How Visual Experience and Task Context Modulate the Use of Internal and External Spatial Coordinate for Perception and Action

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Abstract: Recent studies proposed that the use of internal and external coordinate systems for perception and action may be more flexible in congenitally blind when compared to sighted individuals. To investigate this hypothesis further, we asked congenitally blind and sighted people to perform, with the hands uncrossed and crossed over the body midline, a tactile temporal order judgment and an auditory Simon task. Crucially, both tasks were carried out under task instructions either favoring the use of an internal (left vs. right hand) or an external (left vs. right hemispace) frame of reference. In the internal condition of the temporal order judgment task, our results replicated previous findings (Röder, Rösler, & Spence, 2004) showing that hand crossing only impaired sighted participants' performance, suggesting that blind people did not activate by default a (conflicting) external frame of reference. However, under external instructions, a decrease of performance was observed in both groups, suggesting that even blind people activated an external coordinate system in this condition. In the Simon task, and in contrast with a previous study (Röder, Kusmierek, Spence, & Schicke, 2007), both groups responded more efficiently when the sound was presented from the same side of the response ("Simon effect") independently of the hands position. This was true under the internal and external conditions, therefore suggesting that blind and sighted by default activated an external coordinate system in this task. Together, these data demonstrated that both sighted and blind individuals were able to activate internal and external information for perception and action.

The multisensory nature of our experience poses a number of challenges that the human mind has to solve to be able to correctly perform spatial localization and goal-directed actions. Each sensory modality is initially tied to a specific frame of reference (eye-centered for visual information, head-centered for auditory inputs, and skin-based for tactile information). To efficiently act in the environment, the brain has to remap all sensory information into a common coordinate system (Driver & Spence, 1998; Heed

& Azañón, 2014). The most widespread experimental paradigms that have been used to examine the nature of this common coordinate system are, arguably, the tactile temporal order judgment (TOJ) task (Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001) and the visual or auditory Simon task (Simon, 1969; Simon & Rudell, 1967).

In the TOJ task, participants have to determine, with their hands uncrossed or crossed over the body midline, which of their two hands receives a tactile stimulus first. The fact that hand crossing impairs participants' performance has received different explanations. For instance, tactile information may be processed in external space (taking for granted that each hand is in the congruent space) before being projected back onto skin location by taking into account body posture (external-first framework; Kitazawa, 2002; Kitazawa et al., 2008; Yamamoto & Kitazawa, 2001). Alternatively, tactile input could be initially represented into skin-based coordinates and then automatically remapped into external coordinates (internal-first framework: Cadieux, Barnett-Cowan, & Shore, 2010; Shore et al., 2002; see also Driver & Spence, 1998). A third possibility is that the internal and external reference frames are concurrently activated and integrated during a TOJ task (see also Tamè, Wühle, Petri, Pavani, & Braun, 2017, for a similar hypothesis in a tactile mislocalization task). The localization of touch, within this integration framework, depends on task's demands and on the relative weight attributed to each coordinate system (Badde & Heed, 2016; Badde, Heed, & Röder, 2014, 2016; Badde, Röder, & Heed, 2014, 2015; Heed, Buchholz, Engel, & Röder, 2015). Although somewhat different in their implementation, all these theoretical accounts suggest the mandatory activation of external coordinates in a task which is seemingly achievable without taking body posture into account (Heed & Azañón, 2014).

In an auditory Simon task, participants are required to press a left or a right response key depending on the pitch of a sound presented from either a left or a right loudspeaker (Röder, Kusmierek, Spence, & Schicke, 2007; Simon & Rudell, 1967; Simon & Small, 1969). Even if the stimulus location is irrelevant to the task, participants' response times (RTs) are usually faster when the sound is presented in the same relative location as the response button. The so-called Simon effect is observed while individuals respond with their hands crossed over the body midline, suggesting that auditory spatial information automatically activates an external coordinate system.

In contrast to sighted individuals, congenitally blind (CB) people do not manifest any crossing effects in the TOJ task (Crollen, Albouy, Lepore, & Collignon, 2017; Crollen, Lazzouni, et al., 2017; Röder, Rösler, & Spence, 2004), and also show a reversed Simon effect when responding with crossed hands in an auditory Simon task. When determining the pitch of a sound, blind people indeed respond faster with the hand contralateral to the sound source in a crossed posture (Röder et al., 2007). While these data were first interpreted as evidence that vision drives the development of the external coordinate system, some authors recently proposed that the differences between blind and sighted people could be due to different weighting of internal and external coordinate systems (Badde et al., 2015; Crollen, Albouy, et al., 2017; Heed & Azañón, 2014; Heed, Möller, & Röder, 2015). While internal and external information is automatically integrated in the sighted, the blind would, in contrast, preferentially rely on an

internal frame of reference and would only use the external coordinate system when the task involves action (in contrast to perception) or external instructions (in contrast to internal instructions: Badde et al., 2015; Crollen, Albouy, et al., 2017; Heed & Azañón, 2014; Heed, Möller, et al., 2015; Schubert, Badde, Röder, & Heed, 2017). In a recent tactile congruency task, Schubert et al. (2017) asked sighted and CB participants to localize tactile targets on the palm or on the back of one hand, while ignoring simultaneous tactile distractors at congruent or incongruent locations on the other hand. Participants' hands either both faced down, or one faced down and one up. Target locations had to be reported either anatomically ("palm" or "back" of the hand) or externally ("up" or "down" in space). Under anatomical instructions, performance was more accurate for anatomically congruent than incongruent target–distractor pairs. In contrast, under external instructions, performance was more accurate for externally congruent than incongruent pairs. Importantly, these results were observed in sighted as well as in blind individuals, therefore suggesting that blind people are able to integrate internal and external information during tactile localization. Spatial integration may therefore be flexibly adapted by top–down information (task instruction) even in the absence of early visual experience.

While the results of Schubert et al. (2017) are in line with the observation that blind people do not show any crossing effect in a tactile TOJ task emphasizing internal instructions (Crollen, Albouy, et al., 2017, Crollen, Lazzouni, et al., 2017; Röder et al., 2004), they are at odds with the data of Röder et al. (2007) highlighting, in the blind, a reversal of the Simon effect under external instructions. The authors indeed demonstrated, in the blind, a spatial compatibility effect between the external location of a stimulus and the internal location of a response (the hand used to respond) under task's instructions emphasizing an external frame of reference (press a left or right response key depending on the bandwidth of pink noise).

In the present study, we wanted to examine this discrepancy by requiring CB and sighted participants to perform a tactile TOJ and an auditory Simon task under internal and external instructions. If integration favors external coordinates in the sighted, a crossing hand deficit should be observed in both instructions' conditions in the TOJ task. A classic Simon effect should similarly be observed in both instructions' conditions of the Simon task. If the weighting scheme of internal and external coordinate systems is more flexible in the blind, the participant's pattern of performance should be instruction dependent, each task instruction emphasizing the weighting of the corresponding reference frame.

Method

Participants

Fourteen CB participants and 15 sighted controls (SCs) took part in the study. The CB group was composed of four females and 10 males (two ambidextrous, two left-handed, and 10 right-handed) ranging in age from 21 to 59 years old with a mean age of 37 years ($SD = 9.61$). CBs were totally blind or had only rudimentary sensitivity for brightness differences but never experienced patterned vision. In all cases, blindness was attributed to peripheral deficits with no additional neurological problems (see Table S1 in the online supplemental materials for details). The SC

group was matched to the CB group in terms of age, $t(27) = 0.48$, $p = .63$, and sex, $\chi^2 = 0.03$, $p = .87$] The sighted group was composed of four females and 11 males (two left-handed, 13 right-handed) ranging in age from 23 to 53 years old with a mean age of 34 years ($SD = 8.26$). Sighted participants were blindfolded when performing the tasks. The sample size was determined by the number of blind participants we were able to recruit in a 6 months period. All the procedures were approved by the Research Ethics Boards of the Catholic University of Louvain (Belgium–Projet, 2016-26: "Weighting of Anatomical and External Spatial Reference Frames") and the experiments were undertaken with the understanding and written consent of each participant.

TOJ Task

A similar procedure as the one applied by Crollen, Albouy, et al. (2017) was used in this task for the presentation of the stimuli. A pneumatic tactile stimulator was used to send two successive tactile stimuli (10 ms) to the participants' left and right middle fingers (see Crollen, Albouy, et al., 2017, for a detailed description of the stimulator). Participants had to localize the first stimulation under two different instruction conditions. In the *internal condition*, they had to use foot pedals to determine the hand that they perceived to have been stimulated first. If the left hand was stimulated first, participants had to press the pedal under their left foot (and inversely for the right hand). In the *external condition*, participants had to use foot pedals to determine the hemispace that they perceived to have been stimulated first. If the left hemispace was stimulated first, participants had to press the left foot pedal

while the right pedal had to be pressed if the right hemispace was stimulated first (see Figure 1).

In both conditions, stimuli were delivered at varying stimulus onset asynchronies (SOAs): —200, —90, —55, —30, —15, 15, 30, 55, 90, 200. Negative values indicated that the first stimulus was presented to the participant's left hand (internal instructions) or left space (external instructions); positive values indicated that the first stimulus was presented to the participant's right hand (internal instructions) or right space (external instructions). The hands of the participants could be either uncrossed or crossed over the body midline (see Figure 1). Legs were always in the uncrossed position. Participants had to respond within a random interval ranging from 3,000 to 4,000 ms (from the onset of the target) and wore noise-canceling headphones to mask any sounds made by the operation of the tactile stimulators. Each SOA was presented 18 times in six blocks of 60 stimuli (three successive blocks in the uncrossed posture and three successive blocks in the crossed position), with the order of the hands position counterbalanced across participants. Prior to the start of the experiment, participants performed two practice blocks of 10 trials each, one with the hands uncrossed and one with the hands crossed. Stimuli were delivered using E-Prime 2.0. The two feet pedals were 50 cm away from each other.

Simon Task

In the Simon task, participants had to use response keys to determine the bandwidth of a sound delivered to either a left or a right loudspeaker. Each trial started with a 250-ms warning tone
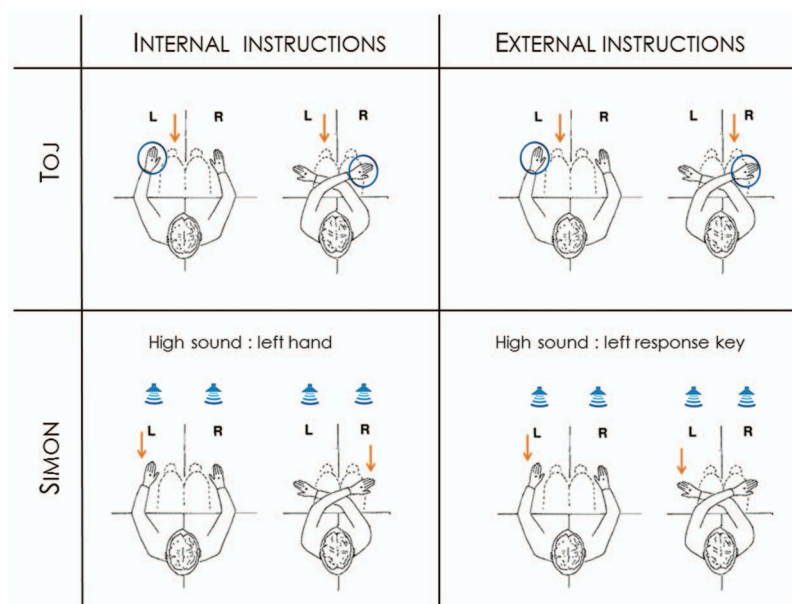

Figure 1. Top row: Temporal order judgment (TOJ) task under internal (left panel) and external instructions (right panel). The circle represents the location of the first stimulation. The arrow represents the expected answer which varies, depending on the instruction, in the crossed posture. Bottom row: Simon task under internal (left panel, high sound associated with a left-hand press) and external instructions (right panel, high sound associated with a left-key press). The arrow represents the expected answer which varies, depending on the instruction, in the crossed posture. Figure adapted with permission from Smania and Aglioti (1995). L = left; R = right. See the online article for the color version of this figure.

(1000 Hz, 73 dB) presented simultaneously in the left and right loudspeakers. Then, after 800 –1,000 ms, the target stimulus (high vs. low sound) was presented. Two different sounds (Target 1: 500 –5000 Hz, 71 dB; Target 2: 500 –15000 Hz, 74 dB] served as the target stimuli (duration =100 ms). The next trial started 1,000 –1,200 ms after the response on the preceding trial. As previously, participants had to perform the Simon task under internal versus external instruction conditions. In the internal condition, high and low sounds were associated with specific hand presses. This condition moreover comprised two response assignments. Half of the participants had to associate high sounds with a left-hand press, and low sounds with a right-hand press. For the other half of the participants, the reverse assignment was used: The low sounds were associated with a left-hand press and the high sounds were associated with a right-hand press. In the *external condition*, high and low sounds were associated with specific key presses. This condition also comprised two response assignments. Half of the participants had to associate high sounds with the left response key, and low sounds with the right response key. For the other half of the participants, the reverse assignment was used: the low sounds to the left key and the high sounds to the right key.

In both instruction conditions, response keys were placed 40 cm in front of each participant's body and 25 cm away from the body midline in the left and right hemispaces. Both instruction conditions were performed either with the hands in a parallel posture (i.e., uncrossed posture) or with the arms crossed over the body midline (i.e., crossed posture; see Figure 1). Hand posture was altered after three blocks; half of the participants started with the uncrossed posture and the other half with the crossed hand posture. Stimuli were delivered using E-Prime software running on a Dell XPS computer using a Windows XP operating system (Brussels, Belgium). The stimuli were presented in a randomized order in six blocks of 60 trials each (i.e., 15 trials of each of the four conditions: low vs. high sound × left vs. right loudspeaker) in each instruction condition. Before the eight experimental blocks, each participant completed two blocks of 16 practice trials, one with their hands uncrossed and the other with their hands crossed. Instructions emphasized accuracy and speed which were recorded by the computer.

General Procedure

Participants completed two testing sessions, separated by approximately 1 week of interval. The internal instructions of both tasks were performed during one testing session; the external instructions of both tasks were performed during the other session. Presentation order of the instruction's conditions was counterbalanced across participants.

Results

TOJ Task

The mean percentages of "right" responses (right hand in the internal condition and right space in the external condition) were calculated for each participant, SOA, and posture and transformed into their standardized z-score equivalents. These z-score measures were then used to calculate the best-fitting linear regression lines of each participant—by only including

the intermediate 8 points (i.e., —90 to 90 ms) to avoid ceiling effects (see Crollen, Albouy, et al., 2017; Shore et al., 2002). The slopes of each individual line were then submitted to an analysis of variance (ANOVA) with group (CB, SC) as the between-subjects variable and posture (uncrossed vs. crossed) and instruction (internal vs. external) as within-subject factors. One blind participant was removed from the analyses because he fell asleep during testing.

Results of the ANOVA showed a significant effect of instruction, $F(1, 26) = 13.74$, $p = .0001$, $\eta_p^2 = .35$. The slopes were indeed steeper in the internal condition ($M \pm SE = 0.76 \pm 0.05$) than in the external one ($M \pm SE = 0.53 \pm 0.06$). A posture effect, $F(1, 26) = 28.04$, $p = .001$, $\eta_p^2 = .52$, demonstrated that participants performed better with the hands uncrossed ($M \pm SE = 0.90 \pm 0.006$) than with the hands crossed ($M \pm SE = 0.38 \pm 0.097$). A significant group effect, $F(1, 26) = 7.85$, $p = .009$, $\eta_p^2 = .23$, showed that blind individuals performed better ($M \pm SE = 0.78 \pm 0.07$) than their sighted peers ($M \pm SE = 0.51 \pm 0.07$). A significant Posture × Group interaction, $F(1, 26) = 9.13$, $p = .006$, $\eta_p^2 = .26$, highlighted a larger difference between the crossed and uncrossed postures in the sighted group. Finally, an interaction between posture and instruction, $F(1, 26) = 14.32$, $p = .001$, $\eta_p^2 = .35$, demonstrated a larger difference between the crossed and uncrossed postures in the external instruction condition (see Figure 2). Bayesian statistics were also calculated using JASP Version 0.8.0.0 (JASP Team, 2016). According to these statistics and in support of the previously reported ANOVA, the model that best described our data corresponded to the (Instruction + Posture + [Instruction × Posture] + Group + [Posture × Group]) model (see Table S2 in the online supplemental materials). Additional analyses demonstrated that the posterior mass was not centered on the three main effects models.

To further examine the results, two ANOVAs with group (CB, SC) as the between-subjects variable and posture (uncrossed vs. crossed) as the within-subject factor were then carried out separately for the internal and external conditions of the task. In the internal condition, the posture effect was significant, $F(1, 26) = 8.33$, $p = .008$, $\eta_p^2 = .24$, as well as the group effect, $F(1, 26) = 5.74$, $p = .02$, $\eta_p^2 = .18$. Participants performed better in the uncrossed posture ($M \pm SE = 0.90 \pm 0.006$) as compared to the crossed-hands position ($M \pm SE = 0.61 \pm 0.009$). Blind individuals were more accurate ($M \pm SE = 0.87 \pm 0.07$) than their sighted peers ($M \pm SE = 0.64 \pm 0.07$). There was finally a significant posture x group interaction, $F(1, 26) = 6.88$, $p = .01$, $\eta_p^2 = .21$, showing that while sighted people showed a steeper slope in the uncrossed posture ($M \pm SE = 0.91 \pm 0.07$) as compared to the crossed position of the hands ($M \pm SE = 0.36 \pm 0.18$), there was no difference between the uncrossed ($M \pm SE = 0.88 \pm 0.01$) and crossed positions ($M \pm SE = 0.86 \pm 0.02$) in the blind group. In the external condition of the task, the same effect of posture, $F(1, 26) = 33.75$, $p = .0001$, $\eta_p^2 = .56$, and group, $F(1, 26) = 5.76$, $p = .02$, $\eta_p^2 = .18$, as well as the same Posture × Group interaction, $F(1, 26) = 6.54$, $p = .02$, $\eta_p^2 = .20$, were found. In this condition of the task, a posture difference was found in both groups, $t(14) = —6.23$, $p = .0001$ in the sighted group; $t(12) = —2,18$, $p = .05$ in the blind group, but the difference between both postures was larger in the sighted group ($M \pm SE = —1.07 \pm 0.17$) than in the blind group ($M \pm SE = —0.42 \pm 0.19$), $t(26) = —2.56$, $p = .02$ (see Figure 2).
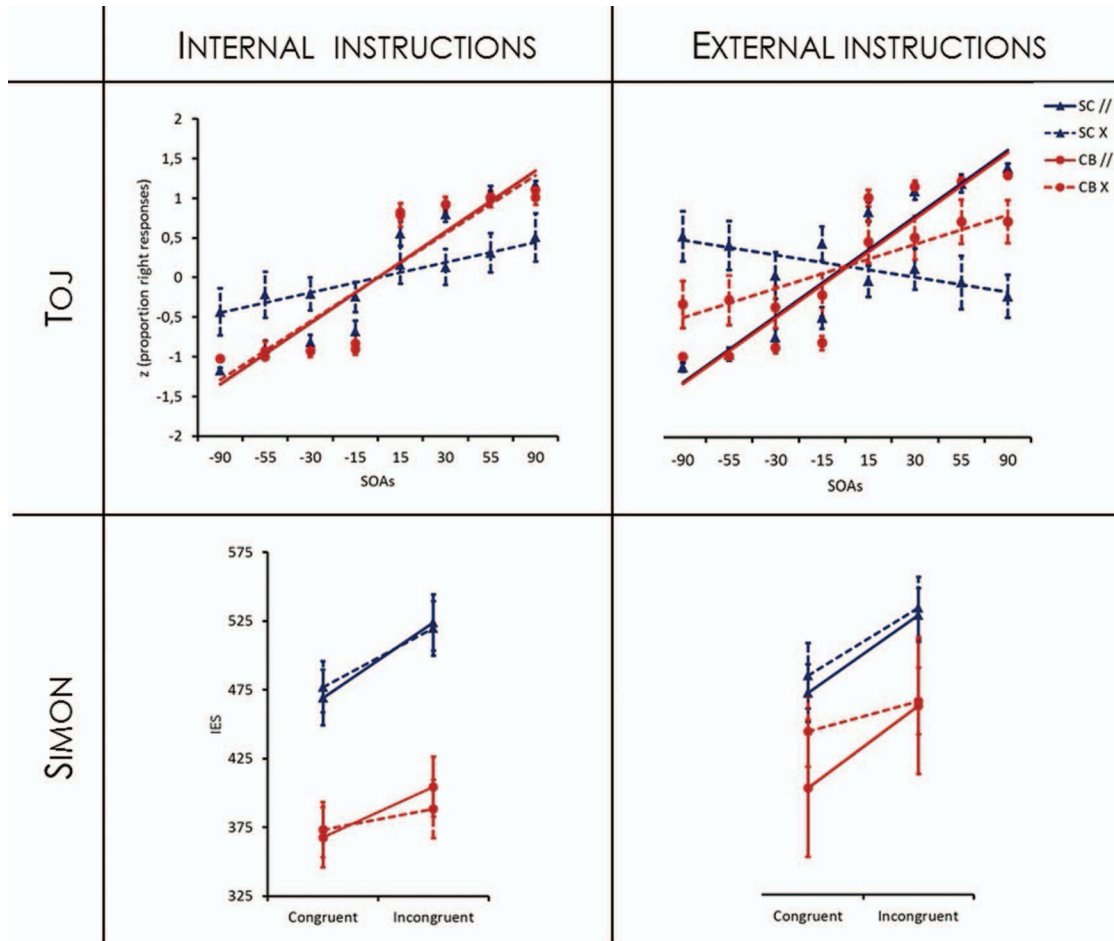
Figure 2. Top row: Slopes of the temporal order judgment (TOJ) task under internal (left panel) and external instructions (right panel). The proportion of right-hand responses was calculated in the internal condition, while the proportion of right-space responses was calculated in the external condition. Bottom row: Inverse efficiency scores in the Simon task under internal (left panel) and external instructions (right panel). Sighted controls (SCs) are represented in blue (dark gray); congenitally blind (CB) in red (light gray); double slashes (//) represent the uncrossed posture (straight lines); X represents the crossed posture (dashed lines). Bars represent standard errors of the mean. SOA = stimulus onset asynchrony. See the online article for the color version of this figure.

Simon Task

In experiments emphasizing accuracy and processing speed, as it is the case in the present task, it is common to combine both response speed and accuracy into a single score performance to obtain a general index of performance that discounts possible criterion shift or speed/accuracy tradeoff effects (Crollen, Dormal, Seron, Lepore, & Collignon, 2013; Röder et al., 2007; Townsend & Ashby, 1978). Participants' performance was therefore analyzed by measuring inverse efficiency scores (IESs), which were obtained by dividing RTs by correct response rates. A blind participant was removed from the analyses because his RTs were 3 *SD* larger than the blind group mean RT.

A 2 (Condition: congruent, incongruent) $\times$ 2 (Position: uncrossed, crossed) $\times$ 2 (Instruction: internal vs. external) repeated-measures ANOVA with group (SC vs. CB) as a between-subjects factor was then carried out on the IES measure. Results first demonstrated a group effect, $F(1, 26) = 10.23$, $p = .004$, $\eta^2_p = .28$,

with blind individuals ($M \pm SE = 413.68 \pm 20.01$) performing better than their sighted peers ($M \pm SE = 501.13 \pm 18.63$). We also observed an effect of instruction, $F(1, 26) = 13.63$, $p = .0001$, $\eta^2_p = .34$, with participants performing better under the internal instructions ($M \pm SE = 440.48 \pm 13.71$) than under the external ones ($M \pm SE = 474.33 \pm 15.10$). A significant instruction x group interaction, $F(1, 26) = 8.37$, $p = .008$, $\eta^2_p = .24$, nevertheless indicated that the instruction effect was essentially present in the blind group. There was also a significant effect of condition, $F(1, 26) = 91.65$, $p = .0001$, $\eta^2_p = .78$, suggesting the presence of the Simon effect; participants indeed performed better in the congruent condition ($M \pm SE = 436.32 \pm 14.13$) than in the incongruent one ($M \pm SE = 478.49 \pm 13.56$). The Condition $\times$ Group interaction was marginally significant, $F(1, 26) = 3.85$, $p = .06$, $\eta^2_p = .13$, suggesting that the Simon effect tended to be less pronounced in the blind than in the sighted group. Finally, interactions between instruction and condition, $F(1, 26) = 5.23$, $p =$

.03, $\eta^2_p = .17$, and between posture and condition, $F(1, 26) = 9.63$, $p = .005$, $\eta^2_p = .27$, were observed. The difference between the incongruent and congruent conditions was larger, $t(27) = -2.18$, $p = .04$, under external instructions ($M \pm SE = 47.59 \pm 5.80$) than under internal instructions ($M \pm SE = 37.98 \pm 4.32$). Similarly, the Simon effect was larger, $t(27) = -2.92$, $p = .007$, when participants responded with the hands uncrossed ($M \pm SE = 52.31 \pm 3.98$) as compared to the crossed position ($M \pm SE = 33.26 \pm 6.94$; see Figure 2).

The ANOVA conducted here therefore demonstrated that the blind participants performed better than the sighted. This difference between both groups was larger in the internal condition of the task. But, more interestingly for our purposes, our results failed to replicate the significant reversal of the Simon effect in the blind group as previously observed by Röder et al. (2007) in the crossed hands posture with external instructions. To confirm this failure to replicate, we applied the method recently described by Masson (2011) to compute the posterior probabilities for the null hypothesis (no interaction between condition and group) and Hypothesis 1 (interaction between condition and group). This analysis indicated that the posterior probabilities were .43 for the null hypothesis (i.e., the null hypothesis has 43% chance of being true) and .57 for Hypothesis 1. According to Raftery's (1995) classification of evidence into weak (.50 –.75), positive (.75–.95), strong (.95–.99), and very strong (>.99), the probability values obtained for this interaction therefore provide weak support for Hypothesis 1 and weak support for the presence of a reversed Simon effect in the blind group.

To further confirm our results, we acquired another set of fully independent data on the same task on 11 CB and 11 SC that did not participate in the main experiment. This set of data also demonstrated the presence of a canonical Simon effect in the blind and sighted groups while responding with hands uncrossed and crossed over the body midline, under external instructions (see the Appendix).

Discussion

In this study, blind and sighted participants were required to perform two different tasks (TOJ vs. auditory Simon tasks) under two different instruction conditions. In the internal condition, emphasis was put on the hand used to respond (which hand received the first tactile stimulation in the TOJ task vs. association of high and low sounds with the left and right hands in the Simon task). In the external condition, target locations had to be reported in external space (which space received the first tactile stimulation in the TOJ vs. association of high and low sounds with the left and right hemispaces). Moreover, both tasks were performed with the hands uncrossed or crossed over the body midline to challenge the congruency between anatomical and external coordinate systems under equal sensory stimulation. We wanted to investigate whether the use of internal and external coordinate systems depend on task's demands in perception and action tasks, and the role visual experience plays in weighting the internal and external coordinate systems.

Overall, our results demonstrated a significant effect of instructions in the TOJ task. Congenitally blind and sighted participants performed better under internal instructions than under external ones. This general internal "advantage" is well in line with the idea

that tactile information is initially processed in a skin-based or anatomical reference frame (Azañón, & Soto-Faraco, 2008; Shore et al., 2002; Yamamoto & Kitazawa, 2001). Touch may therefore be originally organized in a homuncular, skin-based fashion in primary somatosensory cortex and afterward transformed and integrated into external space (Badde & Heed, 2016; Heed, Buchholz, et al., 2015).

In sighted people, a crossing hand deficit was observed irrespective of the instruction. The performance of the participants was indeed better in the uncrossed position than with the hands crossed over the body midline. This crossing hand deficit has been repeatedly observed in sighted people (Crollen, Albouy, et al., 2017, Crollen, Lazzouni, et al., 2017; Röder, Heed, & Badde, 2014; Shore et al., 2002; Yamamoto & Kitazawa, 2001) and demonstrated a difficulty in adjusting the perception of tactile inputs with the spatial position of the hands. This difficulty seems moreover to be independent of the effector used to respond as it not only occurs when responses are given with the stimulated hand (Crollen, Albouy, et al., 2017; Crollen, Lazzouni, et al., 2017; Röder et al., 2014), but also when participants respond with a foot pedal as here (see also Azañón, Camacho, & Soto-Faraco, 2010; Heed, Backhaus, & Röder, 2012; Yamamoto, Moizumi, & Kitazawa, 2005), when they respond verbally (Pagel, Heed, & Röder, 2009; Hermosillo, Ritterband-Rosenbaum, & van Donkelaar, 2011), or when they have to look toward the limb that was stimulated first (Yamamoto & Kitazawa, 2001).

In the blind, crossing the hands did not lead to a decrement of performance in the internal condition of the task. This result replicates previous reports suggesting that the automatic external remapping of touch depends on early visual experience (Röder et al., 2014; Crollen, Albouy, et al., 2017; Crollen, Lazzouni, et al., 2017). However, we reported for the first time that a crossing hand deficit might be observed in CB people during a TOJ task when target locations have to be reported externally. The observation of this crossing-hand deficit in the external condition of the task supports the idea that blind individuals are able to activate external information while making tactile localization (Heed et al., 2015; Schubert et al., 2017). When required by the task, CB humans therefore integrate internal and external spatial coordinates but they do so by probably using lower default weights for externally coded information (Badde & Heed, 2016). This specific weighting scheme can be advantageous in some specific tasks such as the TOJ. Even in the external condition of the task, it is interesting to note that crossing the hands less dramatically affected the blind than the sighted performances. The slope of the external condition in the blind was indeed less steep than the one observed in the sighted (which was actually completely inverted; see Figure 2). However, this particular weighting scheme may also be detrimental in other situations, like when blind individuals have to readily integrate audiotactile information in the crossed posture, putatively due to the less integrated default spatial coordinates of these two modalities (internal by default for touch and external by default for sound in the blind while both stimulation activate an external frame of reference in the sighted; Collignon, Charbonneau, Lassonde, & Lepore, 2009).

It has recently been demonstrated that RTs in a tactile detection task are faster when tactile stimuli are presented to the side of the body ipsilateral to the body part used to respond (Tamè & Longo, 2015). This advantage, the crossed-uncrossed difference is thought

to reflect interhemispheric interactions. According to this hypothesis, it is more demanding to integrate information coming from different hemispheres than to integrate information coming from the same hemisphere. It is interesting to note that this hypothesis could explain in itself why performances of both blind and sighted participants were worst in the crossed position of the external condition of the TOJ task. In this particular condition, the stimulated hand and the motor effector did indeed not project to the same hemisphere, creating a sensorimotor integration "cost" (and therefore lower performances). As this cost is eliminated when vision of the body is present (Tamè, Carr, & Longo, 2017), blindfolding sighted participants may have further impaired their performance, supporting the idea that sighted people preferentially use a visuospatial coordinate system when processing touch.

In the Simon task, sighted and blind participants demonstrated a classic Simon effect: Performances of both groups were better when the location of the sound (left vs. right loudspeaker) was congruent with the location of the response key in external space irrespective of the hand position (crossed vs. uncrossed) and instruction conditions (internal vs. external). Even if the Simon effect was less pronounced in the blind group than in the sighted, our results did not replicate previous data reporting a reversal of the Simon effect in the blind with external instructions (Röder et al., 2007). This result demonstrates that auditory inputs activate an external coordinate system irrespective of the participants' early visual experience (see also the Appendix for a replication of this effect in an independent sample of blind individuals). It is important to note that the Simon and TOJ tasks present different characteristics in terms of input stimuli. While the TOJ task necessarily involves skin-based coordinates, the Simon task necessarily involves the computation of external coordinates because the auditory stimuli originate in external space. Our two tasks therefore allocated, by default, different weights to the internal and external coordinate systems. While the sighted performances were congruent with this default weighting scheme (better performances under internal instructions in the TOJ, preferential use of external coordinates in the Simon task), visual deprivation seems to modulate it. Indeed, blind people performed better under internal instructions even in a task emphasizing the use of an external frame of reference (i.e., Simon task). As blind participants nevertheless demonstrated a classic Simon effect which reflects a spatial compatibility effect between the external location of a stimulus and the external location of a response, our data support recent studies showing that blind individuals are able to use external coordinates in specific circumstances, for example, when time encoding is required (Bottini, Crepaldi, Casasanto, Crollen, & Collignon, 2015) or when the task involves action such as bimanual movements (Heed & Röder, 2014) and motor sequence learning (Crollen, Albouy, et al., 2017).

As in the TOJ task, there was a significant effect of group in the Simon task, suggesting that blind participants performed better than their sighted peers. Moreover, while the sighted performances were not influenced by task's instructions, blind individuals were more efficient while performing the task under internal instructions. Gori and colleagues recently demonstrated that auditory localization might be impaired or delayed in the blind under specific circumstances (Cappagli, Cocchi, & Gori, 2017; Gori, Sandini, Martinoli, & Burr, 2014; Vercillo, Burr, & Gori, 2016; Vercillo, Tonelli, & Gori, 2018). Bisection of auditory triplets was indeed shown to be more difficult in the blind when external acoustic landmarks were used or when participants had to reproduce the spatial distance between two sounds. In contrast, blind people demonstrated normal performances when they had to localize sounds with respect to their own hand or when they had to judge the distances of sounds from their finger (Vercillo et al., 2018). Internal coordinates therefore seem particularly important for the blind, who, independently of the nature of the task, better think about spatial relationships in internal terms. Early visual deprivation might therefore reduce the default activation of external space. In conclusion, our data suggest that both sighted and CB individuals can integrate internal and external information for perception and action but the weight attributed to each coordinate system depends on the task and instruction at play.

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Appendix

Simon Task's Data Acquired in Montreal

Method: Participants

Eleven CB participants and 11 SC from Montreal (Canada) were required to perform the Simon task under external instructions (same procedure as previously described). The CB group was composed of three females and eight males ranging in age from 21 to 61 years old with a mean age of 42 years ($SD = 13.74$). Participants were totally blind or had only rudimentary sensitivity for brightness differences but never experienced patterned vision. In all cases, blindness was attributed to peripheral deficits with no additional neurological problems. The SC group was matched to the CB group in terms of age and sex. This group was composed of four females and seven males ranging in age from 21 to 68 years old with a mean age of 43 years ($SD = 14.13$). Sighted participants were blindfolded when performing the tasks. All the procedures were approved by the Research Ethics Boards of the University of Montreal and the experiments were undertaken with the understanding and written consent of each participant.

Results

The IES values were entered in a 2 (Group: CB, SC) $\times$ 2 (Condition: congruent, incongruent) $\times$ 2 (Hand Posture: crossed, uncrossed) repeated-measures ANOVA with group as the between-subjects factor. This analysis demonstrated the following results (see Figure A1): (a) a main effect of posture, $F(1, 20) = 5.98$, $p = .02$, $\eta^2_p = .23$, indicating that participants responded faster in the uncrossed position ($M \pm SE = 455.25 \pm 23.16$) than with their hands crossed over the body midline ($M \pm SE = 480.08 \pm 25.01$); (b) a main effect of condition, $F(1, 20) = 63.01$, $p = .0001$, $\eta^2_p = .76$, and post hoc analyses indicated that the congruent trials ($M \pm SE = 444.63 \pm 23.82$) were responded faster than the incongruent ones ($M \pm SE = 490.70 \pm 23.65$); (c) a marginal effect of group, $F(1, 20) = 3.38$, $p = .08$, $\eta^2_p = .14$, suggesting that the blind tended to perform better ($M \pm SE = 424.35 \pm 33.32$) than their sighted peers ($M \pm SE = 510.97 \pm 33.32$); and (d) a marginally significant Condition $\times$ Group interaction, $F(1, 20) = 3.50$, $p = .08$, $\eta^2_p = .15$. The Simon effect was present in both groups, but the difference between the congruent and incongruent
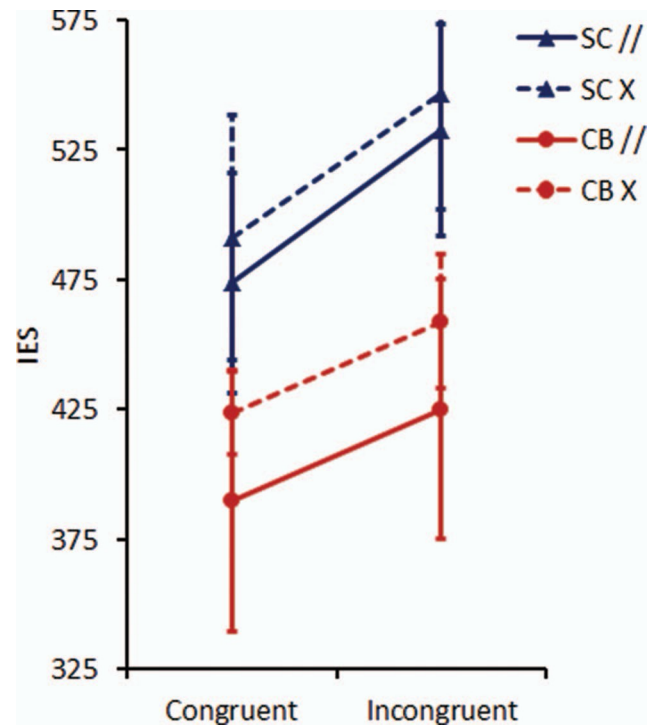

Figure A1. Group mean inverse efficiency scores (IES) with standard errors of the means in the Simon task for the congenitally blind (CB) and their sighted control (SC) group (data coming from a participants' sample in Montreal). See the online article for the color version of this figure.

conditions tended to be larger in the sighted group. No other effect was significant, supporting our observation that the Simon effect did not reverse in the blind while responding with crossed hands.