The shared numerical representation for action and perception develops independently from vision

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Abstract

Humans share with other animals a *number sense*, a system allowing a rapid and approximate estimate of the number of items in a scene. Recently it has been shown that numerosity is shared between action and perception as the number of repetitions of self-produced actions affects the perceived numerosity of subsequent visual stimuli presented around the area where actions occurred. Here we investigate whether this interplay between action and perception for numerosity depends on visual input and visual experience. We measured the effects of adaptation to motor routines (finger tapping) on numerical estimates of auditory sequences in sighted and congenitally blind people. In both groups, our results show a consistent adaptation effect with relative under- or over-estimation of perceived auditory numerosity following rapid or slow tapping adaptation, respectively. Moreover, adaptation occurred around the tapping area irrespective of the hand posture (crossed or uncrossed hands), indicating that motor adaptation was coded using external (not hand centred) coordinates in both groups. Overall, these results support the existence of a generalized interaction between action and perception for numerosity that occurs in external space and manifests independently of visual input or even visual experience.

Keywords: Numerosity perception, adaptation, cross-modal perception, blindness, external remapping

1. Introduction

Humans excel at processing and manipulating numbers, an ability supporting many of our most salient cultural achievements. Even if the exact processing of symbolic numbers might be specific to humans, converging evidence suggests that many animals possess the ability to rapidly estimate the approximate number of items in a scene (Dehaene, Dehaene-Lambertz, & Cohen, 1998; Nieder, 2005). Such a number sense is phylogenetically ancient (Butterworth, Varma, & Laurillard, 2011; Dehaene, 2011), governed by the Weber's law (Anobile, Cicchini, & Burr, 2014) and likely innate, as suggested by studies showing that chicks and new-born infants (less than 3 days old) show habituation to numerosity (de Hevia, Veggiotti, Streri, & Bonn, 2017; Jordan & Brannon, 2006; Lipton & Spelke, 2004; Rugani, Fontanari, Simoni, Regolin, & Vallortigara, 2009; Rugani, Regolin, & Vallortigara, 2007). 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 stimulation (Hersh & Dehaene, 1998).

The existence of a number sense has recently found psychophysical support in adaptation paradigms. Exposure to either very high or very low numerical quantities changes the apparent numerosity of stimuli subsequently displayed in the same position, causing a repulsive aftereffect whereby the adapted stimulus is perceived as more numerous (overestimation) if the adaptor included fewer dots, and less numerous (underestimation) if the adaptor contained more dots than the adapted stimulus (Arrighi, Togoli, & Burr, 2014; Burr & Ross, 2008). Several authors have however suggested that adaptation to visual texture density underlies the apparent adaptation to numerosity and therefore that low-level visual mechanisms may explain what is thought to be specific numerosity effects (Dakin, Tibber, Greenwood, Kingdom, & Morgan, 2011; Durgin, 2008; Morgan, Raphael, Tibber, & Dakin, 2014; Tibber, Greenwood, & Dakin, 2012). Cross-modal studies have emerged as a compelling paradigm to distinguish aftereffects of perceived number from visual aftereffects in the visual analysis of texture density (Anobile, Castaldi, Turi, Tinelli, & Burr, 2016; Anobile, Cicchini, & Burr, 2012; Anobile et al., 2014; Pomè, Anobile, Cicchini, Scabia, & Burr, 2019). It was for instance demonstrated that adapting to a series of tones changed the apparent numerosity of visual flashes, and vice-versa, to the same extent as within-modal adaptation (Arrighi et al., 2014).

This concept was recently significantly extended by demonstrating that the numerosity of self-produced actions (hand tapping) distorted the estimates of visual stimulus numerosity presented around the tapping region, with such *motor* adaptation aftereffects occurring in real world, not hand-centred, coordinates (Anobile, Arrighi, Togoli, & Burr, 2016). This result is important as it reveals an interplay between action and perception in the numerical dimension, potentially underlying successful interaction between our body and objects in the environment, for instance when planning the number of movements to execute based on the number of elements in our peri-personal space.

Evidence from several studies indeed supports the idea of a close relation between action and numerical cognition, with numerical information affecting how actions are performed and vice versa. For instance, the numerical magnitude of a stimulus can affect hand grip aperture/closure movements (Andres, Davare, Pesenti, Olivier, & Seron, 2004), sensory-motor training can improve children’s performance in a numerical task (Fischer, Moeller, Bientzle, Cress, & Nuerk, 2011), and finger counting habits can influence number processing (Domahs, Moeller, Huber, Willmes,

& Nuerk, 2010). This interplay between action and numerosity representation is perhaps even more striking when considering how goal-directed actions are guided by numerical information. Indeed, several studies have shown the existence of neuronal populations – mostly in the parietal cortex – encoding the number of actions required to perform a task. For instance, Sawamura et al. (2002) showed that neurons in the posterior parietal cortex of the monkey represented the numerosity of a series of self-produced actions (Sawamura, Shima, & Tanji, 2002). In a subsequent study, Sawamura and colleagues (2010) have shown that inactivating such number-selective neurons increased the rate of errors in producing a specific sequence of movements, without impairing motor abilities per se (Sawamura, Shima, & Tanji, 2010). These results thus show that numerical information has an essential role in guiding behavior. Conversely, our recent study (Anobile, Arrighi, et al., 2016) further demonstrates that the number of movements strongly affects perception, to suggest a bi-directional link between action and perception in numerical cognition.

However, several open questions remain about how such shared mechanism between action and perception for numerosity processing emerges. First, it is not clear whether the interaction occurs only in the presence of sensory inputs belonging to the visual modality. Considering that in most of the cases the motor system prepares and executes goal-directed actions leveraging on visual information (i.e., the number of repetitions of arm movements for picking up a group of cherries scattered on a table depends on the visual estimates of their numerosity), the interaction might be consequently restricted to the visual domain. However, if the interaction between action and perception occurs at a level in which stimulus numerosity is encoded at an abstract level (i.e. regardless of sensory modality), we should observe an interference of the numerosity of self-produced action also for non-visual numerical estimates (i.e., auditory signals). Similarly, it remains unknown whether visual experience is necessary for the emergence of such an abstract sense of number. Indeed, vision is thought to be crucial to link action and perception using an external (world-centred) frame of reference; therefore, it might be possible that visual experience is mandatory to shape such joint numerical representation in external space (Anobile, Arrighi, et al., 2016).

In our study, we thus address the role of visual input and visual experience in shaping the relation between action and perception. First, we investigated whether cross-dimensional numerosity adaptation between action and perception is selective to visual stimuli - supporting the idea of a specific interplay between action and the perception of visual numerical information - or whether it generalizes to different sensory modalities (i.e. audition) - suggesting that the shared mechanisms between action and perception for numerosity operates supra-modally. Indeed, the above-mentioned cross-dimensional studies involved visual inputs and one may critically argue that in the context of such experiments, visual numerosity might be automatically activated even by cross-dimensional inputs (Gebuis, Cohen Kadosh, & Gevers, 2016).

Second, we assessed whether cross-dimensional adaptation between action and perception can be observed in the absence of visual experience (Crollen, Albouy, Lepore, & Collignon, 2017; Crollen, Dormal, Seron, Lepore, & Collignon, 2013). Indeed, it has been suggested that the number sense may develop by anchoring itself onto circuits typically mapping visuo-spatial information (Walsh, 2003). For instance, topographical numerosity maps have been found in occipito-parietal circuits that overlaps with visually responsive regions having visuospatial receptive fields, and the topographic organization of numerical quantities resembles topographic visual field maps (Harvey & Dumoulin, 2017; Harvey, Fracasso, Petridou, & Dumoulin, 2015; Harvey, Klein, Petridou, & Dumoulin, 2013). On the contrary, in case the number sense transcends from basic sensory (visual) processes, numerosity adaptation between action and perception should be independent of visual experience. We addressed this issue by measuring the effects of motor adaptation on numerosity estimates of sequences of sounds in congenitally blind people.

Finally, even in case motor adaptation affected numerosity estimates in congenitally blind subjects, we settled to test whether adaptation would rely on a similar spatial frame of reference in both sighted and blind people. Indeed, numerosity adaptation was found to be spatially selective and coded in external world coordinates. For instance, when asked to rapidly (vs. slowly) tap in mid-air, human adults underestimate (vs. overestimate) the numerosity of visual stimuli subsequently displayed around the tapping region, compared to numerosity estimates for stimuli displayed in the opposite location (where estimates remain veridical). This holds true even when the tapping movements are performed with the hand crossed over the body midline (Anobile, Arrighi, et al., 2016). These results suggest that motor adaption occurs in a reference frame anchored in external world coordinates (e.g., adaptation is selective to the spatial position in which tapping occurs). As opposed to this reference frame anchored to external coordinates, an internal reference frame – anchored to the body irrespective of its position in space – has been shown to be preferentially activated in early blind individuals (Röder, Rösler, & Spence, 2004). Several recent studies on spatial processing have indeed suggested that the lack of early visual experience might alter the development of an external reference frame for the processing of sensory information (Crollen et al., 2013; Röder et al., 2004), that is exactly the coordinate system previous studies have reported motor adaptation to occur in. This reliance on an internal reference frame of early blind individual has been recently demonstrated in the context of the spatial-numerical association of response codes (SNARC) effect (Crollen et al., 2013). According to this effect, responses to small numerosities are faster when provided with a response key located on the left while responses to larger numerosities are faster by using a response key on the right independently from the position of the hands (crossed or uncrossed) the response is provided with, an effect mimicking a spatial organization of numerical magnitudes oriented from left to right (i.e., as in a mental number-line). When sighted participants are asked to cross their hands to the opposite hemispaces, the effect remains bounded to the left and right hemispace, irrespective of the hand position (i.e., faster responses to small numerosities with the *right* hand positioned in the *left* hemispace). Conversely, in early blind participants the effect remains bounced to the effector hand, irrespective from its position in space (i.e., faster responses to small numerosities with the *left* hand positioned in the *right* hemispace). Although the spatial selectivity of the adaptation effect (Arrighi et al., 2014) is conceptually different from the spatial-numerical association of the SNARC effect, if the absence of early visual experience generally disrupts stimulus encoding in an external reference frame, a similar relying on internal coordinates might emerge even in the domain of motor adaptation. In contrast, since it has been shown that the use of an external coordinate system is also used by default when congenitally blind people perform an action (Crollen et al., 2017) (which is not the case with the SNARC effect), it is possible that congenitally blind people will also rely on external coordinate as sighted do for this task.

More in general, spatial abilities has been shown to be altered in absence of early visual experience. While some specific tasks simultaneously manipulating the space/time relative relationship of stimuli in external space has shown deficits in congenitally blind people (e.g., Gori, Sandini, Martinoli, & Burr, 2014; Rieser, Lockman, & Pick, 1980), judgements of the absolute position of sounds in external space appear to be faster (Collignon, Renier, Bruyer, Tranduy, & Veraart, 2006) and more accurate (Battal, Occelli, Bertonati, Falagiarda, & Collignon, 2019) in congenitally blind people. Other differences compared to sighted individuals concern distinctive exploratory strategies, different generation of mental models of the environment, and a stronger reliance on an egocentric and experience-based reference frame (Cattaneo et al., 2008).

We therefore asked congenitally blind and sighted participants to estimate the numerosity of sequences of tones after having performed a short period of slow vs. fast hand tapping movements, with the hands uncrossed or crossed over the body midline. If blindness prevents the default use of an external reference frame, then adaptation effects should *not* be associated with the spatial position of the tapping hand, but rather with the internal reference frame associated to the hand *identity*. On the opposite, in case motor adaptation was coded in external spatial coordinates also in congenitally blind subjects, then adaptation should be linked to the spatial position of the tapping hand.

2. Methods

2.1. Participants

Twenty-eight participants took part in the study: 14 sighted and 14 congenitally blind participants. Both groups were composed of 4 females and 10 males. The age of the congenitally blind individuals ranged from 21 to 49 years old (M = 35.7; SD = 7.78). In the sighted group, age ranged from 23 to 53 years old (M = 35; SD = 8.04). Both groups did not statistically differ in terms of age, t(26) = 0.24, p = 0.81.

The recruitment procedure was identical for the sighted and blind group, and involved contacting potential participants directly and asking if they wish to enroll in the study. Contact information of potential participants was taken from a database available to the researchers at the Catholic University of Louvain (Belgium). Sighted and blind participants were matched according to age, sex, and socio-economic status.

All the blind participants were congenitally and totally blind or with just a rudimentary sensitivity for brightness differences with no pattern vision since birth. In all cases, blindness was attributed to peripheral deficits with no additional neurological or psychological problems. All participants provided an informed consent before participating in the study. Additionally, participants' handedness was assessed with the Edinburgh Handedness Inventory test. Two sighted and two congenitally blind were left-handed; two congenitally blind were ambidextrous, while all the other participants were right-handed. The procedures were approved by the Research Ethics Board of the Catholic University of Louvain (Belgium - Project 2016-26) and are in line with the Declaration of Helsinki. Experimental and analytical procedures were not pre-registered.

Regarding the sample size of the two groups tested in the present study, we based our choice on a previous research employing a similar adaptation technique (Anobile, Arrighi, et al., 2016). Despite the fact that in this previous study an average of seven participants was tested in each condition, in order to ensure enough power to detect an effect in blind participants – which may show higher inter-individual variability – we have doubled a priori the sample size in this study (i.e., 14 participants).

Blind participants were not screened for their ability to localize a sound in space. However, due to the relatively large distance between sound sources used in the experiment to deliver numerical stimuli, and the fact that only one source was used at each time, no difference in sound localization is expected between sighted and blind participants (Battal et al., 2019; Gori et al., 2014).

2.2. Stimuli

All the stimuli used to test numerical estimation performance were generated and delivered using the routines of the Psychophysics toolbox (version 3) for MatLab (version r2015b; The Mathworks, Inc.).

Auditory stimuli were pure tones (500 Hz tones; duration = 40 ms; intensity = 77 dB), with 5-ms ramps at the onset and offset. Stimuli were presented through one of two loudspeakers placed 40 cm in front of each participant's body and 25 cm away from the body midline in the left and right hemi-spaces. Each test sequence included either 16, 17, 18, 19, or 20 tones. To minimize temporal regularity and to avoid fusion of two or more stimuli (i.e., due to a too short inter-stimulus interval; ISI), the ISI between any two consecutive stimuli in a sequence was randomly determined with the constrain of a maximum sequence duration of 2 s, minimum ISI of 40 ms, and a maximum ISI of 290 ms.

2.3. Procedure

The experiment consisted of two phases: an adaption phase followed by a test phase. During the adaptation phase (6 seconds), participants performed a sequence of tapping movements with their dominant hand (right or left according to the participant handedness; ambidextrous participants used the right hand) in one of two possible posture positions. In the uncrossed posture, participants tapped with the dominant hand in an uncrossed position: the right hand in the right hemi-space vs. left hand in the left hemi-space. In the crossed position, the tapping movements had to be performed with the dominant hand crossed relative to the body midline: right hand in the left hemi-space vs. left hand in the right hemi-space.

We also employed two different adaptation conditions. In the fast adaptation condition, participants were required to tap as many times as possible within the 6 seconds adaptation phase, while in the slow adaptation condition, participants were required to tap a few times within the 6 seconds adaptation. An auditory cue (a recorded human voice saying “Go” or “Stop”) was used to indicate the beginning and the end of the adaptation phase. An infrared motion sensor device (Leap motion controller; https://www.leapmotion.com/) running at 60 Hz was used to continuously monitor hand movements and the position of the participant’s hand. When the participant’s hand moved away from the leap motion, the trial was aborted and an auditory signal indicated that the hand had to be put back to the correct position. Note that to minimize sensory feedbacks all subjects were required to tap in air (no tactile feedback) and sighted participants were blindfolded during the task (to ensure no visual feedback).

In the “fast” condition, the tapping frequency was about 4 Hz (~25 taps) and we did not find any difference between the tapping rates for sighted and blind participants, neither in the uncrossed (blind: M = 25.07 ± 7.5; sighted: M = 24.46 ± 6.5, t(26) = 0.22, p = .82) nor in the crossed condition (blind: M = 25.25 ± 5.9; sighted: M = 24 ± 6.5, t(26) = 0.53, p = .60). In the “slow” condition, the tapping frequency was about 1.8-2 Hz as subjects usually performed 10-11 tapping repetitions regardless of the condition (uncrossed or crossed), with again no difference between blind and sighted participants (uncrossed position-blind: M=10.75 ± 2.69; uncrossed position-sighted: M=10.82 ± 2.88, t(26) = 0.07, p = 0.95; crossed position-blind: M=11.18 ± 2.64; crossed position-sighted: M=11.44 ± 2.8, t(26) = 0.18, p = 0.86 - see Supplementary Table 1). The two posture conditions (uncrossed vs. crossed) and the two adaptation conditions (fast vs. slow) were randomly presented twice for a total of 8 experimental blocks (see below).

One second after the end of the adaptation phase, a sequence of sounds (ranging from 16 to 20 tones) was presented to the participant either in the adapted side or in the opposite, non-adapted side (see supplementary figure 1). After the presentation of the entire sequence, participants were required to verbally estimate the number of auditory tones presented. After the estimate was provided, the next trial started after about 1 s. Each numerosity was presented six times for a total of 240 trials presented in 8 separate blocks of 30 trials (two blocks per condition).

2.4. Statistical Analyses

To achieve an overall index of the adaptation effect throughout all the numerosities tested, we first calculated an adaptation effect index (AI) as the ratio between slow and fast adaptation averaged across all presented numerosities (multiplied by 100):

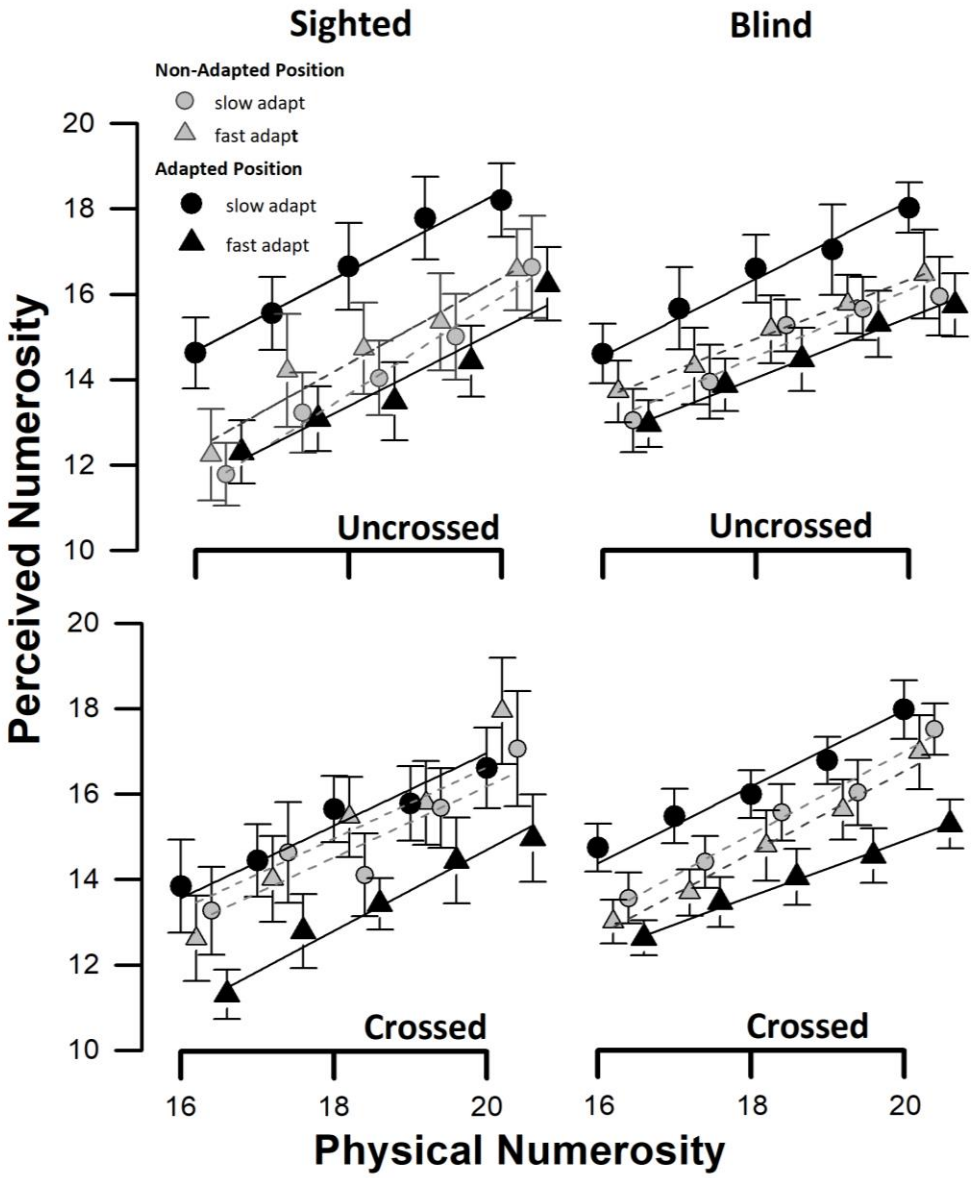
$$\mathrm{AI} = 100 * \left(\left(\frac{1}{n} \sum_{j=1}^{n} \frac{\overline{RS}_j}{\overline{RF}_j} \right) - 1 \right) \qquad \text{Eq. 1}$$

Where *n* is the number of numerosities tested (*n* = 5, with numerosity ranging from 16 to 20), $\overline{RS}$ is the average response after slow adaptation and $\overline{RF}$ is the average response after fast adaptation for each numerosity *j*. Positive AI values indicate an adaptation effect whereby numerical estimates after slow adaptation are higher compared to after fast adaptation, while negative values indicate an effect opposite to the expected adaptation phenomenon. Adaptation indexes were then used to assess the effect across different conditions and groups. To this aim, we employed a mixed model ANOVA including “posture” (uncrossed vs. crossed) and “adaptation/test congruency” (congruent vs. incongruent; i.e., meaning that the test stimulus was presented either at the adapted hemispace, or in the opposite one) as within-subject factors, and “group” (sighted vs. blind) as between-subject factor. This analysis was followed by a series of post-hoc tests comparing the effect obtained in different conditions (paired t-tests when comparing effects within the same group; independent-sample t-tests when comparing effects across groups).

To ensure that the results allow, on the one hand, to confidently conclude that the effect is present in both groups, and, on the other hand, that it does not differ between sighted and blind participants, we additionally performed a Bayesian analysis (e.g., see for instance Ly, Verhagen, & Wagenmakers, 2016). Such an analysis was based on the t-values obtained with the t-tests mentioned above (i.e., comparing the adaptation effects within and across groups), and on a Cauchy prior centred on zero (scale = 0.707) representing the null hypothesis. The Bayes factor (BF) values obtained with this analysis represent a measure of how strongly the data supports either the null hypothesis of no effect or no difference between groups (i.e., low BF values, < 1), or the alternative hypothesis (high BF values, >3). The ANOVA analysis was performed using SPSS (IBM), while t-tests were performed using MatLab (version r2016b; The Mathworks, Inc.). The Bayesian analysis was performed using JASP (JASP Team, 2019).

3. Results

Figure 1 shows the perceived numerosity of sequences of auditory impulses as a function of their physical numerosity for both groups (sighted or blind) in both posture conditions (crossed and uncrossed).



<u>FIG.1</u> *– Effect of motor adaptation on perceived numerosity in sighted (left panels) and blind participants (right panels). Mean responses for each numerosity after slow (black circles) or fast (upward triangles) motor adaptation. The upper panels represent the uncrossed condition (i.e., subjects tapped with the right hand on the right side) and lower panels the crossed condition (i.e., subjects tapped with the right hand on the left side). Continuous dashed lines represent linear fits to the relative data. Error bars represent SEM. Note that individual data points are shifted horizontally for the ease of visualization.*

To assess the effect of adaptation throughout the different numerosities tested, we calculated an adaptation effect index (AI) as the ratio of numerical estimates after slow and fast adaptation, averaged across all numerosities (see *Statistical Analyses*). This index allows to easily quantify the average magnitude of motor adaptation for each participant regardless of subject-specific biases in numerosity estimates likely to occur when subjects are allowed to freely map stimulus magnitude. Results based on the Adaptation Index are shown in figure 2, comparing the performance for both blind and sighted participants, in all conditions.

We thus assessed the adaptation magnitude by performing a mixed model ANOVA with "posture" and "adaptation/test congruency" (i.e., test stimulus presented in either the adapted – congruent – hemispace, or in the opposite – incongruent – one) as within-subject factors, and "group" (sighted vs. blind) as between-subject factor. The results show a significant main effect of adaptation/test congruency ($F(1,26) = 101.26$, $p < 0.001$, $\eta_p^2 = 0.796$), but no main effect of posture ($F(1,26) = 0.708$, $p = 0.408$). We also observed a significant interaction between adaptation/test congruency and posture ($F(1,26) = 4.879$, $p = 0.036$, $\eta_p^2 = 0.158$), reflecting a slightly larger difference in the adaptation effect between congruent and incongruent adaptation/test pairs in the uncrossed posture condition (paired t-test, $t(27) = 2.22$, $p = 0.035$, Cohen's $d = 0.42$). Importantly, we did not observe any main effect of group ($F(1,26) = 0.021$, $p = 0.886$) and no interaction of group with any of the other factors (posture × group, $F(1,26) = 3.16$, $p = 0.087$; adaptation/test congruency × group, $F(1,26) = 1.58$, $p = 0.219$; posture × adaptation/test congruency × group, $F(1,26) = 0.617$, $p = 0.439$).

Moreover, with a series of post-hoc tests, we directly compared the adaptation indexes obtained when the test stimulus was delivered to the adapted (congruent) hemispace against the effects measured when the test stimulus was delivered to the opposite (incongruent) hemispace compared to adaptation. These tests were performed both separately for the different posture conditions and for the sighted and blind group, as well as directly comparing the effect across the two groups. Additionally, frequentist statistics in this context was coupled with a Bayesian analysis aimed to assess whether and to what extent the data actually support the null (i.e., no difference between two conditions/groups) or the alternative (i.e., a difference in the effect of adaptation in two conditions/groups) hypothesis (see *Statistical Analyses*). For both groups of participants, in the uncrossed condition, adaptation was significantly higher when stimuli were presented on the side where the hand had been tapping than on the other side (i.e., congruent vs. incongruent condition; paired t-test, sighted $t(13) = 8.45$, $p < 0.001$, $d = 2.4$, Bayes factor [BF] > 1000, average effect = 19.7% ± 2.8% vs. 2.0% ± 1.9%; blind $t(13) = 7.208$, $p < 0.001$, $d = 2.1$, BF > 1000, average effect = 13.8% ± 2.2% vs. 2.1% ± 1.9%). Similarly, in the crossed condition, a stronger distortion of perceived numerosity occurred when test stimuli were presented in the same hemispace where adaptation was performed (paired t-test, sighted $t(13) = -5.22$, $p < 0.001$, $d = 1.8$, BF = 185, average effect = 14.7% ± 2.7% vs. -0.5% ± 1.7%; blind $t(13) = -3.969$, $p = 0.002$, $d = 1.1$, BF = 26; average effect = 17.1% ± 3.1% vs. 4.3% ± 2.9%).

Moreover, we directly compared the effect of adaptation in the sighted and blind group. In both the uncrossed and crossed condition, the analysis did not show any significant difference between the two groups (independent-sample t-test; $t(26) = 0.55$, $p = 0.58$, and $t(26) = 1.66$, $p = 0.11$, respectively). As this comparison is central to the aim of the study, we performed again a Bayesian analysis to assess whether and to what extent the data actually support the null (i.e., no difference between the two groups) or the alternative (i.e., a difference in the effect of adaptation in the two groups) hypothesis (see Data analysis). With these tests, we observed a Bayes factor (BF) of 0.965 in the uncrossed condition and 0.396 in the crossed condition. Such low BF values thus provide more evidence for the null hypothesis of no difference in the effect between the two groups compared to the alternative hypothesis.

Taken together these results indicate that the reference frame for motor adaptation is coded in external coordinates also in those subjects that have not benefitted from early visual experience.

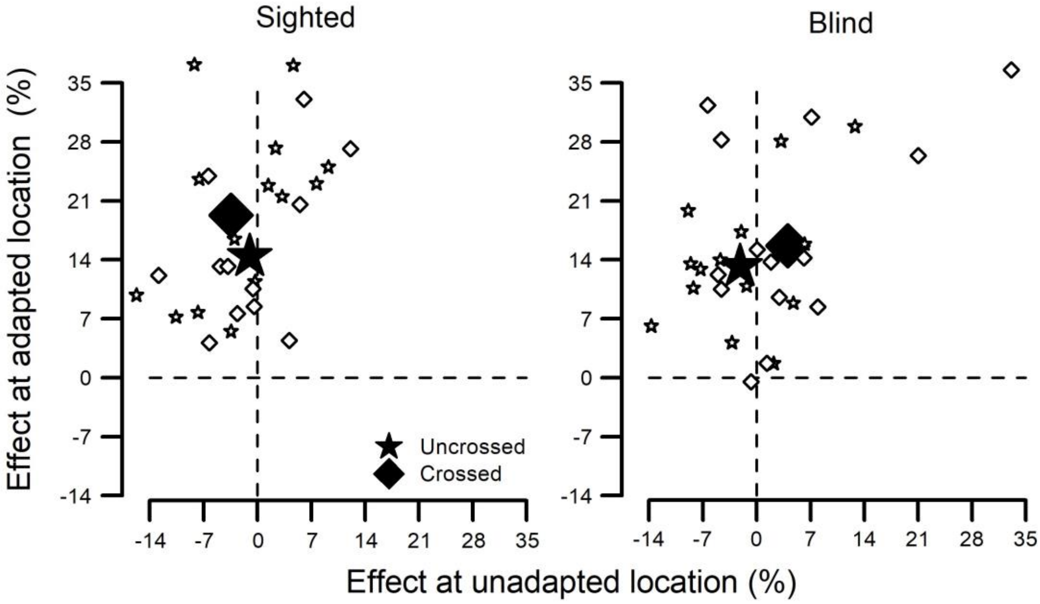


FIG.2 *– Reference frame of motor adaptation. Adaptation magnitudes for each participant in the sighted group (left panel) and the blind group (right panel), plotted as the effect at unadapted location (i.e., incongruent adaptation/test location) against the effect at the adapted location (i.e., congruent adaptation/test location). The larger symbols represent the mean of each group in both postures (star: uncrossed position; diamond: crossed position). Small symbols represent individual data. Dashed lines represent the level of zero adaptation effect.*

4. Discussion

In our study we first investigated whether the interaction between perception and action in numerosity processing is selective for visual inputs or generalizes to other sensory modalities (i.e. audition). We found that estimates of sequences of sounds were strongly biased after the execution of repetitive motor routines. Namely, adaptation to different tapping speeds resulted in a relative difference between numerical estimates, with fast and slow tapping causing an under- or over-estimation (respectively) relative to each other. Changes in perceived numerosity induced by motor adaptation occurred in most participants and were found to be as robust as 15% change in perceived numerosity. These results indicate that the execution of a given number of motor routines biases subsequent numerosity estimates for auditory impulses similarly to what has been previously reported to be the case for visual stimuli (Anobile, Arrighi, et al., 2016). This in turn supports the idea that the motor system might interact with an abstract sense of number processing numerosity regardless of the presentation format (sequential/simultaneous) or sensory modality (Arrighi et al., 2014; Barth, La Mont, Lipton, & Spelke, 2005; Brannon, 2003; V. Izard, Sann, Spelke, & Streri, 2009; Nieder, 2012; Nieder & Merten, 2007).

In general, however, the adaptation effect measured here appears to be embedded in a pattern of overall underestimation of numerosity (i.e., all numerosities tended to be underestimated irrespective of the condition; see figure 1), which was not observed in previous studies (Anobile, Arrighi, et al., 2016). Nevertheless, such an underestimation is not unusual in numerosity estimation tasks (Crollen, Castronovo, & Seron, 2011; Véronique Izard & Dehaene, 2008), and in this context might have been prompted by the use of the auditory modality instead of vision in combination with the use of a higher numerosity range compared to previous studies (i.e., 16-20 as opposed to 6-14 items in Anobile, Arrighi, et al., 2016).

The main goal of the study was to evaluate the role visual experience plays in shaping the development and reference frame used for such motor adaptation. Distortions in perceived numerosity of the auditory impulses induced by motor adaptation were found to be similar in magnitude in sighted and congenitally blind subjects, with no statistically significant difference between the two groups of participants. Crucially, we also showed that the adaptation effects were spatially selective in both groups: only numerosity estimates for stimuli presented in the adapted location were distorted by adaptation, compared to estimates for stimuli presented in the neutral (non-adapted) location which did not show any adaptation effect. The spatial selectivity shown here complements and nicely extends previous studies including visual stimuli (Anobile, Arrighi, et al., 2016; Anobile et al., 2019; Arrighi et al., 2014). This indicates that motor adaptation is coded in external world, not hand-centered coordinates (Anobile, Arrighi, et al., 2016), and this clearly suggests that numerosity adaptation is perceptual in nature as such a spatial selectivity is not expected from a change in judgment criterion or a response bias, and suggests the involvement of perceptual processes coding numerical information in a spatial reference frame instead of a post-perceptual bias.

The use of an external reference frame in early blind participant contrasts with a previous study showing a hand-centred reference frame to process number (Crollen et al., 2013). Indeed, the default use of an anatomical frame of reference following blindness was suggested after the observation of a reversed SNARC effect while congenitally blind had to perform a number comparison task with the hands crossed over the body midline (Crollen et al., 2013). While the present data may first seem at odds with those results, they are well in line with more recent studies showing that blind people are able to use external coordinates when the task involves action (in contrast to mere perception) (Crollen et al., 2017; Crollen, Spruyt, Mahau, Bottini, & Collignon, 2019; Heed, Buchholz, Engel, & Röder, 2015; Heed & Röder, 2014). Bimanual coordination in the congenitally blind is for example constrained by external-spatial factors like in the sighted (Heed & Röder, 2014). External coordinates may similarly affect tactile localization in congenitally blind in the context of an action that requires external spatial coding (Heed et al., 2015). Finally, congenitally blind are able to produce the mirror (the external representation) of a previously learned motor sequence (Crollen et al., 2017). Overall, those experiments, like ours, suggest that congenitally blind rely on an external spatial frame of reference when the task requires a motor action. Note however that the SNARC effect and the effect of adaptation measured here involve two very different concepts of spatialization. In the case of the SNARC effect, the spatialization comes from the association between number and space in a mental number-line oriented from left to right. Such a mapping of numbers onto space has been indeed shown to be a robust cognitive phenomenon, which can be modulated by formal mathematical education (Dehaene, Izard, Spelke, & Pica, 2008) and disrupted by spatial attentional deficits like neglect (Zorzi et al., 2012; Zorzi, Priftis, Meneghello, Marenzi, & Umiltà, 2006; Zorzi, Priftis, & Umiltà, 2002). In the case of the motor adaptation task, instead, we refer to the reference frame in which the effect is carried over to successive stimuli. Namely, adaptation does not follow any association between number and space, but operates only according to the relative position of adaptor and adapted stimulus in space. These different concepts of spatialization – which are likely mediated by different underlying mechanisms – may additionally explain the contrast between previous reports of the use of an internal reference frame in blind participants, and the external spatial coding observed here.

An additional important point to consider is whether the adaptation effect is truly bound to the adaptation position in external coordinates, or whether it is linked to the hand coordinates. In other words, if participants moved their hand right after the adaptation phase, would the effect still occur at the adapted position, or would it follow the hand position in space? Unfortunately, such a question is not easy to answer, as previous studies show that any movement performed after an adaptation phase will reset the adaptation itself, leading to no effect on the subsequent stimuli (Tomassini, Gori, Burr, Sandini, & Morrone, 2012). Although not directly related to the motor adaptation technique used here, several previous studies show that relatively high-level perceptual effects are robust to shifts in reference frames, remaining bound to the spatial position of the stimuli. This is for instance the case in the context of motion adaptation, which has been shown to affect perceived time with a spatially-localized effect occurring irrespective of eye movements (Burr, Tozzi, & Morrone, 2007; Fornaciai, Arrighi, & Burr, 2016), or other visual effects involving information integration in spatial coordinates (Fornaciai, Binda, & Cicchini, 2018). In the context of the present motor adaptation technique, we believe that the effect should remain similarly bound to the spatial position where adaptation occurs, irrespective of subsequent movements displacing the adapting hand. This is however a speculative interpretation, and the nature of the spatial localization of the motor adaptation effect remains an open question.

5. Conclusion

In conclusion, our results show that adaptation to slow or fast tapping movements can change the apparent numerosity of subsequent sequences of sounds in sighted as well as in congenitally blind participants. In both groups, motor adaptation aftereffects were spatially selective with only the stimuli presented in the adapted location being affected by motor adaptation. This result suggests that performing a given number of motor patterns in a given region of space distorts the processing of stimulus numerosity around that area, as if self-produced movements would be able to change the sensitivity of the perceptual mechanisms underpinning numerosity of visual or auditory stimuli. Moreover, the lack of any significant difference between motor adaptation aftereffects for sighted and congenitally blind subjects neither in the magnitude of adaptation, nor in the reference frame (for all participants found to be coded in real world coordinates) suggests that visual experience does not play a key role for the development of an abstract representation of numerosity between action and perception. Our study therefore further unveils the characteristics underpinning a shared representation of numerosity between perception and action by showing abstraction from visual input and visual experience.

Data availability: experimental/analytical materials and data relative to the experiments described in this manuscript are available on Open Science Framework following this link: https://osf.io/9u4v5/

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