Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex

Research report

Blind readers break mirror invariance as sighted do

Adélaïde de Heering ^{a,*}, Olivier Collignon ^{b,c,d} and Régine Kolinsky ^{a,d}

^a Unité de Recherche en Neurosciences Cognitives (UNESCOG), Center for Research in Cognition & Neurosciences (CRCN), Université Libre de Bruxelles (ULB), Belgium

^b Institute of Psychology (IPSY) and Institute of Neuroscience (IONS), Université Catholique de Louvain (UCL), Belgium

^c Center for Mind/Brain Sciences (CIMeC), University of Trento, Italy

^d Fonds de la Recherche Scientifique — FNRS (FRS-FNRS), Belgium

ARTICLE INFO

Article history: Received 19 September 2017 Reviewed 12 November 2017 Revised 7 December 2017 Accepted 9 January 2018 Action editor Roberto Cubelli Published online 31 January 2018

Keywords: Blind Braille Mirror Invariance Reading

ABSTRACT

Mirror invariance refers to a predisposition of humans, including infants and animals, which urge them to consider mirrored images as corresponding to the same object. Yet in order to learn to read a written system that incorporates mirrored letters (e.g., vs. <d> in the Latin alphabet), humans learn to break this perceptual bias. Here we examined the role visual experience and input modality play in the emergence of this bias. To this end, we tested congenital blind (CB) participants in two same-different tactile comparison tasks including pairs of mirrored and non-mirrored Braille letters as well as embossed unfamiliar geometric shapes and Latin letters, and compared their results to those of age-matched sighted participants involved in similar but visually-presented tasks. Sighted participants showed a classical pattern of results for their material of expertise, Latin letters. CB's results signed for their expertise with the Braille script compared to the other two materials that they processed according to an internal frame of reference. They also evidenced that they automatically break mirror invariance for different materials explored through the tactile modality, including Braille letters. Altogether, these results demonstrate that learning to read Braille through the tactile modality allows breaking mirror invariance in a comparable way to what is observed in sighted individuals for the mirrored letters of the Latin alphabet.

© 2018 Elsevier Ltd. All rights reserved.

1. Introduction

Reading is a cultural activity that requires considerable training and which is known to profoundly reorganize the brain and several cognitive functions (for a review, see Dehaene, Cohen, Morais, & Kolinsky, 2015), among which is mirror invariance. Also referred to as mirror generalization, mirror invariance typically refers to humans' (including 3month-old infants, Bornstein, Gross, & Wolf, 1978) and other animals' (monkeys, pigeons and even octopuses) tendency to







^{*} Corresponding author. Center for Research in Cognition & Neurosciences, Université Libre de Bruxelles, Avenue F. Roosevelt, 50 CP 191, B-1050, Brussels, Belgium.

E-mail address: addeheer@ulb.ac.be (A. de Heering).

https://doi.org/10.1016/j.cortex.2018.01.002

^{0010-9452/© 2018} Elsevier Ltd. All rights reserved.

consider mirrored images - produced thanks to the reflection across a given axis - as corresponding to the same object even if they induce different retinal projections (for a review, see e.g., Corballis & Beale, 1976). Mirror invariance is an efficient property of the ventral visual system for the processing of various visual stimuli such as faces, animals and objects because it facilitates view-invariant object recognition (Baylis & Driver, 2001; Dehaene et al., 2010; Freiwald & Tsao, 2010; Logothetis, Pauls, & Poggio, 1995; Pegado, Nakamura, Cohen, & Dehaene, 2011; Rollenhagen & Olson, 2000). It needs however to be overcome during reading acquisition, or at least to be inhibited during letter recognition (e.g., Ahr, Houdé, & Borst, 2016; Borst, Ahr, Roell, & Houdé, 2015; Duñabeitia, Molinaro, & Carreiras, 2011; Perea, Moret-Tatay, & Panadero, 2011), in order for beginner readers of the Latin alphabet to differentiate mirrored letters such as and <d>, for example, and consequently master the script they are exposed to. Consistently, proficient readers of the Latin alphabet are able to discriminate between mirrored patterns, and are consequently unable to ignore mirrored contrasts even when this hinders performance (Fernandes, Leite, & Kolinsky, 2016; Kolinsky & Fernandes, 2014; Pegado, Nakamura et al., 2014), which attests that their visual system automatically encodes mirrored stimuli as being different. This is not the case of preliterate children who are known to make mirror errors when they start reading and writing (e.g., Fernandes et al., 2016) and of adults who either remained illiterate for socioeconomic reasons (Kolinsky et al., 2011; Pegado, Comerlato et al., 2014) or who acquired a script that does not include mirrored characters (Danziger & Pederson, 1998; Pederson, 2003). In addition, it has been shown that, once triggered by literacy, the capacity to break mirror invariance generalizes to non-linguistic visual stimuli (e.g., Fernandes & Kolinsky, 2013; Kolinsky et al., 2011) and that this generalization is stronger for materials that resemble letters such as false-fonts or

geometric shapes compared to pictures of familiar objects (Fernandes et al., 2016; Hannagan, Amedi, Cohen, Dehaene-Lambertz, & Dehaene, 2015; Kolinsky & Fernandes, 2014; Kolinsky et al., 2011; Pegado, Comerlato et al., 2014; Pegado, Nakamura et al., 2014).

Among the brain regions associated to reading is a region of the left ventral occipito-temporal cortex, commonly called the visual word form area (VWFA, Cohen et al., 2002). It is associated with literacy acquisition across different scripts (e.g., Baker et al., 2007; Bolger, Perfetti, & Schneider, 2005; Nakamura et al., 2012; Wu, Ho, & Chen, 2012) and is robustly activated when written strings of a known script are presented to sighted literates (for a review, see e.g., Dehaene & Cohen, 2011). It has been suggested that this region, part of the ventral occipito-temporal stream, is coopted for reading (Dehaene & Cohen, 2007) because it presents appropriate connectivity with the spoken language network (as indicated by functional/structural connectivity and co-lateralization studies, e.g., Bouhali et al., 2014; Cai, Lavidor, Brysbaert, Paulignan, & Nazir, 2008) and because it offers useful properties for written strings recognition such as some degree of abstraction, namely the ability to process letter strings identities irrespective of case, font, size or location in the visual field (e.g., Cohen et al., 2002; Dehaene et al., 2001, 2004; Qiao

et al., 2010; but see; Rauschecker, Bowen, Parvizi, & Wandell, 2012). This brain region has also been described as underlying the ability to perform mirror discrimination of words (Dehaene et al., 2010) and of single letters (Pegado et al., 2011).

In short, acquiring a script that includes mirrored characters pushes sighted individuals to break mirror invariance for the characters they learn to read, and this effect generalizes to visual materials sharing visual similarity with the original script. Is this process limited to the visual modality, or can it generalize to any sensory input used to read, which would then reflect a more general perceptual computation not specifically tight to vision?

In line with this research question, the goal of this study was to test whether the developmental process of breaking mirror invariance depends, or not, on visual experience and visual inputs. The study of congenitally blind individuals provides a unique opportunity to test this hypothesis since most of them learn to read Braille, a written system relying on tactile exploration of embossed dot patterns that, in the same way as some of the Latin letters, are symmetric to each other. It is known that congenitally blind subjects efficiently detect (Cattaneo, 2017) and process the symmetry of tactile patterns (Cattaneo et al., 2010) among which Braille-like displays (Bauer et al., 2015), but their ability to break mirror invariance when they are exposed to a linguistic or a non-linguistic material had never been tested so far. We therefore developed a behavioral protocol specifically dedicated to the tactile exploration of mirrored and non-mirrored pairs of Braille letters and of embossed geometric shapes and Latin letters, and tested a large group of congenital blind (CB) Braille readers. More specifically, CB participants were tested in two same-different judgment tasks of simultaneously presented stimuli. One task assessed their expertise at processing different materials through the measure of their performance on mirrored items whose general orientation had to be taken into account and associated to a "different" response for successful performance (orientation-based task). The other task evaluated their ability to automatically break mirror invariance through mirrored items whose general orientation had to be ignored and associated to a "same" response for successful performance (shape-based task, cf. Fernandes et al., 2016; Kolinsky & Fernandes, 2014). Their results were compared to those of an age-matched group of sighted individuals tested on the same materials but presented visually. Given that these subjects were experts at processing Latin letters, we expected them to show a classical pattern of results for this material, namely a relative ease at considering mirrored items as "different" in the orientation-based task and a relative difficulty at considering mirrored items as "same" in the shape-based task. We also predicted that CB participants would be particularly good at the orientation-based task given their reported tactile acuteness with both Braille and other (including non-meaningful) tactile stimuli (Bauer et al., 2015; Goldreich & Kanics, 2003). Regarding the shape-based task, we foresaw that even though they acquired literacy through the tactile modality and in the absence of vision, CB participants would automatically break mirror invariance for all materials and especially for Braille letters, the material they had the most expertise with.

Table 1 – CB information. Participants' gender (M = male; F = female), age (years), reported type of blindness (0: absence of vision, 1: light perception, 2: color perception), cause of blindness (1: pigmentary retinopathy, 2: Leber amaurosis, 3: Norrie disease, 4: oxygen toxicity, 5: glaucoma, 6: retinal detachment, 7: optical nerve atrophia, 8: corneal distrophia associated with keratite) and reported age of Braille acquisition (years). An objective measurement of Braille expertise is presented in the far right column and represents the averaged number of words (W) and pseudo-words (PW) read out-loud per minute.

Name	Gender	Age	Type of blindness	Cause of blindness	Age of Braille	Mean of W and PW/minute
DD	М	58	1	1	5	50
FE	М	40	0	3	5	42
KT	F	36	0	2	6	27
IT	М	28	1	2	6	28
BL	F	35	1,2	8	9	36
MT	F	43	0	4	5	24
AC	F	45	1	2	6	48
SC	М	39	1	2	6	43
SJ	F	38	1	1	4	32
CC	М	29	1	2	5	21
IL	М	21	1,2	5	6	27
CB	F	43	1	1	5	18
ADB	М	49	1	7	6	39
VS	М	37	0	4	5	26
OL	М	35	1	2	5	33
JW	М	31	0	3	4-5	61
MT	М	30	1	6	5—6	39
PL	М	48	0	4	5—6	52

2. Method

2.1. Participants

The Research Ethics Boards of the department of Psychology of the Université Libre de Bruxelles (Belgium) approved the experiment. A total of 19 French-speaking congenital blind (CB) were tested in this experiment. We excluded one participant from the sample because his averaged percentage of correct responses over the whole experiment was significantly below (X - 2.5 SD) the one of the rest of the group. Thus the final sample included 18 CB individuals (6 female; mean age: 38 years, SD = 8.6), either totally blind (6 participants; Table 1) or with rudimentary sensitivity for brightness differences (10 participants) and/or rudimentary color perception (2 participants) but without any shape perception since birth. They reported no additional neurological problems, to have learned Braille between 4 and 9 years of age and to have no expertise of lower-case Latin letters (Table 1). We evaluated their reading profiles through two reading fluency tests for which they were asked to read aloud as many (Braille) words or pseudo-words as possible in a minute.

Eighteen sighted participants with no visual or tactile experience with Braille were also tested for comparison. They were part of a larger group of 25 participants tested for another study. They were all female, all right-handed and agematched to the CB group [t(35) = .254, p = .801]. They were all expert readers, none of them was familiar with Braille and their vision was normal or corrected to normal.

2.2. Stimuli

Three categories of stimuli were used: Braille letters (B), geometric shapes (S) and lower-case Latin letters (L). The Braille alphabet is the substitution system blind individuals use the most for reading. It is typically acquired during childhood and is composed of Braille characters (called "cells") constructed on the basis of a 2 × 3 matrices of six positions called "dots". One character is distinguishable from the other on the basis of the number of "raised" dots and of their specific arrangement. We chose 7 letters for this study. Critically, all of them were reversible since they can all, as the rest of the Braille alphabet, be mapped onto meaningful representation after mirroring. Accordingly, we also selected 7 geometric shapes and 7 Latin letters from the material used by Fernandes and collaborators (2016) that were the less prone to ink superposition after embossing, among which two were reversible (Fig. 1A).

For the tactile version of the experiment, all 3 materials were centered on 10.5 cm \times 6 cm cards. Braille cells precisely subtended 4 mm \times 8 mm while the superficies increased to 130 \times 131 mm for embossed letters and from 64 \times 248 mm to 240 \times 246 mm for embossed shapes (Fig. 1A). Sighted participants viewed the same stimuli but at 57 cm of a computer screen presented against a white background, with Braille cells, Latin letters and shapes subtending 3 \times 2, 2 \times 1.5 and 6 \times 4 degrees of visual angle, respectively.

2.3. Procedure

In line with Fernandes and collaborators (2013), both CB and sighted participants were presented with a total of six samedifferent tests (3 materials \times 2 tasks), all in one testing session. Participants were involved in two tasks aiming at evaluating differently participants' ability to process symmetry. The shape-based task required participants to consider identical (I) and mirrored (M^1) pairs as "same" and fully *different pairs* (D, in which stimuli varied by both shape and

¹ Mirrored pairs involved symmetry around the vertical axis (HM; left-right flip) in half of the trials and around the horizontal axis (VM; top-down flip) in the other half of the trials.



Fig. 1 – A. Braille cells, embossed geometric shapes and Latin letters used in the experiment, both with CB and sighted participants. The items are not scaled in the figure as they were in the experiment. B. Example of an identical (I: "è"-"è"), a fully different (D: "è"-"à"), a horizontal mirrored (H: "è"-"z"), and a vertical mirrored (V: "è"-"ë") Braille (French) pair.

orientation) as "different" (Fig. 1B). To perform adequately, they had therefore to base their judgment of mirrored pairs on the invariant shape of the constitutive items while ignoring their orientation. Conversely, only I pairs had to be considered as "same" in the orientation-based task, in which both M and D pairs had to be considered as "different". In this task, judgments of mirrored pairs had therefore to be performed on their orientation while ignoring their shape. The shape-based task was always presented before the orientation-based task to ensure that any mirror interference observed on the shapebased task would not be due to previous requirement to take orientation into account. We compensated the unequal number of same/different responses within each task by artificially adding 28 different and 28 identical trials to the shape-based task and orientation-based task, respectively. In this way, in each task, half of the trials required a "same" response and the other half required a "different" response (shape-based task: 42 D, 14 I, 28 M; orientation-based task: 42 I, 14 D, 28 M).

All participants performed the experiment in a sitting position. At the beginning of each task, CB participants were orally instructed that they would have to tactically explore and compare, as accurately and as quickly as possible, pairs of items the experimenter would place in front of them, on a table. The elements of each pair were always placed 26 cm away from each other and 6 cm away from 2 button boxes connected to the E-prime 2.0 software (http://www.pstnet. com/eprime). Then participants were asked to put their thumbs on the button boxes placed right underneath the pairs of stimuli (right thumb on the right button box and left thumb on the left button box) and to lift them simultaneously as soon as they heard a 100 msec beep launched after a 100 msec blank interval, which indicated that they could start to explore the items placed in front of them with their index fingers (right index on the right item, left index on the left item and no transfer allowed between the 2 items). CB subjects quickly learned to use the sound as the confirmation that they could start to explore the stimuli. The tactile exploration phase ended when a same/different response was made (the assignment of same/different responses to the right/left button box was counterbalanced across participants). The intertrial interval was of ~500 msec [490 msec-510 msec].

The sequence of events was identical for sighted participants who viewed pairs of stimuli presented side by side on a computer screen. As blind individuals, they were asked to provide their responses by pressing the response boxes (same/ different responses and right/left button boxes counterbalanced across participants).

Each task started by 8 practice trials followed by 84 randomly presented trials (7 original stimuli \times 4 conditions \times 3 repetitions) separated into 2 blocks of 42 trials. Practice trials had to be performed with a minimum of 75% of correct responses to engage the test trials. Tasks were counterbalanced across participants.

3. Results

To check for task commitment and control for response biases, we first converted participants' mean accuracy scores for each task separately into d' scores adapted for same-different designs (Macmillan & Creelman, 2005). The repeated measure ANOVA performed on these scores revealed a significant main effect of group for each task (both *ps* < .001, see Supplemental Material). Sighted participants performed overall better than CB participants (see Table S1 for proportion of correct responses on mirrored and non-mirrored trials in each group and each task). To control for this overall difference between groups, we calculated normalized indexes for each task separately, based on participants' accuracy scores. As in former studies (Fernandes & Kolinsky, 2013; Fernandes et al., 2016; Pegado, Nakamura et al., 2014), we calculated, for the orientation-based task, mirror drops by contrasting participants' "different" responses on M and D trials, using the formula (M-D)/(M+D). For the shape-based task, we estimated mirror costs by contrasting participants' "same" responses on M and I trials, using the formula (M-I)/(M+I).

Supplemental material presents (a) participants' speed values, because these were exploration times ranging in seconds for CB participants and reaction times ranging in milliseconds for sighted participants, therefore possibly relying on different brain mechanisms; (b) participants' detailed scores on HM and VM trials and (c) Bayes factor analyses for each of the analyses presented here below.

3.1. Orientation-based task

The 3 (material: B - S - L) × 2 (group: blind – sighted) repeated measure ANOVA on participants' mirror drops, which estimate their relative difficulty of having to respond "different" to mirrored pairs compared to fully different pairs, revealed main effects of material [F(2,64) = 22.729, p < .001; $\eta^2 = .372$] and group [F(1,32) = 13.75, p < .001; $\eta^2 = .301$] as well as a significant material by group interaction [F(2,64) = 6.421, p = .003; $\eta^2 = .105$]. We therefore looked at the response pattern of each group separately.

CB participants showed a significant main effect of material $[F(2,34) = 26.335, p < .001; \eta^2 = .608]$ testifying of their expertise with the Braille material, on which they experienced a much weaker mirror drop than on either geometric shapes [t(17) = 6.58, p < .001; Cohen's d = 1.641] or Latin letters [t(17) = 5.941, p < .001; Cohen's d = 1.230], without significant difference between the two latter materials [t(17) = -.8, p = 1; Cohen's d = -1.167]. In fact, they showed a null mirror drop for Braille [unilateral one-sample t-test: t(17) = .000, p = .5; Cohen's d = .000], suggesting that they experienced no difficulty at all with the Braille mirrored pairs. In contrast, mirrored images of embossed shapes and Latin letters induced an important mirror drop that was significantly different from zero [unilateral one-sample ttests: S: t(17) = -7.300, p < .001; Cohen's d = -1.721; L: t(17) = -5.828, p < .001; Cohen's d = -1.374] (Fig. 2A). We

Congenitally Blind

further checked whether CB's expertise with Braille, as estimated by the number of Braille words of pseudo-words they read aloud per minute, had an influence on their mirror drop for Braille. This correlation did not reach significance [two-tailed Pearson correlation: r(16) = -.431, p = .079].

Sighted participants also showed a significant main effect of material [F(2,30) = 5.011, p = .013; $\eta^2 = .250$]. Post-hoc t-tests revealed that their mirror drop was stronger for geometric shapes than for either Latin letters [t(16) = -2.236, p = .040; Cohen's d = -.542] or Braille [t(15) = 2.371, p = .032; Cohen's d = .593], without significant difference between the two latter materials [t(16) = .737, p = .472; Cohen's d = .179]. Moreover, the mirror drop was significantly different from 0 for shapes [unilateral one-sample t-tests: t(16) = -2.375, p = .015; Cohen's d = -.576) and Latin letters (t(17) = -1.890, p = .038; Cohen's d = -.445) but not for Braille (t(16) = -.391, p = .350; Cohen's d = -.095] (Fig. 2A).

In addition, mirror drops did not differ between groups for Braille [t(33) = .286, p = .777; Cohen's d = .097] while significant group differences were observed for geometric shapes [t(33) = -2.092, p = .044; Cohen's d = -.708] and Latin letters [t(34) = -5.366, p < .001; Cohen's d = -1.789]. Finally, it is worth noting that mirror drops did not differ when contrasting each group's material of expertise, namely Braille for CB subjects and Latin letters for sighted participants [t(34) = 1.022, p = .314; Cohen's d = .341].



Sighted

Fig. 2 – A. Mean mirror drop observed on the 3 materials (Braille, geometric shapes, Latin letters) in the orientation-based task. The more negative is the drop, the stronger the difficulties to discriminate mirrored stimuli. B. Mean mirror cost observed on the 3 materials (Braille, geometric shapes, Latin letters) in the shape-based task. The more negative is the cost, the stronger is the interference of mirror contrasts on shape judgments.

3.2. Shape-based task

The 3 (material: B - S - L) × 2 (group: blind – sighted) repeated measure ANOVA on participants' mirror costs which estimates their relative difficulty of having to respond "same" to mirrored (M) pairs compared to identical (I) ones revealed no main effect of material [F(2,68) = .211, p = .810; $\eta^2 = .006$], or of group [F(1,34) = 1.459, p = .235; $\eta^2 = .041$] but a significant material by group interaction [F(2,68) = 3.185, p = .048; $\eta^2 = .085$], which credits for the below-mentioned (group) decomposition.

The main effect of material did not reach significance, in CB participants $[F(2,34) = 1.445, p = .250; \eta^2 = .078]$ or in sighted subjects $[F(2,34) = 1.816, p = .178; \eta^2 = .096]$, indicating that both groups broke mirror invariance for their material of expertise (Braille letters for CB and Latin letters for sighted), and that this effect generalized across materials (Fig. 2B). This result was confirmed by the observation that mirror costs were significant for all materials, in both groups (unilateral one-sample t-tests: ps < .05; Cohen's d between -1.132 and -.450). CB participants' mirror cost for all materials also significantly and negatively correlated with their expertise with Braille, as measured by their reading fluency [a priori one-tailed Pearson correlation: r(16) = -.424, p = .040], especially when CB subjects demonstrated a high expertise with Braille (Fig. 3). Additional group comparisons indicated that the mirror costs only differed between the two groups for Latin letters [sighted > blind: t(34) = 2.468, p = .019; Cohen's d = .823], but not for shapes [t(34) = -1.877, p = .069; Cohen's d = -.626], nor for Braille [t(34) = .724, p = .474; Cohen's d = .241]. In addition, the mirror cost experienced by CB participants for Braille was not stronger than the mirror cost experienced by sighted participants for Latin letters [t(34) = 1.681, p = .102; Cohen's d = .560].

4. Discussion

In this study, we used congenital blindness as a model system to shed light on whether the perceptual mechanisms that enables sighted individuals to discriminate mirrored letters such as and <d> requires visual experience and visual inputs. In particular, we tested if a group of congenital blind subjects, who have



Fig. 3 – Correlations between the CB participants' mirror costs for all 3 materials and the number of Braille words (W) and pseudo-words (PW) they could read aloud in 1 min.

acquired reading through the tactile modality during their childhood, break mirror invariance in the same way as agematched sighted readers do for the Latin alphabet. We did so thank to the use of two tasks. One task indexed mirror discrimination through the evaluation of CB's expertise at processing mirrored and non-mirrored pairs of Braille letters, geometric shapes and Latin letters (orientation-based task: mirrors have to be considered as "different"). Another task assessed their ability to automatically break mirror invariance, namely the tendency to automatically respond "different" to mirrored pairs of the expert script (shape-based task: mirrors have to be considered as "same"). For the orientation-based task, we expected blind participants to show better performance on the mirrored Braille trials relative to fully different Braille trials because, given their reading expertise, we expected their explicit discrimination of the mirrored Braille items to be good. For the shape-based task, we hypothesized that they would show worse performance on mirrored trials relative to identical trials, especially for their material of expertise, in case they would break mirror invariance as sighted do.

Accordingly, we observed in the orientation-based task that CB proficiently processed the items of the reading Braille material. The mirror drop indexes specifically calculated for this task ((M–D)/(M+D)) did indeed not reach significance for this material. We also found that the drops for what were the non-linguistic materials for them - geometric shapes and embossed Latin letters - were much more massive and significantly different from what had been observed for Braille. This result illustrates the extreme difficulty CB subjects have when they have to consider the mirrored items of geometric shapes and Latin letters as "different" even though they pointed, for example, to opposite directions (< vs >; Fig. 1; for similar results on illiterate sighted people, see Fernandes & Kolinsky, 2013). According to us, this difficulty is related to the fact that blind people use an internal system of reference for spatial representations to process the non-linguistic materials, as they do when they touch or process numbers. Studies on tactile stimulus localization indeed demonstrated that whereas sighted people rely on an external spatial frame of reference (i.e., locations are represented within a framework external to the body to locate tactile events), blind individuals preferentially use an anatomical frame of reference to represent spatial relationships (i.e., locations are represented with respect to the position of the body and of the limbs; Collignon, Charbonneau, Lassonde, & Lepore, 2009; Röder, Rösler, & Spence, 2004) even in case of sight restoration after a period of congenital blindness (Ley, Bottari, Shenoy, Kekunnaya, & Röder, 2013). In the same vein, blind and sighted people differ in term of how they process number-space interactions (Crollen, Dormal, Seron, Lepore, & Collignon, 2013). In particular, sighted show a classic SNARC effect under hand-crossed and uncrossed conditions (i.e., small numbers eliciting faster left-sided responses and large numbers eliciting faster rightsighted responses, independently of the responding hand) while, in the blind, the numerical stimulus primes a particular anatomical hand (i.e., small numbers eliciting faster left-hand responses and large numbers eliciting faster right-sighted responses only in the uncrossed condition while the reverse pattern emerges when the blind hands are crossed over their body midline) (Crollen et al., 2013). Importantly, blind

individuals' reliance on an internal frame of reference does however not prevent them from using, as sighted do, an external frame of reference for the spatial representations of time (Bottini, Crepaldi, Casasanto, Crollen, & Collignon, 2015).

That is, blind people have access to both systems of reference and our results suggest that their *default* spatial system of reference might be internal before being unlearnt and externalized as a consequence of Braille reading. The same developmental transition indeed occurs in the sighted brain: while sighted preliterate children and illiterate adults have difficulties discriminating reflections across the object principal axis and across the external vertical axis, the same does not hold true for age-matched literate children and literate adults who only struggle with the former type of reflections (Fernandes, Coelho, Lima, & Castro, 2017; Gregory, Landau, & McCloskey, 2011; Gregory & McCloskey, 2010).

As blind participants, sighted also showed in the orientation-based task a marker of expertise for the material they use on an everyday basis, Latin letters. Their mirror drops were indeed significant but still close to zero for this material. In contrast, they performed much worse with the non-expert material, geometric shapes. Despite their absence of expertise with the Braille material, sighted also showed an absence of mirror drop for Braille cells that we attribute to two contingent factors: their smaller size compared to shapes, which could possibly have increased their efficient processing as wholes (i.e., holistic processing helping gluing independent features into a coherent percept), and their specific format of black dots arranged according to main axes, which is known to overall increase symmetry perception (Wagemans, 1997).

Regarding the shape-based task, we did not find greater interference indexes (mirror costs = (M-I)/(M+I)) in CB or in sighted individuals for their respective material of expertise compared to the other two materials. In fact, and as previously suggested, the effects significantly differed from zero and generalized across materials in sighted as a consequence of literacy acquisition (Fernandes et al., 2016; Hannagan et al., 2015; Kolinsky & Fernandes, 2014; Kolinsky et al., 2011; Pegado, Comerlato et al., 2014; Pegado, Nakamura et al., 2014). The pattern of results was identical for CB. As the exact counterpart of what has been proposed for the sighted brain, we would therefore suggest that, as a consequence of literacy, learning to read Braille through the tactile modality significantly impacts not only CB's judgment of mirrored Braille pairs but also their judgment of similar pairs out of materials that are non-linguistic to them (geometric shapes and Latin letters). This conclusion is supported by two observations. The first one is their null mirror drop for Braille observed in the orientation-based task, which attests of their expertise with this material. The second one is the significant increase of their mirror cost averaged across materials the greater is their fluency with Braille, which attests of the fluctuation of this bias with Braille expertise (for similar results on sighted adults and children, see Fernandes et al., 2016; Pegado, Nakamura et al., 2014).

Overall, the current findings are twofold. On the one hand, they illustrate that blind individuals rely on an internal frame of reference to process, through the tactile modality, materials they do not have expertise with. This phenomenon is manifested in this study by their acute difficulty at judging mirrored pairs of non-linguistic materials as "different" compared to what is observed in sighted. On the other hand, our results emphasize that the ability to automatically break mirror invariance is similar in proficient blind and sighted readers, even though the former have always lacked of visual experience and inputs. Visual experience is therefore not mandatory to trigger the ability to break mirror invariance, suggesting that this effect relates to cognitive and cerebral systems that execute a given function or computation regardless of the sensory input they operate on. In particular, we think of the VWFA as the best candidate to underlie this perceptual bias. It is indeed sensitive to the mirror discrimination of letters in sighted (Pegado et al., 2011) and it shows preferential responses to Braille in early blind people (Büchel, Price, & Friston, 1998; Reich, Swed, Cohen, & Amedi, 2011). If correct, this would indicate that regions of the ventral occipito-temporal stream typically supporting visual processing in sighted individuals can, in the absence of visual input even during early development, reorganize themselves to process inputs from the preserved modalities and maintain similar computational principles as those implemented in the sighted brain (Dormal & Collignon, 2011).

Acknowledgments

We would like to deeply thank all the CB participants who participated in the study. This work was supported by an Interuniversity Attraction Poles (IAP) grant 7/33, Belspo. RK is Research Director and OC is Research Associate of the Fonds de la Recherche Scientifique – FNRS, Belgium.

Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.cortex.2018.01.002.

REFERENCES

- Ahr, E., Houdé, O., & Borst, G. (2016). Inhibition of the mirror generalization process in reading in school-aged children. Journal of Experimental Child Psychology, 145, 157–165.
- Baker, C. I., Liu, J., Wald, L. L., Kwong, K. K., Benner, T., & Kanwisher, N. (2007). Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. Proceedings of the National Academy of Sciences of the United States of America, 104, 9087–9092.
- Bauer, C., Yazzolino, L., Hirsch, G., Cattaneo, Z., Vecchi, T., & Merabet, L. B. (2015). Neural correlates associated with superior tactile symmetry perception in the early blind. Cortex, 63, 104–117.
- Baylis, G. C., & Driver, J. (2001). Shape-coding in IT cells generalizes over contrast and mirror reversal, but not figureground reversal. Nature Neuroscience, 4, 937–942.
- Bolger, D. J., Perfetti, C. A., & Schneider, W. (2005). Cross-cultural effect on the brain revisited: Universal structures plus writing system variation. *Human Brain Mapping*, 25, 92–104.
- Bornstein, M., Gross, C., & Wolf, J. (1978). Perceptual similarity of mirror images in infancy. *Cognition*, 6, 89–116.

Borst, G., Ahr, E., Roell, M., & Houdé, O. (2015). The cost of blocking the mirror generalization process in reading: Evidence for the role of inhibitory control in discriminating letters with lateral mirror-image counterparts. *Psychonomic Bulletin & Review*, 22, 228–234.

Bottini, R., Crepaldi, D., Casasanto, D., Crollen, V., & Collignon, O. (2015). Space and time in the sighted and blind. *Cognition*, 141, 67–72.

- Bouhali, F., Thiebaut de Schotten, M., Pinel, P., Poupon, C., Mangin, J. F., Dehaene, S., et al. (2014). Anatomical connections of the visual word form area. *Journal of Neuroscience*, 34, 15402–15414.
- Büchel, C., Price, C., & Friston, K. (1998). A multimodal language region in the ventral visual pathway. *Nature*, 394, 274–277.
- Cai, Q., Lavidor, M., Brysbaert, M., Paulignan, Y., & Nazir, T. A. (2008). Cerebral lateralization of frontal lobe language processes and lateralization of the posterior visual word processing system. *Journal of Cognitive Neurosciences*, 20, 672–681.
- Cattaneo, Z. (2017). The neural basis of mirror symmetry detection: A review. Journal of Cognitive Psychology, 29, 259–268.
- Cattaneo, Z., Fantino, M., Silvanto, J., Tinti, C., Pascual-Leone, A., & Vecchi, T. (2010). Symmetry perception in the blind. Acta Psychologica, 134, 398–402.
- Cohen, L., Lehéricy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language-specific tuning of visual cortex? Functional properties of the visual word form area. *Brain*, 125, 1054–1069.
- Collignon, O., Charbonneau, G., Lassonde, M., & Lepore, F. (2009). Early visual deprivation alters multisensory processing in peripersonal space. *Neuropsychologia*, 47, 3236–3243.
- Corballis, M. C., & Beale, I. L. (1976). The psychology of left and right. Hillsdale, NJ: Erlbaum.
- 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, 276–283.
- Danziger, E., & Pederson, E. (1998). Through the lookingglass: Literacy, writing systems and mirror-image discrimination. Written Language and Literacy, 1, 153–164.
- Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. Neuron, 56, 384–398.
- Dehaene, S., & Cohen, L. (2011). The unique role of the visual word form area in reading. Trends in Cognitive Sciences, 15, 254–262.
- Dehaene, S., Cohen, L., Morais, J., & Kolinsky, R. (2015). Illiterate to literate: Behavioural and cerebral changes induced by reading acquisition. Nature Reviews Neuroscience, 16, 234–244.
- Dehaene, S., Jobert, A., Naccache, L., Ciuciu, P., Poline, J. B., Le Bihan, D., et al. (2004). Letter binding and invariant recognition of masked words: Behavioral and neuroimaging evidence. Psychological Sciences, 15, 307–313.
- Dehaene, S., Naccache, L., Cohen, L., Le Bihan, D., Mangin, J. F., Poline, J. B., et al. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. Nature Neuroscience, 4, 752–758.
- Dehaene, S., Nakamura, K., Jobert, A., Kuroki, C., Ogawa, S., & Cohen, L. (2010). Why do children make mirror errors in reading? Neural correlates of mirror invariance in the visual word form area. *NeuroImage*, 49, 1837–1848.
- Dormal, G., & Collignon, O. (2011). The functional selectivity in sensory-deprived cortices. Journal of Neurophysiology, 105, 2627–2630.
- Duñabeitia, J. A., Molinaro, N., & Carreiras, M. (2011). Through the looking-glass: Mirror reading. NeuroImage, 54, 3004–3009.
- Fernandes, T., Coelho, B., Lima, F., & Castro, S. L. (2017). The handle of literacy: Evidence from preliterate children ad illiterate adults on orientation discrimination of graspable and non-graspable objects. Language, Cognition and Neuroscience. https://doi.org/10.1080/23273798.2017.1283424.

- Fernandes, T., & Kolinsky, R. (2013). From hand to eye: The role of literacy, familiarity, graspability, and vision-for-action on enantiomorphy. Acta Psychologica, 142, 51–61.
- Fernandes, T., Leite, I., & Kolinsky, R. (2016). Into the looking glass: Literacy acquisition and mirror invariance in preschool and first-grade children. *Child Development*, 87, 2008–2025.
- Freiwald, W. A., & Tsao, D. Y. (2010). Functional compartmentalization and viewpoint generalization within the macaque face-processing system. Science, 330, 845–851.
- Goldreich, D., & Kanics, I. M. (2003). Tactile acuity is enhanced in blindness. Journal of Neuroscience, 23, 3439–3445.
- Gregory, E., Landau, B., & McCloskey, M. (2011). Representation of object orientation in children: Evidence from mirror-image confusions. Visual Cognition, 19, 1035–1062.
- Gregory, E., & McCloskey, M. (2010). Mirror-image confusions: Implications for representation and processing of object orientation. Cognition, 116, 110–129.
- Hannagan, T., Amedi, A., Cohen, L., Dehaene-Lambertz, G., & Dehaene, S. (2015). Origins of the specialization for letters and numbers in ventral occipitotemporal cortex. *Trends in Cognitive Sciences*, 19, 374–382.
- Kolinsky, R., & Fernandes, T. (2014). A cultural side effect: Learning to read interferes with object identity processing. Frontiers in Psychology, 5, 1224.
- Kolinsky, R., Verhaeghe, A., Fernandes, T., Mengarda, E. J., Grimm-Cabral, L., & Morais, J. (2011). Enantiomorphy through the looking glass: Literacy effects on mirror-image discrimination. Journal of Experimental Psychology General, 140, 210–238.
- Ley, P., Bottari, D., Shenoy, B. H., Kekunnaya, R., & Röder, B. (2013). Partial recovery of visual-spatial remapping of touch after restoring vision in a congenitally blind man. Neuropsychologia, 51, 1119–1123.
- Logothetis, N. K., Pauls, J., & Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. *Current Biology*, 5, 552–563.
- Macmillan, N. A., & Creelman, C. D. (Eds.). (2005). Detection theory: A user's guide (2nd ed). Mahwah, NJ: Erlbaum.
- Nakamura, K., Kuo, W. J., Pegado, F., Cohen, L., Tzeng, O. J., & Dehaene, S. (2012). Universal brain systems for recognizing word shapes and handwriting gestures during reading. Proceedings of the National Academy of Sciences of the United States of America, 109, 20762–20767.
- Pederson, E. (2003). Mirror-image discrimination among nonliterate, monoliterate, and biliterate Tamil subjects. Written Language and Literacy, 6, 71–91.
- Pegado, F., Comerlato, E., Ventura, F., Jobert, A., Nakamura, K., Buiatti, M., et al. (2014). Timing the impact of literacy on visual processing. Proceedings of the National Academy of Sciences of the United States of America, 111, E5233–E5242.
- Pegado, F., Nakamura, K., Braga, L. W., Ventura, P., Nunes Filho, G., Pallier, C., et al. (2014). Literacy breaks mirror invariance for visual stimuli: A behavioral study with adult illiterates. Journal of Experimental Psychology: General, 143, 887–894.
- Pegado, F., Nakamura, K., Cohen, L., & Dehaene, S. (2011). Breaking the symmetry: Mirror discrimination for single letters but not for pictures of the Visual Word Form Area. *NeuroImage*, 55, 742–749.
- Perea, M., Moret-Tatay, C., & Panadero, V. (2011). Suppression of mirror generalization for reversible letters: Evidence from masked priming. Journal of Memory and Language, 65, 237–246.
- Qiao, E., Vinckier, F., Szwed, M., Naccache, L., Valabrègue, R., Dehaene, S., et al. (2010). Unconsciously deciphering handwriting: Subliminal invariance for handwritten words in the visual word form area. *NeuroImage*, 49, 1786–1799.

- Rauschecker, A. M., Bowen, R. F., Parvizi, J., & Wandell, B. A. (2012). Position sensitivity in the visual word form area. Proceedings of the National Academy of Sciences of the United States of America, 109, E1568–E1577.
- Reich, L., Swed, M., Cohen, L., & Amedi, A. (2011). A ventral visual stream reading center independent of visual experience. *Current Biology*, 21, 363–368.
- Röder, B., Rösler, F., & Spence, C. (2004). Early vision impairs tactile perception in the blind. *Current Biology*, 14, 121–124.
- Rollenhagen, J. E., & Olson, C. R. (2000). Mirror-image confusion in single neurons of the macaque inferotemporal cortex. *Science*, 287, 1506–1508.
- Wagemans, J. (1997). Characteristics and models of human symmetry detection. TICS, 1, 346–352.
- Wu, C. Y., Ho, M. H., & Chen, S. H. (2012). A meta-analysis of fMRI studies on Chinese orthographic, phonological, and semantic processing. *NeuroImage*, 63, 381–391.