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Research report

Embodied numbers: The role of vision in the development of number–space interactions

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ARTICLE INFO

Article history:
Received 19 August 2011
Reviewed 11 October 2011
Revised 7 November 2011
Accepted 14 November 2011
Action editor Carlo Umiltà
Published online xxx

Keywords:
Numerical cognition
SNARC effect
Blindness
External remapping

ABSTRACT

The strong association between numbers and space is found in the well-documented SNARC effect (Spatial Numerical Association of Response Codes), where responses on small/large numbers are faster in the left/right side of space, respectively. However, little is known about the developmental process through which numbers are mapped onto external physical space. Here we show that early blind individuals, but not late blind or sighted, demonstrate a reversed SNARC effect when performing a numerical comparison task with hands crossed over the body midline. Importantly, this reversed SNARC effect was not observed in any group of participants in a control parity judgment task. The present study therefore demonstrates that early visual experience drives the development of an external coordinate system for the visuo-spatial representation of numbers and further supports the idea that different types of spatial information are engaged in specific numerical tasks.

1. Introduction

In humans, several high level cognitive abilities are considered to be grounded onto more basic and evolutionary inherited sensori-motor functions (Dehaene and Cohen, 2007). A striking example of this concept resides in numerical cognition, where the semantic representation of numbers is thought to be tightly linked to the physical properties of external space (for a review, see Hubbard et al., 2005). A compelling demonstration of the strong association between numbers and space resides in the Spatial Numerical Association of Response Codes (SNARC) effect, referring to the observation that

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doi:10.1016/j.cortex.2011.11.006

Please cite this article in press as: Crollen V, et al., Embodied numbers: The role of vision in the development of number–space interactions, Cortex (2012), doi:10.1016/j.cortex.2011.11.006

responses to small numbers are faster in the left side of space, while responses to large numbers are faster in the right side of space (Dehaene et al., 1990).

This effect has been accounted by the idea that number semantics is organized on a left-to-right oriented mental number line (Dehaene et al., 1993; Dehaene, 1997). According to this view, numerical–spatial interactions result from the spatial compatibility effect occurring between the position of the number on the mental number line and the location of the response (Dehaene et al., 1993; Fischer, 2003; Fischer et al., 2003; Hubbard et al., 2005). Importantly, because the SNARC effect was observed even when participants crossed their hands (i.e., left/right hand in the right/left side of space), numbers were assumed to be mapped onto an external frame of reference (Dehaene et al., 1993; but see Wood et al., 2006), where small and large numbers facilitate responses in the left and right side of space irrespective of the hand of response. This demonstrates that the coordinate frame in which the SNARC effect arises is eye- or world-centered rather than hand-based.

However, the development of this intrinsic association between numbers and external space remains elusive. Recently, researchers have investigated the role of visual experience in the development of such connection by comparing the performance of early blind and sighted individuals in number comparison and parity judgment tasks (Castronovo and Seron, 2007; Szücs, and Csépe, 2005). Because blind and sighted participants displayed a similar SNARC effect, the authors suggested that vision was not a necessary prerequisite for the development of an internal representation of numbers mapped onto external physical space. However, because the authors did not include a crossed-hands condition, these studies cannot disambiguate whether the SNARC effect emerges from the use of similar coordinate frames in both populations. Indeed, such effect could be triggered by the use of eye- or hand-based coordinates. This is of major importance since recent experiments with blind individuals have suggested that the default-use of an external coordinate system in space for perception and action depends on early visual experience (Collignon et al., 2009a, 2009b; Röder et al., 2004, 2007, 2008). For example, Röder et al. (2004) demonstrated that when participants were required to determine the temporal order of two tactile stimuli, one applied to either hand, sighted and late blind participants' performance was impaired in a crossed when compared to an uncrossed-hands posture, but performance of early blind participants remained unchanged across posture changes. The authors argued that the automatic external remapping of touch in sighted and in late blind induces a conflict between external and body-centered coordinates, leading to a decrease in performance. However, in the early blind, an absence of the externalization process of touch protects them from the detrimental effect of the crossed-hands posture. Therefore, since early visual experience drives the default-use of an external frame of reference for perception and action, and if numerical cognition is grounded on such basic sensori-motor abilities, early blind individuals should use an anatomically anchored reference system (i.e., hand-based) when performing a SNARC paradigm whereas sighted participants should use an eye- or world-centered coordinate frame of reference.

In the present study, early blind, late blind and sighted controls were asked to perform a numerical comparison task to 5, either with hands parallel or with hands crossed over the body midline. Because the default-use of an external coordinate system for perception and action depends on early visual experience (Collignon et al., 2009a, 2009b; Röder et al., 2004, 2007, 2008), crossing hands was expected to reverse the SNARC effect in early blind individuals in the numerical comparison task. Moreover, in order to test for the specificity of this effect, participants were also required to carry out a parity judgment task. Since this latter task is thought to primarily depend on verbal–spatial associations rather than on visuo-spatial associations with numbers (van Dijck et al., 2009), a classic SNARC effect was expected to be observed irrespective of hand posture in every group of participants.

2. Method

2.1. Participants

One group of sighted and two groups of blind participants (early and late blind) took part in the present study. The sighted control group was composed of 7 females and 6 males ranging in age from 24 to 61 with a mean age of 42 (Standard deviation (SD) = 11). The early blind group was composed of 4 females and 7 males ranging in age from 29 to 62 with a mean age of 46 (SD = 11). The late blind group was composed of 7 females and 8 males ranging in age from 31 to 61 with a mean age of 48 (SD = 8). The three groups did not statistically differ in terms of age. Unlike the early blind, all late blind participants had experienced functional vision before sight loss. The mean age at onset of blindness in the late blind group was 29 (range: 7–53) and the mean duration of blindness before participating in the study was 19 (range: 2–47). At the time of testing, the participants in both blind groups were totally blind or had only rudimentary sensitivity for brightness differences and no patterned vision. In all cases, blindness was attributed to peripheral deficits with no additional neurological problems (see Table 1 for details). Procedures were approved by the Research Ethics Boards of the Centre for Interdisciplinary Research in Rehabilitation of Greater Montreal (CRIR) and Université de Montréal. Experiments were undertaken with the understanding and written consent of each subject. None of the subjects reported neurological or psychological problems, and none was taking psychotropic medication at the time of testing. Sighted participants were blindfolded when performing the tasks.

2.2. Numerical comparison task

In this task, participants were asked to judge whether an orally presented number was smaller or larger than 5. The verbal numerals used were numbers 1–9 (except for 5). Stimuli lasted 450 msec, had identical auditory properties (44,100 Hz, 16 bits, stereo) and were played at a comfort intensity level through loudspeakers placed in front of the participant.

Participants were instructed to respond as quickly and accurately as possible in a forced two-choice paradigm 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. The task comprised two

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Table 1 – Characteristics of the blind participants.

Participants	Gender	Age	Handedness	Onset	Cause of blindness
EB1	F	29	A	6 Months	Retinopathy of prematurity
EB2	M	41	R	0	Retinopathy of prematurity
EB3	M	62	R	0	Rubella of the mother during pregnancy
EB4	M	59	R	0	Congenital cataract
EB5	F	58	R	0	Retinopathy of prematurity
EB6	M	52	R	2 Months	Medical accident
EB7	M	31	R	2 Years	Retinoblastoma
EB8	F	33	R	10 Months (left eye) 3 Years (right eye)	Retinoblastoma
EB9	M	48	R	0	Thalidomide
EB10	M	42	R	0	Leber's congenital amaurosis
EB11	F	54	R	0	Retinopathy of prematurity
LB1	M	53	L	51	Diabetic retinopathy
LB2	F	47	R	44	Glaucoma + cataract
LB3	F	54	R	19	Aniridia
LB4	M	48	R	32	Accidental detachment of the retina
LB5	M	42	R	17	Bilateral section of optical nerve
LB6	F	61	R	52	Stevens Johnson Syndrome + Sulfa Antibiotics
LB7	M	31	R	15	Bilateral section of optical nerve
LB8	F	55	L	8	Accidental detachment of the retina
LB9	F	59	R	53	Retinitis pigmentosa
LB10	M	55	R	44	Diabetic retinopathy
LB11	M	55	L	26	Bilateral section of optical nerve
LB12	F	36	R	20	Glaucoma
LB13	M	48	R	16	Glaucoma + congenital cataract
LB14	M	43	R	7	Fibroplasia
LB15	F	42	R	38	Microphthalmia + cataract

Note: M = male; F = female; L = left-handed; R = right-handed; A = ambidextrous.

response assignments. In the first condition, "smaller than 5" response was assigned to the left response key, while "larger than 5" response was assigned to the right response key. In the second condition, the reverse assignment was used: the "larger than 5" response to the left key and the "smaller than 5" response to the right key. Moreover, participants were asked to perform the task either with their hands in a parallel posture (i.e., 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 (i.e., crossed posture) (see Fig. 1). Each participant completed 4 blocks of trials [response mode (2) × posture (2)]. The order of response mode and posture conditions was counterbalanced across participants. During testing, subjects sat in a silent room with the head restrained by a chin rest. Stimuli were delivered and reaction times were recorded using Presentation software (Neurobehavioral Systems Inc.) running on a Dell XPS computer using a Windows XP operating system. Each verbal numeral was presented 16 times in each condition, giving a total of 512 stimuli [number (8) × presentation (16) × response mode (2) × posture (2)] randomly presented in 4 experimental blocks. The inter-stimuli interval ranged from 1500 to 2500 msec. Trials for which subjects did not respond were considered as omissions.

2.3. *Parity judgment task*

The procedure used in the parity judgment task was exactly the same as the one used for the comparison task, except that participants were asked to judge the parity of the verbal numerals presented. As for the comparison task, response mode and posture was counterbalanced across participants (see Fig. 1).

2.4. *Statistical analyses*

In experiments equally emphasizing accuracy and processing speed, as it is the case in the present study, it is common to combine both response speed and accuracy into a single score performance in order to obtain a general index of performance that discounts possible criterion shift or speed/accuracy tradeoff effects. Participants' performance was therefore analyzed by measuring inverse efficiency scores (IES), which were obtained by dividing response times (RT) by correct response rates (Townsend and Ashby, 1978). Because the SNARC effect predicts a negative relation between the magnitude of the number and the difference in RT between the right and the left-sided responses, dIES were computed by subtracting the median IES for the left response key from the median IES for the right response key (Fias et al., 1996). A classic SNARC effect should be reflected by a negative relation between number magnitude and dIES: small numbers should elicit faster left-sided responses (i.e., positive dIES) and large numbers should elicit faster right-sided responses (i.e., negative dIES).

dIES were first entered in an exploratory 3 (Group: early blind, late blind, sighted) × 2 (Magnitude: small, large) × 2 (Hand posture: crossed, uncrossed) × 2 (Tasks: numerical comparison, parity judgment) Linear Mixed Model (LMM) with

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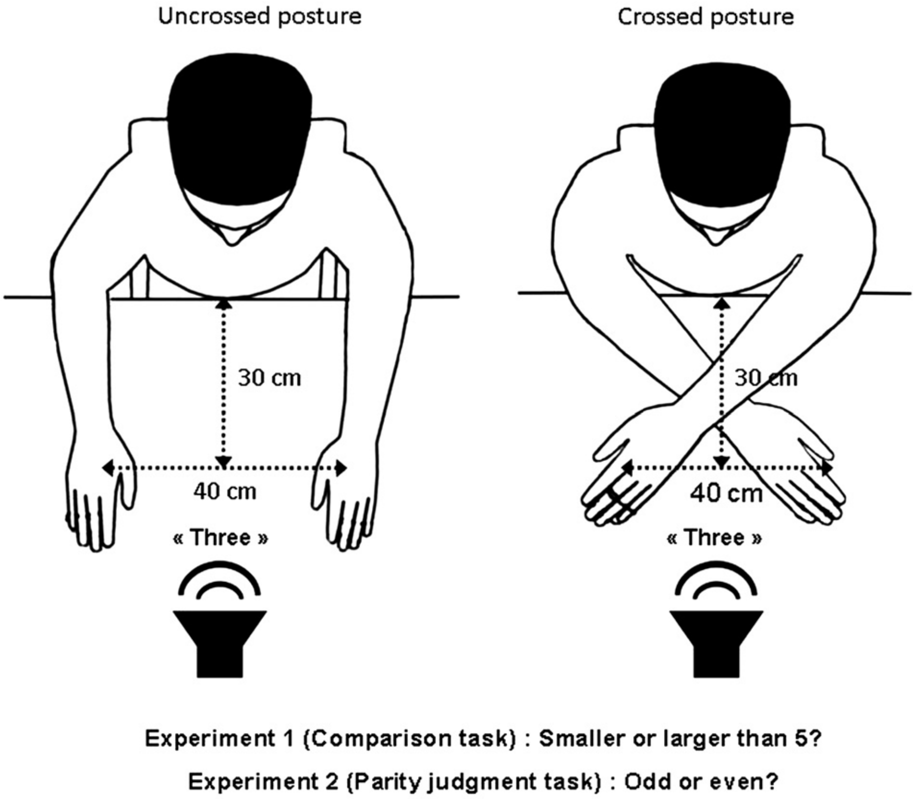

Fig. 1 – **Methodology of the numerical comparison and parity judgment tasks.**

participants as a random factor. Because this analysis revealed that number and space interacted with the group and task factors (the interaction magnitude × hand posture × task and the interaction group × magnitude × hand posture × task were both significant, $p_s < .05$), two separate follow-up LMM were performed for the numerical comparison and parity judgment tasks respectively.

dIES were processed with LMM as well as with General Linear Model (GLM). Both analyses led essentially to the same conclusions. However, as LMM does not require observations to be independent with constant variance (as the GLM does), and as this model presents the advantage to allow the specification of random and fixed factors, only results of the LMM are reported in the "Results" section of this paper. Bonferroni post-hoc analyses were performed when appropriate.

3. Results

3.1. *Numerical comparison task*

The LMM performed on the dIES demonstrated the following results (see Fig. 2): (1) a main effect of magnitude, $F(1, 612) = 31.21$, $p < .001$; indicating that small numbers were, overall, responded to faster with the left response key while large numbers were responded to faster with the right response key; (2) a group × magnitude interaction, $F(2, 612) = 8.63$, $p < .001$. Post-hoc analyses indicated that the difference between small and large numbers was more pronounced in the sighted controls than in the early blind [$p < .01$]. The late blind did not differ from the two other groups [$p_s > .1$]; (3) a magnitude × hand posture interaction, $F(1, 612) = 15.38$, $p < .001$; indicating that the magnitude effect was more pronounced in the uncrossed posture than in the crossed posture; (4) a group × magnitude × hand posture interaction, $F(2, 612) = 5.89$, $p < .01$. In order to further decompose this last interaction, a LMM on the dIES was performed for each group separately. In the sighted controls and late blind groups, only the magnitude factor was significant [$F(1, 204) = 26.75$, $p < .001$ in sighted controls; $F(1, 236) = 21.70$, $p < .001$ in late blind]. In both groups, a classic SNARC effect was thus observed irrespective of the hand posture (see Fig. 2). Importantly, in the early blind, the interaction between magnitude and hand posture was significant, $F(1, 172) = 16.675$, $p < .001$. When the early blind performed the comparison task with hands uncrossed, a classic SNARC effect was observed, whereas when they performed the task with crossed hands, the SNARC effect was reversed: small numbers elicited faster right-sided responses while large numbers elicited faster left-sided responses (see Fig. 2). LMM performed independently on the accuracy scores (right accuracy score - left accuracy score; i.e., dAccuracy) and on the reaction times (right reaction time - left reaction time; i.e., dTR) led to similar results (see Supplemental data).

3.2. *Parity judgment task*

Due to technical problems, the data of one sighted participant were not recorded in the parity judgment task. The analyses

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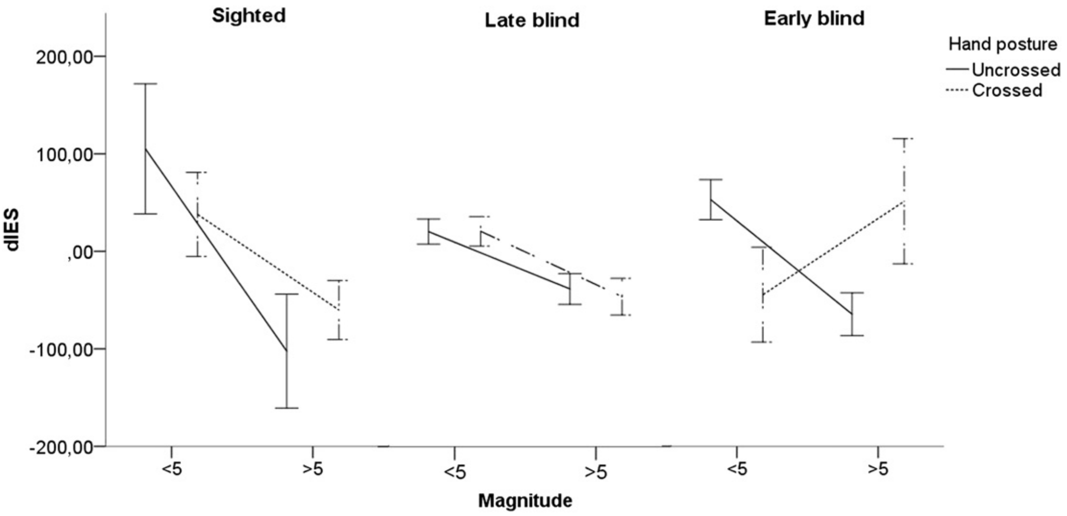

Fig. 2 – dIES (see Method) for sighted controls, late blind and early blind individuals in the numerical comparison task.

reported in this section are therefore performed on 12 sighted controls, 11 early blinds, and 15 late blinds. As in the previous task, dIES were computed and submitted to a 3 (Group: early blind, late blind, sighted) × 2 (Magnitude: small, large) × 2 (Hand posture: crossed, uncrossed) LMM with participants as a random factor. This analysis only highlighted a main effect of magnitude, $F(1, 596) = 9.45$, $p < .01$, indicating the presence of a SNARC effect independent of hand posture (see Fig. 3). As in the previous task, the LMM performed on dAccuracy and dTR independently led to similar conclusions (see Supplemental data).

4. Discussion

The study of visually deprived individuals represents a unique opportunity to test the intrinsic relation between numerical cognition and basic sensori-motor abilities. In the first experiment of the present study, early blind, late blind and sighted controls were asked to perform a numerical comparison task to 5. The task was carried out either with hands parallel or with hands crossed. Sighted and late blind participants showed a classic SNARC effect in the uncrossed and crossed conditions (Dehaene et al., 1993): small numbers elicited faster left-sided responses while large numbers elicited faster right-sided responses, independently of the responding hand (left or right). Our data therefore support the idea that the crossed-hands posture did not preclude the SNARC effect from occurring in sighted controls (Dehaene et al., 1993) and extended this observation to the case of late blind. These results indicate that in both groups, the SNARC effect elicited in a number comparison task depends on eye- or world-centered coordinates rather than hand-based coordinates. These results contrast with the ones of Wood et al. (2006) showing an absence of SNARC effect in a crossed posture. According to these authors, two relevant spatial frames of reference are available in SNARC tasks: the representational and the hand-based frame of reference. Within this framework, the SNARC effect should be a weighted sum of the activation of both coordinate systems: when hands are crossed, there is a conflict between world-centered and body-centered coordinates. If the saliency of both coordinates is

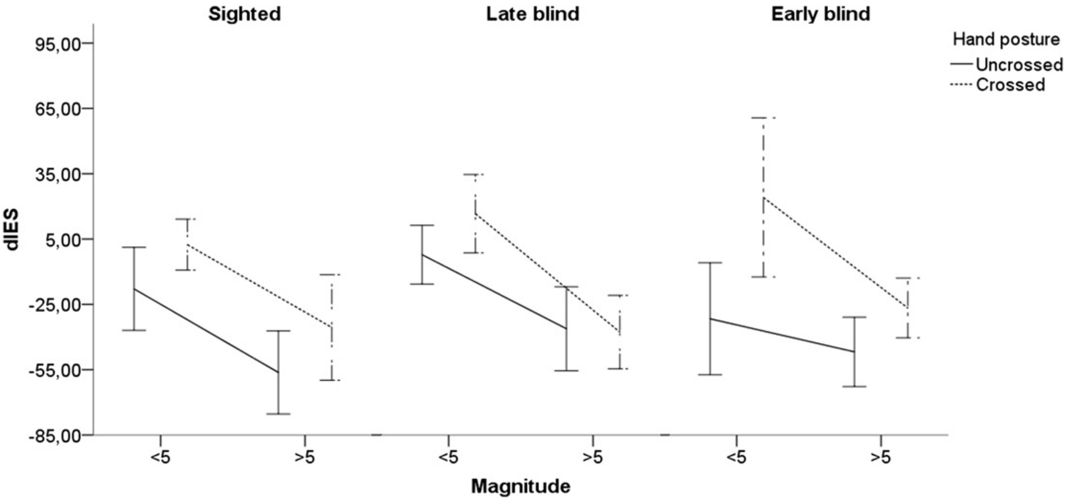

Fig. 3 – dIES (see Method) for sighted controls, late blind and early blind individuals in the parity judgment task.

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approximately equal, a null SNARC effect should therefore be observed. In contrast, if the weights of both coordinates are unequal, a SNARC effect should be observed in the direction of the coordinate system which is the most salient. In line with this theory, visual feedback of the response assignment is an important factor determining the direction of the SNARC effect in crossed-hands posture. Therefore, if the saliency of visual input regarding hand-based coordinates is high, both hand-based and hand-independent frames of reference should influence the SNARC effect. In contrast, if the saliency of the visual input is low (as it is the case with blindfolded sighted participants), the hand-independent frame of reference should influence the SNARC effect by more than the hand-base coordinate system. The lack of visual input could therefore account for the fact that a classic SNARC effect was observed in our experiment with blindfolded sighted participants or late blind individuals in a crossed-hands posture but not in Wood et al. (2006)'s study.

In the early blind, in contrast to sighted controls and late blind, the numerical stimulus primed a particular anatomical hand: small numbers elicited faster left-hand responses while large numbers elicited faster right-hand responses, regardless of where in space hands were placed. In other words, early blind individuals showed a classic SNARC effect in the uncrossed condition and a reversed SNARC effect in the crossed condition (Fig. 2). These results indicate the use of hand-based coordinates in the early blind and are in line with recent experiments demonstrating that early visual deprivation prevents the default-use of an external coordinate system in space for perception and action (Collignon et al., 2009a, 2009b; Röder et al., 2004, 2007, 2008). For example, Röder et al. (2007) have documented that the lack of developmental vision affects the occurrence of the Simon effect (Simon, 1969). Such an effect refers to the observation that responses to a stimulus are faster and more accurate when the position of the stimulus in external space is compatible with the side of the response. While the Simon effect is typically observed irrespectively of whether sighted participants respond with hands parallel or crossed, it appears to be reversed in congenitally blind individuals when performing the task in the crossed position. Hence, whereas the sighted and the late blind use a stimulus-location/response-location mapping (i.e., an external coordinate system) where stimulus location facilitates responses on the same side of space irrespective of the anatomical hand responding, congenitally blind participants use a stimulus-location/response-hand mapping (i.e., a body-centered coordinate system), where stimulus location facilitates responses given by the congruent anatomical hand irrespective of the position of this hand in external space. By showing that early blind individuals display a reversed SNARC effect in the crossed posture, our data extend such observations to the field of numerical cognition. In other words, as previously observed for physically lateralized stimuli (Röder et al., 2007), it appears that numbers are mapped onto physical space based on a body-centered coordinate system in early blind individuals whereas they are mapped onto an extra-corporal coordinate system in late blind and sighted controls. The similarity between our results obtained with numbers and those of previous studies investigating sensorimotor functions (Collignon et al., 2009a, 2009b; Röder et al., 2004, 2007, 2008) further supports the idea that numerical cognition relies on more "basic" sensori-motor foundations (Dehaene and Cohen, 2007). In sum, in a spatial context, it appears that numerical stimuli, as it is the case for tactile/proprioceptive stimuli (Azañón and Soto-Faraco, 2008), are automatically remapped into external coordinates beyond an initial body-centered representation stage. This automatic remapping is acquired during development as a consequence of visual input (Röder et al., 2004). In sighted controls, crossing hands induces a conflict between the anatomical coordinates of the responding hand and the external coordinate of the stimulus (i.e., the number) that has to be processed. In the early blind, in contrast, crossing hands does not induce such a conflict because early visual deprivation prevents the automatic remapping process of numbers in external coordinates, inducing the early blind to map numerical and sensory stimuli into the body-centered representation only.

Moreover, as blind participants are Braille readers and as Braille is read from left-to-right, our findings also support the idea that the SNARC effect may actually be determined by the orientation of reading habits (Dehaene et al., 1993). More particularly, the nature of the spatial representation of numbers is compatible with the main effector that early blind and sighted controls use to read: while reading and the SNARC effect are, by default, eye-centered in sighted people, they are, by default, hand-based in blind individuals.

Neuroimaging studies of the Simon effect, on another hand, consistently find posterior parietal lobe activations (Rusconi et al., 2007), a key region for numerical operations (Hubbard et al., 2005, 2009). In fact, converging evidence in animal and human studies have suggested that the neural underpinnings of numerical–spatial interactions reside in parietal structures commonly involved in the allocation of attention to external physical space and to internal representation of numbers (Hubbard et al., 2005, 2009). In sighted individuals, it is generally assumed that the parietal cortex gathers inputs from different modalities to integrate them into a unique and predominantly eye-centered representation of external space (e.g., Andersen, 1997; Andersen and Bueno, 2002). However, following an early visual deprivation, this neural network undergoes a profound reorganization. For example, occipital brain regions were shown to be extensively involved in auditory spatial processing (Collignon et al., 2001, 2007; Gougoux et al., 2005). Recently, Collignon et al. (2009a, 2009b) used transcranial magnetic stimulation (TMS) in order to induce a virtual lesion of either the right intra-parietal sulcus (rIPS) or the right dorsal extrastriate occipital cortex (rOC) in blind and sighted subjects performing a sound lateralization task. They observed that TMS applied over rIPS disrupted the spatial processing of sound in sighted subjects but surprisingly had no influence on the performance in blind individuals at any timing. In contrast, TMS applied over rOC mainly disrupted the spatial processing of sounds in blind participants. This study suggests a major contribution of rOC in the spatial processing of sound, but also points to lesser involvement of rIPS in this ability in blind participants. The results of the present study may similarly suggest that early visual deprivation also changes the neural responsiveness of the parietal cortex to the spatial coding of numbers.

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The data of our parity judgment task, on the contrary, demonstrated that sighted controls, late blind and early blind participants showed a classic SNARC effect in the parallel as well as in the crossed-hands posture. This finding is compatible with the idea that the SNARC effect does not necessarily need the metaphor of the mental number line to be explained, but may also be situated at a categorical level (Gevers et al., 2006, 2010; Proctor and Cho, 2006; Santens and Gevers, 2008). A recent theoretical framework has indeed developed the idea that different types of spatial information might be engaged in different numerical tasks. Studies on the topic have demonstrated that the SNARC effect disappears under spatial load during magnitude comparison tasks whereas it disappears under verbal load during parity judgment tasks (Herrera et al., 2008; van Dijck et al., 2009). Based on these studies, the SNARC effect was assumed to primarily originate from visuo-spatial associations in magnitude comparison tasks while it was assumed to primarily arise from verbal associations in parity judgment tasks. According to this theoretical framework, the SNARC effect does not necessarily map onto a visuo-spatial coding, but might, in specific circumstances, be located at a categorical level where numerical representation is linked to language (e.g., concepts such as “small” and “left”, “large” and “right”) rather than to physical space (Gevers et al., 2006, 2010; Proctor and Cho, 2006; Santens and Gevers, 2008). Because the default-use of an external coordinate system is a visuo-spatial phenomenon (Röder et al., 2007), it was therefore expected that blind individuals would show, in the crossed-hands posture: (1) a reversed SNARC effect in the task that primarily depends on visuo-spatial associations (i.e., magnitude comparison task) and (2) a classic SNARC effect in the task that primarily requires verbal associations (i.e., parity judgment task).

In line with previous studies (Castronovo and Seron, 2007; Szücs and Csépe, 2005), we observed that blindness does not prevent the capacity to generate mental representations in an “analog” format (such as the left-to-right oriented mental number line). However, our results demonstrated that blindness affects the nature of the spatial reference frame in which this mental number line occurs: while the SNARC effect of sighted participants relies on an association between numbers and an external visuo-spatial frame of reference, the SNARC effect of congenitally blind individuals principally relies on an association between numbers and an anatomical coordinate system. Therefore, a dissociation between sighted and blind performance only appears in tasks relying on the use of visuo-spatial coordinates (the comparison task), but not in tasks involving a spatial language component (the parity judgment task).

To conclude, our findings provide a compelling demonstration that early visual experience drives the development of an external coordinate system for the visuo-spatial coding of numbers and further support the idea that different types of spatial information are engaged in different numerical tasks (van Dijck et al., 2009).

Acknowledgments

Authors wish to thank the Institut Nazareth and Louis Braille for their help in recruiting the blind participants. This research was supported by a starting grant of the Research Centre of the University Hospital Sainte-Justine (OC). GD is a Ph.D. student and VC a postdoctoral researcher, both supported by the Belgian National Funds for Scientific Research.

Supplementary data

Supplementary data related to this article can be found online at doi:10.1016/j.cortex.2011.11.006.

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Please cite this article in press as: Crollen V, et al., Embodied numbers: The role of vision in the development of number–space interactions, Cortex (2012), doi:10.1016/j.cortex.2011.11.006