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Review article

How visual is the « number sense »? *Insights from the blind*

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ABSTRACT

Is vision a necessary building block for the foundations of mathematical cognition? A straightforward model to test the causal role visual experience plays in the development of numerical abilities is to study people born without sight. In this review we will demonstrate that congenitally blind people can develop numerical abilities that equal or even surpass those of sighted individuals; despite representing numbers using a qualitatively different representational format. We will also show that numerical thinking in blind people maps onto regions typically involved in visuo-spatial processing in the sighted, highlighting how intrinsic computational biases may constrain the reorganization of numerical networks in case of early visual deprivation. More generally, we will illustrate how the study of arithmetic abilities in congenitally blind people represents a compelling model to understand how sensory experience scaffolds the development of higher-level cognitive representations.

1. A visuo-spatial number sense?

Our ability to accurately process numerical information enable us to process food quantity, time, money and it allows humans to understand complex properties of the environment, build sophisticated engineering and architectural design and send people to the moon. Number processing is therefore an important human cognitive achievement which is nevertheless assumed to rest on a set of core knowledge that humans share with other animals (Rugani et al., 2009, 2008; Spelke, and Kinzler, 2007). For instance, there is ample evidence suggesting that the foundations of numerical processing might be rooted in general visuo-spatial mechanisms (Burr and Ross, 2008; Hubbard et al., 2005; Ross and Burr, 2010; Simon, 1999; Stoianov and Zorzi, 2012).

Vision, when compared to the other senses, present many advantages to access numerical information. For instance, vision allows to simultaneously and accurately process a large amount of information while audition and touch are limited in the amount of information that can be apprehended at the same time (Anobile et al., 2016; Dakin et al., 2011). Accordingly, a strong link between some aspects of visual perception and numerical thinking has been highlighted in the literature. Performances in tasks evaluating visual working memory (Bull et al., 2011; Le Fevre et al., 2010), visual attention (Anobile et al., 2013), visuo-spatial mental rotation (Reuhkala, 2001), basic visual perception (Lourenco et al., 2012; Tibber et al., 2013; Zhou et al., 2015) and visual movement perception (Sigmundsson et al., 2010) were indeed associated with mathematical achievement. Like other primary visual features, numerosity is susceptible to adaptation: several seconds of exposure to a small/large numerosity changes the apparent numerosity of subsequent stimuli viewed in the same position, causing a “repulsive” after-effect by inducing the perception of larger/smaller numerosity, respectively (overestimation vs. underestimation effect; Burr and Ross, 2008; Ross and Burr, 2010). It has even been suggested that such numerical adaptation is relying on visual perception itself (Dakin et al., 2011; Morgan et al., 2014; but see Arrighi et al., 2014). Finally, visuo-spatial deficits such as the one observed in specific genetic disorders (22q11.2 deletion syndrome, fragile X and Turner syndrome; Mazzocco et al., 2016), in hemineglect (Dormal et al., 2014) and in non-verbal learning disability (NVLD) patients (Crollen and Noël, 2015; Crollen et al., 2015; Gomez et al., 2015, 2017) were often associated with problems in basic numerical and arithmetical abilities.

In addition to these links between vision and numerical thinking, many analogies between the processing of numbers and the processing of visual space were also reported. When participants have to make a numerical discrimination task, such as deciding whether a number is smaller or larger than 5, better performances are observed when participants respond to small numbers with a left keypress and to large numbers with a right keypress (see Wood et al., 2008, for a review). Importantly, because the so-called Spatial-Numerical Association of Response Codes or SNARC effect (Dehaene et al.,

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1993) 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 -visual- 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.

Another stream of evidence supporting the idea that numbers and visual space interact with each other come from the number bisection task. This task is the numerical counterpart of the line bisection task (Calabria and Rossetti, 2005; Fischer, 2001) which has been widely used to investigate visuo-spatial attention. It requires participants to bisect a line into two parts of equal length. Right-handed people tend to systematically bisect lines slightly to the left of the objective midline (leftward bias or pseudo-neglect effect; see Jewell and McCourt, 2000). Interestingly, similar visuo-spatial biases occur when control participants are required to indicate (without calculating) the number midway between two others presented auditorily or as Arabic digits, (i.e., number bisection task; Cattaneo et al., 2011; Longo and Lourenco, 2007, 2010; Priftis et al., 2006; Vuilleumier et al., 2004; Zorzi et al., 2002).

An intrinsic connection between numbers and visual space has also been suggested in tasks involving subitizing (Kaufman et al., 1949; Piazza et al., 2011), counting (Simon, 1999) and arithmetic problem solving (Masson and Pesenti, 2014; McCrink et al., 2007). Subitizing is the immediate apprehension of the exact number of items in small sets and has been linked to a non-numerical mechanism of visuo-spatial object individuation (Piazza et al., 2011). Counting, on another hand, involves a visuo-spatial attention search mechanism to isolate the items already counted from those which remained to be counted (Gelman and Gallistel, 1978; Simon, 2011). Arithmetic was finally associated with spatial shifts of visuo-spatial attention (Knops et al., 2009a, b; Masson and Pesenti, 2014; Mathieu et al., 2016; McCrink et al., 2007; Pinhas and Fischer, 2008; Simon, 1999) along the mental number line (Dehaene and Cohen, 1991; Gallistel and Gelman, 1992; Hubbard et al., 2005; Restle, 1970). As small numbers are represented on the left of the line and large numbers on the right, addition problems were assumed to involve a rightward displacement while subtraction problems were assumed to involve a leftward displacement. The so-called “operational momentum effect” is related to the visual phenomenon known as “representational momentum,” in which the location of a linearly moving object that vanishes without warning is systematically shifted in the direction of the object motion (Ashida, 2004; Freyd and Finke, 1984).

Finally, imaging and electrophysiological studies have shown that the underlying neural architecture of number representations closely resembles that of low-level visuo-spatial processes (e.g., Harvey et al., 2013; Shum et al., 2013). Magnitude processing begins in the early visual stream and numerosity-sensitive retinotopic maps are present in areas V2 and V3 (Cavdaroglu et al., 2015; Fornaciai et al., 2017; Roggeman et al., 2011). For instance, ultra-high-field functional magnetic resonance imaging and neural-model-based analyses revealed topographic numerosity map in occipital (visual) regions (Harvey and Dumoulin, 2017). Such close intertwining between numerical and visual perception has raised the possibility that vision may play a foundational role in the acquisition and development of numerical representations and skills. The human visual system could therefore scaffold the detection of numerosity and numerosity changes (Park et al., 2016).

2. Absence of visual experience does not prevent numerical thinking

Evidence from congenitally blind individuals offers a unique opportunity to causally test whether vision plays a foundational role in the development of the concept of numbers. Indeed, if vision is critical for the scaffolding of numerical cognition, then blind people should present atypical numerical behavior. Alternatively, if the “number sense” mostly develops based on abstract representations that can be acquired through other sensory systems and through language, then blind people should show typical numerical abilities.

There are examples of famous blind mathematicians, at least anecdotally suggesting that proficient numerical abilities can develop in the absence of vision. Bernard Morin, for instance, demonstrated in the nineteen-sixties how a sphere could be turned inside out and already suggested that his achievement required a special sort of spatial perception and imagination. Nicholas Saunderson, who worked as Lucasian Professor, a post also held by Isaac Newton and Stephen Hawking, was a blind mathematician able to carry out mentally long and intricate mathematical calculations by using his acute sense of touch. If these cases are anecdotal, recent empirical evidence have demonstrated that blind people are proficient in various numerical tasks (Rinaldi et al., 2018). When asked to enumerate quickly and accurately the number of fingers stimulated, blind people display the same counting (Crollen et al., 2014) and subitizing range (Ferrand et al., 2010) as sighted controls. Blind and sighted people also present the same bisection effects in several auditory number bisection tasks (Blini et al., 2013; Cattaneo et al., 2011, 2010; Rinaldi et al., 2015), the same numerosity adaptation effects with relative under- or over-estimation of perceived auditory numerosity respectively following rapid or slow motor adaptation (Togoli et al., 2020), the same auditory approximate numerosity comparison abilities (Kanjlia et al., 2018) and the same SNARC effect while performing an auditory parity judgement task with the hands uncrossed (Castronovo and Seron, 2007a; Crollen et al., 2013; Szücs and Csépe, 2005). Blind individuals were even shown to outperform sighted people in numerosity estimation involving an ecologic footstep production task, keypress estimation or auditory events estimation (Castronovo and Delvenne, 2013; Castronovo and Seron, 2007b; Ferrand et al., 2010) and calculation tasks (Dormal et al., 2016a,b). Altogether, these data do not support the hypothesis that vision is necessary for the development of advanced numerical abilities. In contrast, they suggest that numerical abilities are not tied to the visual modality and demonstrate that numerical concepts can be acquired through non-visual senses such as touch and audition and/or higher cognitive functions such as language (Dormal et al., 2016a,b; Crollen et al., 2017).

How much of the number sense is linked to ontogenic sensory experience versus innate phylogenetic predisposition is a question that remains highly debated in the field (Toomarian and Hubbard, 2018). Even if the exact processing of symbolic numbers might be specific to humans, converging evidence suggests that symbolic number representations acquire their numerical meaning through being mapped onto non-symbolic representations. Accordingly, it has been shown that many animals such as chicks and new-born infants (less than 3 days old) show habituation to numerosity (de Hevia et al., 2017; Jordan and Brannon, 2006; Lipton and Spelke, 2004; Rugani et al., 2008, 2009) and possess the ability to rapidly estimate the approximate number of items in a scene (Dehaene et al., 1998; Nieder, 2005). Such a number sense is therefore phylogenetically ancient (Butterworth et al., 2011; Dehaene, 2011), and likely innate. Based on these observations, it was suggested that the human mind and brain are endowed with an automatic ability to extract magnitude information from sensory (visual) stimulation (Dehaene, 2011).

However, it remained debated whether visuo-spatial processes were crucial for the optimal development of numerical skills. Evidence from sensory deprived people offers a unique opportunity to address this question. As we have shown above, blind people are able to develop a core sense of number refuting the idea that the development of the number concept is necessarily scaffolded by visuo-spatial development. The phylogenetically older approximate number system does therefore not need vision to develop but can express its innate predisposition differently in case of visual deprivation.

3. Absence of visual experience alters the format of numerical representation

While the quantitative results mentioned above demonstrate that vision is not a mandatory prerequisite for the development of numerical abilities, it does not indicate whether blind and sighted people rely on the same cognitive mechanisms or whether blind people compensate for their lack of vision with the use of alternative strategies to represent numerical estimates. To our knowledge, no study so far has systematically examined how blind people acquire mathematical skills. However, as blind students lack visual perception, there are only two kinds of sensory information that support learning mathematics, in addition to language: tactile-kinesthetic and auditory, which act as a compensation for the lack of vision. It is therefore possible that the use of these compensatory mechanisms shape some qualitative properties (the format) of numerical representations. Moreover, comparing blind people who lost sight early in life along with individuals who lost vision later in life (late-onset blind individuals) allows to probe how experience at different developmental periods shapes the properties of the mental representation of numbers.

For example, when asked to determine whether an auditory number is smaller or larger than 5, early blind people were shown to present a classic SNARC effect when responding with the hands uncrossed and a reversed SNARC effect when responding with the hands crossed over the body midline (see Fig. 1). In the early blind, and in contrast to sighted controls and late blind individuals, the numerical stimulus therefore primed a particular anatomical hand. Small numbers elicited faster right-hand responses, regardless of where in space the hands were placed. Inversely, large numbers elicited faster left-hand responses (Crollen et al., 2013; see Fig. 1A). The results of this experiment indicate the use of hand-based coordinates in the early blind only and therefore suggest that early (and not late) visual deprivation prevents the default-use of an external coordinate system (Collignon et al., 2009a, b; Crollen et al., 2017, 2019a,b,c; Röder et al., 2008, 2007; Röder et al., 2004). Interestingly, when the same participants were required to perform a parity judgement task (i.e., determine whether the number presented is odd or even), sighted controls, late blind and early blind participants showed a classic SNARC effect in the parallel as well as in the crossed-hands posture (see Fig. 1B). This result therefore contrasts with those observed in the magnitude comparison task (Crollen et al., 2013) and therefore supports, as suggested for sighted people, that different spatial information is involved in different tasks: visuo-spatial information in the comparison task vs. verbal-spatial information in the parity judgment task (Gevers et al., 2010, 2006; Proctor and Cho, 2006; Santens and Gevers, 2008). Within this context, early blindness was suggested to shape the coordinate system onto which numbers are mapped but specifically in tasks relying on visuo-spatial processes (not in tasks relying on verbal processes).

Early visual experience also plays an important role in implementing the sensori-motor habits that drive the development of finger-counting, a procedure often used by sighted while learning counting and basic arithmetic (Butterworth, 1999, 2005). Compared with sighted controls, blind children indeed used their fingers

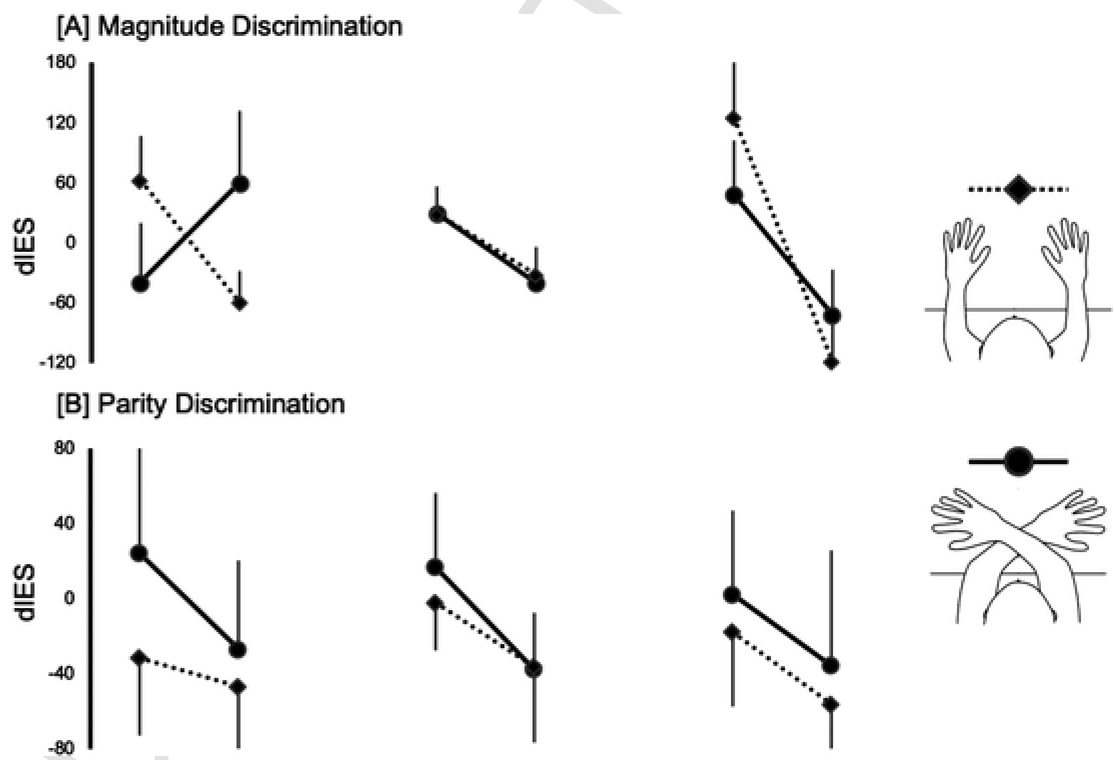

Fig. 1. Congenitally blind (left lines), Late blind (middle lines) and sighted participants (right lines) performances in a number comparison task (A) and in a parity judgement task (B). Performance are represented by inverse efficiency scores (IES), which were obtained by dividing response times (RT) by correct response rates. 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. A classic SNARC effect is reflected by a negative relation between number magnitude and dIES. In the number comparison task (A), a classic SNARC effect was observed in every group in the uncrossed position (dotted lines) and in late blind and sighted individuals in the crossed position (continuous lines). The SNARC effect was, in contrast, reversed when congenitally blind performed the task with the hands crossed over the body midline. In the parity judgment task (B), a classic SNARC effect was observed in every group and in both hand's conditions.

less spontaneously to count and in a less canonical way to count and to show quantities (Crollen et al., 2011). Even more surprisingly and in contrast to what was observed in sighted, blind adults' counting performances (e.g., count how many letters there are between B and M) were not disrupted by the realization of hand movements preventing the use of finger-counting (Crollen et al., 2014). These results demonstrate that the absence of vision precludes the development of a typical finger numeral representation and suggest that the use of canonical finger-counting strategies relies on the visual recognition of particular hand shapes. Importantly, these results show that finger counting is not a mandatory building block to develop advanced numerical skills (Andres et al., 2008; Fayol and Seron, 2005) since blind people who do not rely on fingers to count (Crollen et al., 2011, 2014) have optimal arithmetic skills (Dormal et al., 2016a,b).

If blind children do not rely on finger counting to develop a concept of numerosity, what strategies are they using? Based on previous research blind children are assumed to rely on enhanced auditory working memory to achieve numerical thinking and manipulation and compensate for their lack of vision (Raz et al., 2007; Röder et al., 2001; Siegel and Ryan, 1989; Cornoldi et al., 2009, for similar results with adults in a mental imagery task). Indeed, enhanced working memory abilities in blind people has been assumed to play an important role in the development of the blind's numerical cognition (Castronovo and Delvenne, 2013; Dormal et al., 2016a,b). However, no significant correlation between these 2 processes has never been highlighted so far. This absence of correlation is nevertheless maybe related to the sensitivity of the memory tasks used or to the small sample of blind participants tested in the different studies.

The studies reported above suggest that early visual deprivation does not prevent the development of the number concept but nevertheless affects its underlying properties. In the next part of this review paper, we will see that the foundations of the brain architecture supporting arithmetic processing are likely established through a dynamic interaction between intrinsic organizational factors and environmental conditions and experiences.

4. The neural foundations of arithmetic processing in the blind

Neuroimaging and electrophysiological studies in humans and other animals have shown that the underlying neural architecture of number representations shares properties with those supporting low-level visual processes (e.g., Harvey et al., 2013; Shum et al., 2013). For instance, a multivariate classifier algorithm was shown to be able to infer the direction of left versus right eye movements based on activity recorded in the posterior parietal cortex, and then generalize to sort out subtraction versus addition trials, whether performed with symbols or with sets of dots (Knops et al., 2009a). This study suggests that a region involved in processing eye movement is partially co-opted for solving symbolic and non-symbolic numerical problems, which has been suggested as an instance of "cortical recycling" of a visuo-motor area for a more abstract mathematical use (Knops et al., 2009a; Dehaene and Cohen, 2007). Interestingly, topographic numerosity map (numerotopy) in which neural numerosity preferences progress gradually across the cortical surface (Harvey and Dumoulin, 2017; Harvey et al., 2017, 2013), analogous to sensory maps, have been found in occipital and parietal regions known to display retinotopic mapping (Harvey and Dumoulin, 2017). These regions typically support visuo-spatial cognition (Sack, 2009) and are highly connected to the visual cortices (Uddin et al., 2010). Together, these data suggest that the neural basis of numerical thinking may, at least partially, anchor onto evolutionary ancient low-level visual processes (Dehaene and Cohen, 2007; Hannagan et al., 2015).

What would happen to those regions in case of early visual deprivation? Recently, several studies examined the brain activity of blind and sighted people while performing arithmetic tasks and found common activation in both groups in the classic number-responsive prefrontal and intraparietal regions (Amalric et al., 2018; Crollen et al., 2019a,b,c; Kanjlia et al., 2016). The observation of common activity in both groups suggest that the functional specialization of those regions for arithmetic processing does not depend on visual experience (Kanjlia et al., 2016). However, the observation of similar neural networks for arithmetic processing does not mean that the same cognitive mechanisms or the same representational format are implemented in blind and sighted people in those common regions as we have seen above that congenital blindness qualitatively influences how numbers are represented in the blind's mind (Crollen et al., 2013, 2014, 2019a,b,c). In other words, it might well be that numerical representations in parietal regions intertwin with visuo-spatial or fingers-related maps (Gruber et al., 2001; Zago et al., 2001) in the sighted due to their prominent role in developing arithmetic concepts in this population while those regions anchor onto different perceptual (eg. tactile) or cognitive (e.g. working memories) representation in congenitally blind people due to reorganizations induced by the absence of developmental vision.

In contrast to sighted individuals, congenitally blind people additionally activate their occipital cortex during numerical thinking (see Fig. 2). The recruitment of occipital regions by arithmetic processing in congenitally blind has been used as an evidence that the occipital cortex is functionally flexible early in life (Lane et al., 2015) and capable of repurposing itself toward unrelated cognitive functions apparently distant from visual processes (Kanjlia et al., 2016; Bedny, 2017). This latter argument however relies on the idea that arithmetic and visual processes do not entertain some computational relation. However, as outlined before, several studies have suggested that some specific arithmetic operations are preferentially rooted in specific networks depending on their link with visuo-spatial strategies (Campbell and Timm, 2000; Dehaene and Cohen, 1997; Hecht, 1999; LeFevre et al., 1996; Siegler and Shrager, 1984). For instance, it has been suggested that visuo-spatial procedures are mainly used to solve subtractions (Campbell and Xue, 2001) and

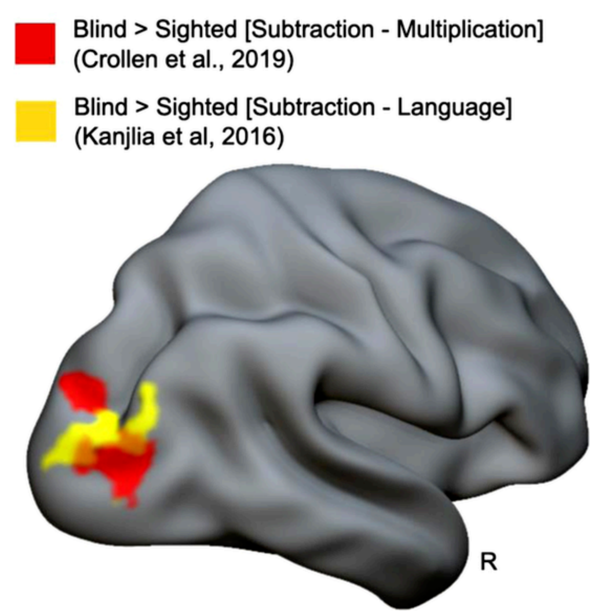

Fig. 2. Activation of the occipital cortex observed in congenitally blind people performing "subtraction" operations. The map is derived from the data of 2 separate studies (Crollen et al., 2019 and Kanjlia et al., 2016).

that subtraction principally engages a network of dorsal parieto-frontal regions (Chochon et al., 1999; Mathieu et al., 2018a; 2018b; Piazza et al., 2007; Prado et al., 2014, 2011) presumably due to the “spatial” strategies used to solve such operations (Siegler and Shrager, 1984). Like subtraction, multiplication requires the mental manipulation of symbolic numbers, yet it is believed to rely on a distinct temporo-parietal network (Chochon et al., 1999; Mathieu et al., 2018a, b; Prado et al., 2011, 2014; Zhou et al., 2007) presumably because multiplications are solved by direct fact retrieval (Cooney et al., 1988). It is therefore possible that early visual deprivation selectively affects the brain organization of visuo-spatial arithmetic operations (subtraction) while keeping intact the neural network involved in the arithmetic operations learned by rote verbal memory (multiplication). This later assumption was recently supported by a study contrasting the brain activity of blind and sighted participants while performing subtraction vs. multiplication arithmetic operations (Crollen et al., 2019a,b,c). As predicted, both groups activated separate brain number network for operating subtraction (i.e., a bilateral dorsal network) versus multiplication (i.e. Temporal regions). However, while no between-group difference was observed for the multiplication task, enhanced activity in the right dorsal occipital cortex was observed in the blind when solving subtraction problems (Crollen et al., 2019a,b,c) (see Fig. 2). Since subtraction is known to rely on “spatial” strategies (Knops et al., 2009a, 2009b; Masson and Pesenti, 2014; McCrink et al., 2007; Pinhas and Fischer, 2008), and because the reorganized regions are known to be involved in visuo-spatial processes in the sighted (Ungerleider and Haxby, 1994), these results suggest a maintenance of functional tuning after sensory deprivation (Dormal and Collignon, 2011). Supporting this idea, a high degree of overlap was observed between the right dorsal regions selectively activated for both subtraction and auditory localization (Collignon, Vandewalle, Voss, Albouy, Charbonneau, Lassonde, & Lepore,; Crollen et al., 2019a,b,c). We infer from this partially common activation that both tasks build on the intrinsic endowment of this region for spatial processing (Collignon et al., 2007, 2011). Moreover, these reorganized regions exhibit increased functional connectivity with a dorsal parieto-frontal network typically involved in spatial attention and shown to be selective for subtraction in both blind and sighted people (Crollen et al., 2019a,b,c). Interestingly, the right middle occipital gyrus was the main cluster specifically activated in congenitally blind people when contrasting arithmetic subtraction with language processing (Kanjlia et al., 2016), a region in the close viscinity with the regions showing selective subtraction activity in the study of Crollen et al. (2019a,b,c) as illustrated in Fig. 2.

These data therefore align with the suggestion that the neural basis of numerical thinking may, at least partially, anchor onto evolutionary ancient processes like those involved in visuo-spatial processing (Dehaene and Cohen, 2007) or shape features sensitivity for the number form area (Abboud et al., 2015; Hannagan et al., 2015). This bias for some specific perceptual/cognitive processes are combined with an intrinsic connectivity profile that is specific to each region (Hannagan et al., 2015). For instance, it was demonstrated that when blind people are presented with numbers encoded using a sensory-substitution device, they show activation in a region overlapping with the number form area in sighted people (Abboud et al., 2015). Using resting-state fMRI in the blind and sighted, the authors further show that the areas with preference for numerals exhibit distinct patterns of functional connectivity with parietal areas involved in processing quantities. In case of visual deprivation, specific occipital regions cannot develop based on low-level visual features. However, the specific bias some regions have to carry out a specific computation in combination with an idiosyncratic connectivity profile with other brain regions involved in a similar functional network create a pressure for this region to keep its intrinsic function even in early blind people (Collignon et al., 2011; Hannagan et al., 2015). This would suggest that the specificity for symbolic number form in the ventral ‘visual’ stream can emerge independently of visual experience, likely under the influence of the distinct connectivity patterns that the number form area has with parietal regions. This view contrasts with the suggestion that occipital recruitment for arithmetic processing would demonstrate that brain regions are pluripotent at birth and that occipital regions in the blind now involves in distant perceptual/cognitive operation than the ones they have been genetically predisposed to (Bedny, 2017).

More generally, we presume that even if high-level cognitive operations colonize the occipital cortex of blind individuals, they do so by recycling a neuronal niche that shares functional similarities with the reorganized function (e.g., subtraction in dorsal occipital regions; Crollen et al., 2019a,b,c). Exactly like it is supposed that evolutionary more ancient parietal circuits are recycled to support arithmetic processing during development, we suggest that, in absence of competitive visual input during development, this neuronal recycling process extends to right dorsal circuit which also represents a suitable neuronal niche to remap numerical processing onto more ancient but computationally compatible circuits (Collignon et al., 2012, 2009). This idea is consistent with other examples of cross-modal plasticity preserving the original function of visual brain areas. Visual motion area hMT+/V5, a region dedicated to processing visual motion in the sighted reorganizes in the blind to process auditory motion (Dormal et al., 2016a,b; Jiang et al., 2016; Poirier et al., 2006). Right dorsal occipital regions typically involved in visuospatial localization in the sighted are active when blind individuals localize sounds (Collignon et al., 2011). Similarly, ventral occipito-temporal regions typically involved in category-specific mapping also seem to partially preserve their functional tuning in case of congenital visual deprivation (Mattioni et al., 2020; Pietrini et al., 2004; Reich et al., 2011; Van den Hurk et al., 2017). In sum, even if the occipital cortex of blind individuals extends its tuning toward non-visual inputs (Bavelier and Neville, 2002), intrinsic network organization narrowly constrains the expression of this cross-modal plasticity (Collignon et al., 2009; Hannagan et al., 2015).

This assumption however needs to be investigated further in the future. To do so, one could examine whether the same kind of brain plasticity dissociation could be observed with other numerical tasks and other numerical stimuli. A functional magnetic resonance imaging study for example recently showed that merely perceiving a "+" sign triggers activity in brain regions that support the orienting of spatial attention in sighted adults (Mathieu et al., 2018b) and in sighted children (Mathieu et al., 2018a). Interestingly, this activity was shown to increase with age and was operation-specific because it was not observed with '×' signs. It could therefore be interesting to: 1) test whether the dissociation between the “+” and the “x” sign could also be observed in the occipital cortex of the blind; 2) investigate whether the developmental neural changes that occur in sighted children can also be observed in blind children.

We recently assessed the role visual experience plays in shaping the neural correlates of tactile spatial localization. For this purpose, sighted and congenitally blind participants were scanned while performing Temporal Order Judgments (TOJ) judgments with the hands uncrossed or crossed over the body midline (Crollen et al., 2017). In practice, this task requires participants to judge which of their two hands receive a tactile stimulation first. At a behavioral level, we observed that crossing the hands massively disrupted TOJ performance in the sighted but not in blind group (Crollen et al., 2017b,2019a,b,c), replicating previous data (Röder et al., 2004).

At the brain level, we observed that the crossed posture, when compared with the uncrossed posture, elicited significantly more activity in the parietal and premotor areas in sighted participants, but not in blind participants (Crollen et al., 2017b). Therefore, another way to further examine the dissociation between visuo-spatial and verbal numerical tasks would be to ask blind participants to perform, in an fMRI scanner, a number comparison task and a parity judgment task with the hands uncrossed and crossed over the body midline. As already mentioned in the previous section, early blindness seems to shape the coordinate system onto which numbers are mapped but specifically in tasks relying on visuo-spatial processes (not in tasks relying on verbal processes). Future studies should therefore examine whether early visual deprivation could change the neural responsiveness of the parietal cortex to the spatial (not verbal) coding of numbers as it has already been observed with the spatial localization of touch (Crollen et al., 2017b).

Finally, while rote arithmetic operations with small numbers have a greater reliance on left-lateralized regions, presumably encoding numbers in a verbal format, approximation and exact calculation with large numbers put heavier emphasis on the left and right parietal cortices, which may encode numbers in a non-verbal quantity format (Stanescau-Cosson et al., 2000). It could therefore be worth to study whether blindness could specifically affect only one of these networks.

5. Conclusions and perspectives: could our understanding of numerical thinking in the blind be used to train the sighted?

Numbers play an important role in our daily lives, they are used in a variety of contexts (e.g., to use mobile phones, cook, deal with money, tell time, etc.) and are most of the time accessed and processed through the visual modality. This supremacy of vision lead to the assumption that vision was critical for the acquisition and the development of numerical representations and skills (Klahr and Wallace, 1973; Simon, 1999). However, and as reviewed in this paper, a new line of research examining the impact of early visual deprivation on numerical cognition demonstrates that vision is not a necessary prerequisite to develop efficient numerical abilities.

First, at the behavioral level, blind people were shown to develop similar subitizing (Ferrand et al., 2010), counting (Crollen et al., 2011, 2014), estimation (Castronovo and Seron, 2007b) and arithmetic performances (Dormal et al., 2016a,b) as compared to their sighted peers. Second, at the neural level, it was demonstrated that specific arithmetic operations activated selective networks in blind as in sighted participants: a parieto-frontal network for subtraction and superior temporal regions for multiplication (Crollen et al., 2019a,b,c). This observation of common task-related activity in sighted and congenitally blind not only supports the idea that arithmetic is processed within distinct cerebral pathways (Dehaene and Cohen, 1997) but also suggests that vision does not have a foundational role in setting-up this functional segregation. The evidence that the neural representation of numbers is not tied to visual abilities or experience thus demonstrate that numerical concepts can be acquired through non-visual mechanisms (Crollen et al., 2017; Dormal et al., 2016a,b).

However, the fact that early blind people perform equally well as sighted controls or that similar brain regions were activated in blind and in sighted individuals during the same numerical task does not mean that the underlying representation was similar across both groups. In this paper, we showed that even if the lack of vision did not preclude the development of various numerical skills (Castronovo, 2014; Crollen and Collignon, 2016; Dormal et al., 2016a,b), some qualitative properties of the number representation nevertheless appeared to be shaped by early blindness. For example, while sighted participants associate numbers to an external frame of reference, congenitally blind individuals principally rely on an egocentric coordinate system (Crollen et al., 2013). In contrast to sighted people, blind individuals do moreover neither rely on finger-counting to develop their counting and arithmetic skills (Crollen et al., 2011, 2014).

We have shown that studying numerical cognition in blind individuals shed new lights on our theoretical knowledge on the development of numerical concepts without vision. Beyond this, the study of blind individuals could also constitute the starting point for elaborating programs that could help the development of mathematical abilities in children at risk. Given their visual deprivation, blind people necessarily develop alternative strategies to learn the concept of numbers. In this paper, we already mentioned two possibilities: 1) the use of general cognitive factors such as language and working memory; 2) the use of touch and object manipulation (Crollen et al., 2017). As blind individuals are able to develop good numerical skills, it is worth examining whether their alternative strategies could be taught to sighted with arithmetic difficulties in order to boost their mathematics understanding. In line with this, it has already been demonstrated that a working memory training could improve mathematics performance in preschool children (Passolunghi and Costa, 2018) and middle school students presenting learning difficulties (Zhang et al., 2018). On another hand, the haptic modality might provide alternatives to mathematics understanding by providing a connection between concrete referents and abstract concepts. Integration of sensory information across modalities can moreover confer behavioral advantages by decreasing perceptual ambiguity, improving reaction time, and increasing processing accuracy relative to unisensory stimuli (i.e., the multisensory integration hypothesis). Converging evidence across species, developmental periods, tasks, and amodal properties suggests that the organizing influence of intersensory redundancy in guiding early attention, perception, and cognition likely constitutes a general developmental principle. It allows naïve perceivers to selectively attend to related aspects of stimulation that constitute unitary events and ignore concurrent stimulation from unrelated events (Bahrick and Lickliter, 2002).

In line with this idea, some studies already demonstrated that the addition of the haptic exploration could help healthy adults and children to learn some abstract concepts more effectively (for handwriting quality, see Bara and Gentaz, 2011; for visual-auditory associations, see Fredembach et al., 2009; for geometry, see Pinet and Gentaz, 2008). In the numerical field, we have recently tackled this question by examining whether touch could boost the development of arithmetic in normally-developing children (Crollen et al., 2019a,b,c). This study compared the efficiency of 4 arithmetic training methods differing according to 2 factors: 1) the perceptual modalities involved in processing the arithmetic operations (touch + vision vs. vision only), and 2) the spatial disposition of the materials used (linear or left-to-right oriented vs. non-linear or random). Interestingly, while the effect of spatial disposition was not significant, results demonstrated that the multisensory training condition led to a significantly larger performance's improvement than did the visual training alone. Blindness could therefore be used as a window to create mathematics teaching program that could not only be used by mathematics teachers in formal schooling but that could also be used by therapists working with sighted children presenting mathematics learning difficulties. This is reminiscent of what Vygotsky wrote: *"If a blind or deaf child achieves the same level of development as a normal child, then the child with a defect achieves this in another way, by another course, by other means. For the pedagogue, it is particularly important to know the uniqueness of the course, along which he must lead the child. The key to originality transforms the minus of the handicap into the plus of compensation"* (in Rieber, and Robinson, 2013, p.158).

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