoding phase, a classification phase and a control phase (see Fig. 1). During the encoding phase participants heard a list of five words, all referring to fruits and vegetables. They heard the list twice and they were asked to keep it in mind, in the correct order, during the entire block. At the beginning of this phase an acoustic signal indicated that the block began. After two seconds the list was played. Within the list, each word was played after two seconds from the onset of the previous word (ISI = 1350 msec). Then, another acoustic signal indicated the beginning of the second repetition of the list. Afterwards a pause of two and a half seconds was given to allow rehearsal before the start of the classification phase. The elements in each list were selected randomly, with the only constraint that a word could not appear more than once in every given sequence (see Supplementary information for a test *a posteriori* of the equal distribution of items in each of the 5 list positions).

During the classification phase all the 10 words were presented twice, one after the other, in pseudo-randomized order, avoiding that the same word was repeated twice in a row. For each trial participants had to decide whether the word was among the five words they were keeping in mind, and, if yes, they had to classify the item as fruit or vegetable. They did so by pressing one of two response keys placed 30 cm in front of each participant's body and 20 cm away from the body midline in the left and right hemi-spaces (see Fig. 2). If the word was not included in the memorized sequence, they had to ignore it and wait for the following trial (Go-Nogo task). The response code (e.g., left key–fruit and right key–vegetables, or vice-versa) was counterbalanced across subjects. Moreover, participants were asked to perform the task either with their hands in a uncrossed posture or with their arms crossed over the body midline so that the left hand was on the right response key and the right hand was on the left response key.

In the control phase participants heard the same five words they heard at the beginning of the block and they had to decide whether the words were presented in the same order, or not. In this second case the difference was quite subtle: at a random location, the order between two adjacent words was changed. The experiment consisted of a total of 32 blocks,

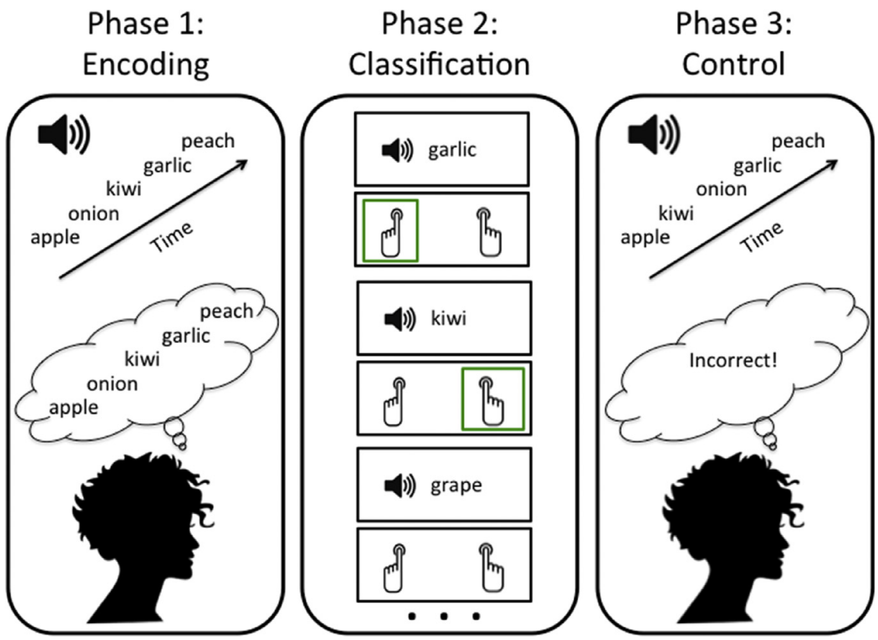

Fig. 1 – Task design. Each experimental block consisted of three phases. (1) During the Encoding phase participants memorized the word sequence; (2) During the Classification phase all words were played in pseudorandomized order and participants classified (as fruit or vegetables) only words that were included in the memorized sequence (Go-Nogo task); (3) During the Control phase participants listen again to the same words they heard in phase 1 and guessed whether they were presented in the same order.

performed in two sessions, one in the uncrossed posture and one in the crossed posture. The order of sessions was counterbalanced across participants. In each session they took a pause of two minutes after the 8th block.

In order to encourage an accurate performance, if participants responded incorrectly in the control phase of a given block, they had to repeat the block at the end of the session.

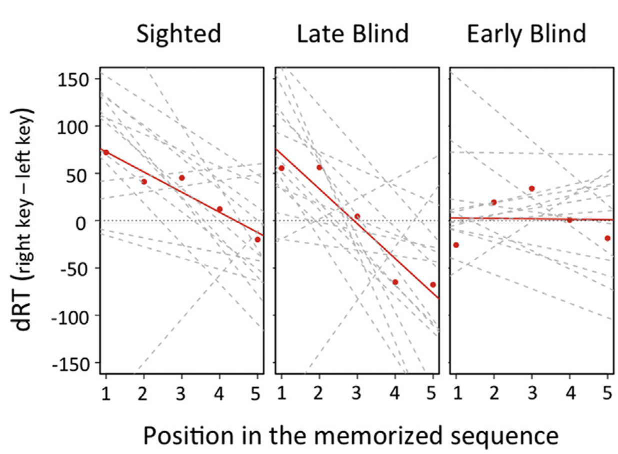

Fig. 2 – Ordinal Position Effect. dRT is calculated subtracting Left Key RTs from Right Key RTs. A positive value of dRT indicates faster left-key responses, a negative value indicates faster right-key responses. The continuous line indicate the overall OPE regression, dashed lines indicates the OPE for each participant.

3. Results

3.1. *Reaction time analysis*

Incorrect blocks (those that received a wrong response in the Test Phase) and incorrect trials during the classification phase were excluded from the analysis (van Dijck & Fias, 2011; Ginsburg et al., 2014). Finally, also no-go trials (in which participants did not have to respond) were excluded. RTs longer than 2.5 SD from the individual mean (separately for the crossed and uncrossed condition) were excluded. This led to the exclusion of 2% of the correct trials for SC, 2% for EB and 2% for LB.

Average RTs (log transformed) were computed for each condition and in each participant and subjected to a $2 \times 5 \times 2$ repeated measures ANOVA with Posture (uncross, cross), Position in the sequence (1–5) and Response Side (left *vs* right) as within subject variables.

Analysis of the results of sighted participants (Fig. 2, left panel) showed a main effect of Position [$F(4, 56) = 7.47$, $p < .001$], and a marginal effect of Response Side [Left-key responses tended to be faster; $F(1, 14) = 3.52$, $p = .08$]. We also found a significant Position by Response Side interaction [$F(4, 56) = 3.13$, $p = .02$] indicating a Ordinal Position Effect: Items at the beginning of the sequence were classified faster with the left hand and items at the end of the sequence with the right hand. The 3-way interaction Position by Response Side by Posture was not significant [$F(4, 56) = .07$, $p = .99$] suggesting that the OPE did not vary between the cross and uncross posture.

LB participants (Fig. 2, central panel) showed a similar pattern. We found a main effect of Position [$F(4, 56) = 6.22$, $p < .001$] and a significant Position by Response Side interaction [$F(4, 56) = 8.39$, $p < .001$]. The 3-way interaction Position by Response Side by Posture did not reach significance [$F(4, 56) = 1.30$, $p = .28$].

EB participants (Fig. 2, right panel), instead, showed a different pattern of results. We found a main effect of Position [$F(4, 54) = 2.69$, $p = .04$] and no other significant main effect or interaction.

Since we did not find any interaction between posture and OPE in none of the groups (all Fs < 1.30, all p-vals > .28) we collapsed the data across postures (uncrossed, crossed) for further analyses. To substantiate the difference in OPE across groups we ran a Mixed ANOVA with Position and Response Side as within-subjects factors, and Group (sighted, LB, EB) as between-subjects factor. The 3 way interaction Position by Response Side by Group was significant [$F(8, 164) = 2.53$, $p = .01$]. Planned comparison showed that the same interaction was significant between sighted and EB [$F(4, 108) = 2.73$, $p = .03$], LB and EB [$F(4, 108) = 3.88$, $p = .005$], but not between sighted and LB [$F(4, 112) = 1.36$, $p = .25$].

Given that we saw some degree of variability in our data, with a few participants showing an opposite effect compared to other participants, in the same group, we decided to run additional analysis to control for the presence of outliers. For each group we excluded participants that showed an OPE that was greater or smaller than 2 SD compared to the group mean. The individual slope of the regression of dRTs over Sequence Position (shown in Fig. 2) was used as a measure of OPE: A negative slope represents a left-to-right canonical OPE, whereas a positive slope represent a right-to-left OPE. This procedure led to the exclusion of 2 participants, one SC and one LB. No outlier was found in the EB group. If anything, analysis following the exclusion of these outliers reinforced the previous ones in all their aspects (see Supplementary material). The following analyses were therefore conducted without including these two outliers.

In order to assess if participants adopted a serial search strategy when recovering information in WM (van Dijck & Fias, 2011; Ginsburg et al., 2014), we tested whether latencies increased progressively from the first to the last position (independently of response side). Average RTs for each serial position were computed for each group (in milliseconds, SC: 1109, 1188, 1152, 1186, 1169; LB: 967, 1000, 992, 1026, 1003; EB: 954, 999, 996, 999, 966). A series of polynomial contrasts (see Supplemental information for graphical representation) showed that a linear regression gave a slightly better fit than a quadratic one in the sighted (Akaike information criterion – AIC: 911 *vs* 912) and LB (AIC: 916 *vs* 918) groups, in line with previous reports (van Dijck & Fias, 2011; Ginsburg et al., 2014; but see Rinaldi et al., 2015). Yet, in all cases, the difference between models did not reach significance (all Fs < 1, all p-vals > .05). On the contrary, a quadratic regression gave a slightly better fit than a linear one in the EB group (AIC: 933 *vs* 934), although the difference was again not significant [$F(1) = .66$, $p = .41$]. Similarly, the interactions between each polynomial and the variable Group were not significant (all Fs < 1, all p-vals > .05).

In sum, the pattern of RTs did not show a clear tendency toward a linear increase, typical of full serial scanning strategies (van Dijck & Fias, 2011). This seems be due to the fact that the first and the last items in the sequence tended to be recalled faster than the others, a pattern better fitted by a quadratic function, which is a typical effect in serial recall (primacy and recency effects; see for instance Rinaldi et al., 2015). A recency effect seems to be more pronounced in EB than in the other two groups, although statistics suggest that this difference is likely to be anecdotal.

Yet, to test whether the OPE (or lack thereof) was related to the extent of which participants sequentially access items in WM, we correlated the slopes of the sequential access with the slopes of the OPE, for each participant. We could not find any relationship between these two factors (all $r < .37$, all p-vals > .19) and, if anything, in EB and LB the relationship trends in the opposite way, with a smaller OPE (less negative slopes) associated with the increasing of sequential access (Fig. 3).

Additionally we tested whether, for LB, the OPE effect was predicted by the onset of total blindness and/or by the duration of blindness. None of these two factors correlated with the OPE effect (see Supplementary information).

3.2. *Accuracy analysis*

The accuracy value was established, for each participant, by weighting the level of accuracy in the test phase (Whether they remembered correctly the WM-sequence) with the level of accuracy during the classification task (How many classification errors they did).

The performance of EB (Proportion Correct = .86, SD = .09) was not different from LB performance [PC = .81, SD = .10; $t(26) = 1.40$, $p = .17$] but EB were more accurate than sighted [PC = .73, SD = .14; $t(27) = 2.96$, $p = .006$]. The performance of the sighted and LB were only marginally different [$t(28) = 1.81$, $p = .08$].

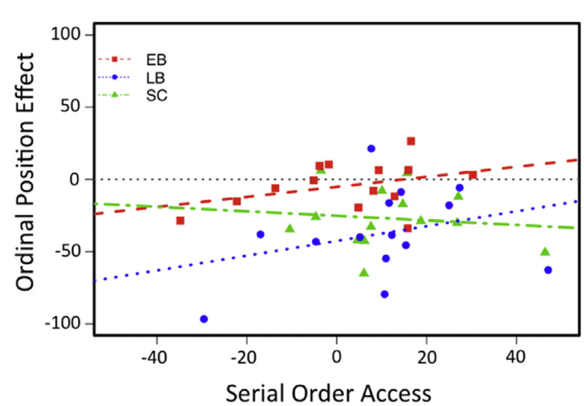

Fig. 3 – Serial access predicting OPE, a negative OPE indicates a canonical left-to-right organization of items in WM. Serial access is represented here by the slope of the regression of RTs over ordinal position in WM. A positive slop (right side of the x axis) indicates that RTs increased with the increasing of the ordinal position in the list (i.e., first items classified faster than last items) suggesting serial access.

For each of the 3 groups we tested whether the OPE correlated with Accuracy. We took the slope of the OPE for each subject and regress it over accuracy (Fig. 4). In none of the case we could find a significant correlation between accuracy and WM-effect (all p-vals > .29). This suggests that the greater accuracy of EB participants in the WM task is unlikely to be the reason of the observed difference in the WM-effect.

4. Discussion

In this study we tested the role of visual experience in establishing and shaping the association between serial order in WM and space. Blind (both early and late) and sighted individuals took part in a WM task in which they had to classify as fruit or vegetable items that they were holding in WM. They did so by pressing two keys, one on the right and one on the left of their body midline. In keep with previous results, sighted and LB spontaneously showed a clear association between item position in WM and space, the OPE: Left-key responses were faster for early items in the list whereas later items facilitated right-key responses. By asking participants to perform the test both with parallel and crossed hands, we were able to demonstrate for the first times that the OPE observed in the sighted and in LB relies on the use of an external spatial frame of reference.

In striking contrast, EB participants did not show any association between space and serial order in WM. The lack of OPE in EB cannot be simply due to a difference of performance in the task: Although EB were more accurate than the sighted in the test, their performances were identical to the ones of the LB who showed a clear OPE. Moreover, the accuracy in the task did not correlate with the OPE in any of the three groups, excluding the hypothesis that more accurate participants show a smaller OPE.

Our results suggest that visual experience is instrumental in establishing the link between serial order in WM and space. Functional vision allows to offload WM by structuring information in spatial media where items are stored and can be retrieved by directing visual-spatial attention to different locations, often serially, and with a canonical direction (e.g., left-to-right). This is the case for all kinds of lists, telephone numbers, schedules or diagrams. This is the way information is presented to us on computer or television screens, lectures, whiteboards at school, etc. All these spatialized practices of memory offload and externalization may indeed facilitate the development of an analogical spatial medium where items are virtually located when we consciously keep them in our mind's eye (Jaynes, 1976). In contrast to sighted people, the experience of EB individuals with spatially structured external memory devices is fairly limited. For instance, memory offload is often obtained, in this population, via recordings or vocal notes that are not spatially organized and that may limit the spatial structuring of items in WM. The limited possibility to retrieve information by "looking" where information is stored provides an interesting parallel with a specific aspect of the OPE, namely that the effect of spatialization seems to emerge during item retrieving (Ginsburg et al., 2014). In fact, if a list of items is maintained in WM but the items do not have to be retrieved during the classification task, the OPE does not emerge (see Ginsburg et al., 2014 and the next paragraph). In other words, the spatialization seems to take place when people "look" whether and where a particular item is stored (Ginsburg et al., 2014), which is an analog of everyday mnemonic behavior for sighted people but not for blind people.

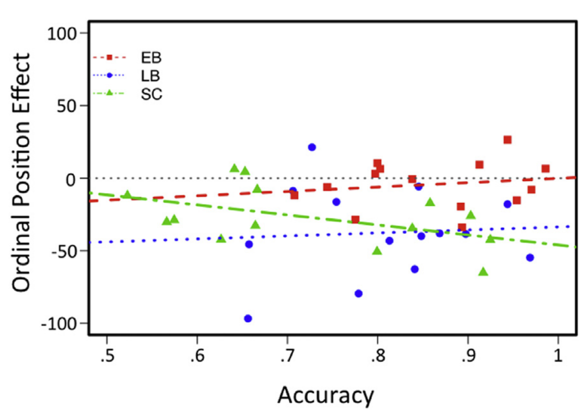

Fig. 4 – Accuracy predicting OPE.

Yet, although blind people cannot write and read in print, they can do it in braille. Braille is read from left to right and can provide a spatialized experience of sequential information. Moreover, some blind individual may use braille typers or braille slates to store and retrieve information, at least when these devices are available (and mostly before the age of smartphones). Yet, at least three aspects have to be considered: (i) the use of these devices for memory offload, especially in the case of short and transient information (lists, telephone numbers, addresses), is quite limited compared to the widespread use of written notes in the sighted population (see Tables 2a and 2b in the Supplementary information); (ii) braille hardly allows for self-produced schematic and diagrammatic representations, which may be an important physical analog of spatialized information in our mind; (iii) retrieval of information in braille is necessarily sequential, whereas visual spatial layouts can be glanced simultaneously. This last point becomes of interest considering the quite surprising fact that serial access to items in WM did not correlate whatsoever with the OPE effect (Fig. 3). This may suggest that the OPE emerges thanks to a vision-like simultaneous representation of information that is independent from sequential encoding and maintenance. This sort of simultaneous representation of information is thought to be less common in blind people's mind (Cattaneo et al., 2008). There is substantial evidence that early lack of vision induces a more sequential representation of space, also in terms of higher-level cognition (Cornoldi, Beni, De Roncari, & Romano, 1989; Noordzij, Zuidhoek, & Postma, 2006; see Cattaneo et al., 2008 for a review). For instance, Noordzij et al. (2006) tested the ability to form spatial mental models of described environment in sighted and blind people. Whereas blind people performed better after a route-like description compared to a survey-like description, the opposite was true for sighted people. Furthermore, Cornoldi et al. (1989) showed that both blind and sighted participants performed well in tasks that required to imagine two simultaneously interacting objects. Yet, when the number of objects increased to 3 or 4, blind people performance worsened considerably whereas sighted performance remained high.

Maybe the most surprising example of spatial WM impairment in blind people comes from an auditory spatial bisection task (Gori, Sandini, Martinoli, & Burr, 2014). In this task participants heard three sounds in succession. The first and the third sounds always came from a left-located and a right-located speaker, respectively. The second sound came from a speaker in an intermediate position between the two other speakers. Subjects had to report whether the second sound was closer to the left (first) or the right (third) sound. In order to perform this task, the sounds have to be abstracted from temporal succession and their locations should be compared onto each other, a process that may be facilitated by a simultaneous representation of spatial locations. Whereas blindfolded sighted people performed well in this task, congenitally blind people produced extremely poor performances (e.g., 5 out of 9 simply could not do the task). The difficulty for EB individuals to develop efficient processes for simultaneously treating information reflects their perceptual (mostly sequential) experience of the world and may also play a role in reducing the OPE.

That is, the way we habitually organize and experience information in the external world may bias the way we store and retrieve information in our memory. Interestingly, blindness has an impact on the spatial structure of verbal WM only when it is acquired early in development. This result suggests that, once acquired, the spatial organization of verbal WM is resilient to change, even after a long period of total blindness.

5. Cognitive maps in the blind mind: comparison with previous results

Previous studies have shown that spatial-temporal (Bottini et al., 2015) and spatial-numerical (Crollen et al., 2013) association can develop in people who have never experienced functional vision (although visual experience may influence the spatial coordinate system used to represent those concepts; Crollen & Collignon, 2012). The lack of spatialization of items in WM in EB suggests that the OPE is not simply an instance of the MTL or the MNL, but that it is based on partially different mechanisms.

Indeed, the association between serial order in WM and space could be considered as a special case of time–space association, with temporal succession (of items in the list) mapped onto the lateral axis (left-right). Yet, if the OPE was due to the fact that people access items in WM in temporal succession, we should have found a correlation between serial scanning behavior and OPE: The more people access items in the memorized list as a temporal series, the more the effect should be evident. Yet, this is not the case across all the 3 groups (see Fig. 4). Accessing items in WM as a temporal sequence does not seem to be necessary for the emergence of OPE.

It has been suggested, otherwise, that the OPE is the mechanisms on which the SNARC effect builds on (van Dijck & Fias, 2011). That is, when people judge the magnitude of a digit compared to "five" they encode in WM the digits (1–9) that are used in the experiment, to facilitate task execution. It might be this temporary association between numerical items and space in WM that produces the SNARC effect, rather than the long term semantic representation of numbers (Dehaene et al., 1993). If OPE and the SNARC effect result from the same underlying processing mechanism, EB should show a OPE effect since they show a SNARC effect (Castronovo & Seron, 2007; Crollen et al., 2013) but as seen here, this is not the case. Moreover, if OPE and the SNARC effect shared similar underlying mechanisms, they should be sensitive to the same task demands (Ginsburg et al., 2014), but, again, this is not the case. Ginsburg et al. (2014) performed an experiment in which participants engaged in a Go-Nogo WM task like the one described here, but with digits instead of words. Participants had to keep in mind a series of 5 numbers (e.g., 74194) and then classify the digits as larger/smaller than five during a Go-Nogo classification phase. Replicating previous results they found a strong OPE (digits at the beginning of the sequence–left key, digits at the end–right key; independently of their magnitude), but a weak and non-significant SNARC effect (smaller digits-left key, larger digits-right key; independently of their position in the sequence). This result seems at first to support the hypothesis that the SNARC effect is actually an instance of the OPE effect: it is the order of digits in WM, and not their magnitude, that is grounded in space. Nevertheless, in a second experiment, they asked participants to classify all the digits presented in the classification phase, including those that were not part of the memorized sequence (All-In task). Everything else was the same, including the fact that participants had to keep a 5-digit sequence in WM. In this case the pattern of result was reversed. In the All-In version of the task, the OPE effect was not significant whereas the SNARC effect emerged strongly. The authors concluded that the SNARC effect does not completely result from temporally created position–space associations in WM, otherwise SNARC and OPE should be susceptible to the same task demands. Consistently with this hypothesis, in a follow-up study it was shown that the OPE and the SNARC effect can be observed simultaneously under certain conditions (Ginsburg & Gevers, 2015). SNARC and OPE are not mutually exclusive, which suggests they rely, at least in part, onto different mechanisms (Ginsburg & Gevers, 2015; Ginsburg et al., 2014). In conclusion, it is worth pointing out that an indication of the independence between SNARC and OPE comes from the hand-posture manipulation in the present experiment. Indeed, whereas crossing hands seems to reduce or nullify the SNARC effect in the sighted population (Wood et al., 2006) and reverse it in the EB (at least in a magnitude comparison task; see Crollen et al. 2013), it had no effect on the OPE as observed here.

To sum up, spatial-numerical and spatial-temporal associations appear to be based, at least in part, on different mechanisms compared to space–position associations in WM. Additionally, previous results from our group suggest that that lack of vision has a different impact on the spatialization of different abstract domains such as numbers and time (Bottini et al., 2015; Crollen et al., 2013). Consistently, the present results show that lack of vision (and its consequences on how people interact with the world) impacts on the spatial organization of verbal WM in a different way compared to spatial-temporal and spatial-numerical associations. This confirms the heterogeneous nature of spatial cognitive maps, and the different role of visual experience in their implementation: (i) visual experience does not seem to impact on the expression of the MTL (Bottini et al., 2015), (ii) visual experience does influence the spatial frame of reference of the magnitude SNARC effect (allocentric frame of reference in the sighted, egocentric frame of reference in the EB; Crollen et al., 2013), and finally (iii) the absence of visual experience reduces the spatialization of ordered items in verbal WM (see Fig. 2). Indeed, if the structure of cognitive maps is in part organized in analogy with domain-relevant experiential practices (such as reading, writing, externalize WM loads, etc.), these effects should differ to the extent that different sensorimotor abilities, like different cultural habits, make such experiences different (Casasanto, 2011; Casasanto & Bottini, 2014b; Jaynes, 1976).

Our data should not be taken as evidence that developmental vision is strictly necessary to spatially organize items in WM, and that blindness mandatorily prevents the emergence of the OPE. Other cultural and experiential factors can indeed contribute to the development of a spatial representation of serial order, even with lack of vision. These may include formal education, parental guidance, idiosyncratic strategies, or the extensive use of particular devices such as portable braille displays. Moreover, the spatialization of items in WM can assume various configurations that may vary from person to person. Although the left-to-right configuration is the most canonical, some people may develop a preference for a top-to-bottom organization of sequences in WM (see Abrahamse et al., 2014, for preliminary results) as well as other configurations. Consistently, the presence of two outliers in the sighted and LB group, with an abnormally strong positive slope (i.e., right-to-left organization) suggests that in some cases people may show idiosyncratic ways to use cognitive maps. Such inter-individual variability may be exacerbated in EB because of their non-canonical experience and representation of space triggered by the lack of a systematic way to represent items simultaneously "in front" of them due to the absence of vision. In contrast, sighted people use a more spatially systematic way to spatialize items on external objects in front of them like on whiteboards, notes, computers, typically following orthographic conventions, at least for linguistic material.

6. Conclusions

Although both sighted and EB individuals can successfully retain a list of items in verbal WM and perform mental operations on it, they do so using a different representational format: Whereas, sighted and LB consistently organize WM items in space (with early items in the list mapped onto leftward location and later items onto rightward location in our sample), EB do not show such consistent spatial mapping. Therefore, verbal WM is less spatialized in EB compared to sighted. The observation of similar OPE in sighted and LB suggests that the experience of vision, even if lost at one point in development, pervasively shape the spatial structure of the verbal WM. Blindness can modulate the way people use spatial schemas to represent non-spatial concepts, and may do so by encouraging or discouraging typical experiential patterns that are subsequently internalized to scaffold abstract cognition (Casasanto, 2011; Jaynes, 1976). That is, part of our cognitive machinery is analogically organized on the basis of the way we perceive and behave in the physical world. The different sensorimotor experiences of EB and their consequences on how they interact with the external world will therefore impact on analogical cognitive processes related to the representation of those interactions with the world.

Acknowledgements

This work was supported by a European Research Council starting grant (MADVIS grant #337573) attributed to OC. We are also extremely thankful to our participants and the Unione Ciechi e Ipovedenti in Milano and Trento, and the Blind Institute of Milano.

Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2016.08.007.

REFERENCES

Abrahamse, E., van Dijck, J.-P., Majerus, S., & Fias, W. (2014). Finding the answer in space: The mental whiteboard hypothesis on serial order in working memory. *Frontiers in Human Neuroscience, 8*(November), 932. http://dx.doi.org/10.3389/fnhum.2014.00932.

Adachi, I. (2014). Spontaneous spatial mapping of learned sequence in chimpanzees: Evidence for a SNARC-like effect. *PloS One, 9*(3), e90373. http://dx.doi.org/10.1371/journal.pone.0090373.

Bottini, R., Crepaldi, D., Casasanto, D., Crollen, V., & Collignon, O. (2015). Space and time in the sighted and blind. *Cognition, 141*, 67–72. http://dx.doi.org/10.1016/j.cognition.2015.04.004.

Caramazza, A., & Hillis, A. E. (1990). Spatial representation of words in the brain implied by studies of a unilateral neglect patient. *Nature, 346*(6281), 267–269. http://dx.doi.org/10.1038/346267a0.

Casasanto, D. (2008). Similarity and proximity: When does close in space mean close in mind? *Memory & Cognition, 36*(6), 1047–1056. http://dx.doi.org/10.3758/MC.36.6.1047.

Casasanto, D. (2009). Embodiment of abstract concepts: Good and bad in right- and left-handers. *Journal of Experimental Psychology. General, 138*(3), 351–367. http://dx.doi.org/10.1037/a0015854.

Casasanto, D. (2011). different bodies, different minds: The body specificity of language and thought. *Current Directions in Psychological Science, 20*(6), 378–383. http://dx.doi.org/10.1177/0963721411422058.

Casasanto, D., & Boroditsky, L. (2008). Time in the mind: Using space to think about time. *Cognition, 106*(2), 579–593. http://dx.doi.org/10.1016/j.cognition.2007.03.004.

Casasanto, D., & Bottini, R. (2014a). Mirror reading can reverse the flow of time. *Journal of Experimental Psychology. General, 143*(2). http://dx.doi.org/10.1037/a0033297.

Casasanto, D., & Bottini, R. (2014b). Spatial language and abstract concepts. *Wiley Interdisciplinary Reviews: Cognitive Science, 5*(April), 139–149. http://dx.doi.org/10.1002/wcs.1271.

Casasanto, D., & Jasmin, K. (2012). The hands of time: Temporal gestures in English speakers. *Cognitive Linguistics, 23*(4), 643–674. http://dx.doi.org/10.1515/cog-2012-0020.

Castronovo, J., & Seron, X. (2007). Semantic numerical representation in blind subjects: The role of vision in the spatial format of the mental number line. *The Quarterly Journal of Experimental Psychology, 60*(1), 101–119. http://dx.doi.org/10.1080/17470210600598635.

Cattaneo, Z., Vecchi, T., Cornoldi, C., Mammarella, I., Bonino, D., Ricciardi, E., et al. (2008). Imagery and spatial processes in blindness and visual impairment. *Neuroscience and Biobehavioral Reviews, 32*(8), 1346–1360. http://dx.doi.org/10.1016/j.neubiorev.2008.05.002.

Cornoldi, C., Beni, R., De, Roncari, S., & Romano, S. (1989). The effects of imagery instructions on total congenital blind recall. *European Journal of Cognitive Psychology, 1*(4), 321–331. http://dx.doi.org/10.1080/09541448908403092.

Crollen, V., & Collignon, O. (2012). Embodied space in early blind individuals. *Frontiers in Psychology, 3*(August), 1–3. http://dx.doi.org/10.3389/fpsyg.2012.00272.

Crollen, V., Dormal, G., Seron, X., Lepore, F., & Collignon, O. (2013). Embodied numbers: The role of vision in the development of number-space interactions. *Cortex, 49*(1), 276–283. http://dx.doi.org/10.1016/j.cortex.2011.11.006.

Dehaene, S., Bossini, S., & Giraux, P. (1993). The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General, 122*(3), 371–396.

van Dijck, J.-P., Abrahamse, E. L., Majerus, S., & Fias, W. (2013). Spatial attention interacts with serial order retrieval from verbal working memory. *Psychological Science, 24*(9), 1854–1859. http://dx.doi.org/10.1177/0956797613479610.

van Dijck, J.-P., & Fias, W. (2011). A working memory account for spatial-numerical associations. *Cognition, 119*(1), 114–119. http://dx.doi.org/10.1016/j.cognition.2010.12.013.

Drucker, C. B., & Brannon, E. M. (2014). Rhesus monkeys (*Macaca mulatta*) map number onto space. *Cognition, 132*(1), 57–67. http://dx.doi.org/10.1016/j.cognition.2014.03.011.

Fuhrman, O., & Boroditsky, L. (2010). Cross-cultural differences in mental representations of time: Evidence from an implicit nonlinguistic task. *Cognitive Science, 34*(8), 1430–1451. http://dx.doi.org/10.1111/j.1551-6709.2010.01105.x.

Ginsburg, V., & Gevers, W. (2015). Spatial coding of ordinal information in short- and long-term memory. *Frontiers in Human Neuroscience, 9*(5), 1–10. http://dx.doi.org/10.3389/fnhum.2015.00008.

Ginsburg, V., van Dijck, J.-P., Previtali, P., Fias, W., & Gevers, W. (2014). The impact of verbal working memory on number-space associations. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 40*(4), 976–986. http://dx.doi.org/10.1037/a0036378.

Gori, M., Sandini, G., Martinoli, C., & Burr, D. C. (2014). Impairment of auditory spatial localization in congenitally blind human subjects. *Brain, 137*(1), 288–293. http://dx.doi.org/10.1093/brain/awt311.

von Hecker, U., Hahn, U., & Rollings, J. (2016). Spatial representation of coherence. *Journal of Experimental Psychology: General, 145*(7), 853–871.

Jaynes, J. (1976). *The origin of consciousness in the breakdown of the bicameral mind*. Boston: Houghton-Mifflin.

Loetscher, T., Bockisch, C. J., Nicholls, M. E. R., & Brugger, P. (2010). Eye position predicts what number you have in mind. *Current Biology, 20*(6), 264–265. http://dx.doi.org/10.1016/j.cub.2010.01.015.

Miles, L. K., Nind, L. K., & Macrae, C. N. (2010). Moving through time. *Psychological Science, 21*(2), 222–223. http://dx.doi.org/10.1177/0956797609359333.

Müller, D., & Schwarz, W. (2007). Is there an internal association of numbers to hands? The task set influences the nature of the SNARC effect. *Memory & Cognition, 35*(5), 1151–1161. http://dx.doi.org/10.3758/BF03193485.

Noordzij, M. L., Zuidhoek, S., & Postma, A. (2006). The influence of visual experience on the ability to form spatial mental models based on route and survey descriptions. *Cognition, 100*(2), 321–342. http://dx.doi.org/10.1016/j.cognition.2005.05.006.

Oberauer, K. (2009). Design for a working memory. In B. H. Ross (Ed.), *The psychology of learning and motivation* (pp. 45–100). Amsterdam: Elsevier.

Ouellet, M., Santiago, J., Israeli, Z., & Gabay, S. (2010). Is the future the right time? *Experimental Psychology, 57*(4), 308–314. http://dx.doi.org/10.1027/1618-3169/a000036.

Pitt, B., & Casasanto, D. (2016). Reading experience shapes the mental timeline but not the mental number line. In D. Grodner, D. Mirman, A. Papafragou, & J. Trueswell (Eds.), *Proceedings of the 38th Annual Conference of the Cognitive Science Society* (pp. 2753–2758). Austin, TX: Cognitive Science Society.

Rinaldi, L., Brugger, P., Bockisch, C. J., Bertolini, G., & Girelli, L. (2015). Keeping an eye on serial order: Ocular movements bind space and time. *Cognition, 142*, 291–298. http://dx.doi.org/10.1016/j.cognition.2015.05.022.

Rinaldi, L., Di Luca, S., Henik, A., & Girelli, L. (2016). A helping hand putting in order: Visuomotor routines organize numerical and non-numerical sequences in space. *Cognition, 152*, 40–52. http://dx.doi.org/10.1016/j.cognition.2016.03.003.

Rusconi, E., Kwan, B., Giordano, B. L., Umiltà, C., & Butterworth, B. (2006). Spatial representation of pitch height: The SMARC effect. *Cognition, 99*(2), 113–129. http://dx.doi.org/10.1016/j.cognition.2005.01.004.

Saj, A., Fuhrman, O., Vuilleumier, P., & Boroditsky, L. (2013). Patients with left spatial neglect also neglect the "Left Side" of time. *Psychological Science*, (November)http://dx.doi.org/10.1177/0956797612475222.

Santiago, J., Lupiáñez, J., Pérez, E., & Funes, M. J. (2007). Time (also) flies from left to right. *Psychonomic Bulletin & Review, 14*(3), 512–516.

Shaki, S., & Gevers, W. (2011). Cultural characteristics dissociate magnitude and ordinal information processing. *Journal of Cross-Cultural Psychology, 42*(4), 639–650. http://dx.doi.org/10.1177/0022022111406100.

Slepian, M. L., Masicampo, E. J., & Ambady, N. (2015). Cognition from on high and down low: Verticality and construal level. *Journal of Personality and Social Psychology, 108*(1), 1–17. http://dx.doi.org/10.1007/s11002-014-9324-z.

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review, 55*, 189–208.

Wood, G., Nuerk, H., & Willmes, K. (2006). Crossed Hands and the SNARC effect: A failure to replicate Dehaene, Bossini and Giraux (1993). *Cortex, 42*(8), 1069–1079.