Task demands affect spatial reference frame weighting during tactile localization in sighted and congenitally blind adults

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Abstract Task demands modulate tactile localization in sighted humans, presumably through weight adjustments in the spatial integration of anatomical, skin-based, and external, posture-based information. In contrast, previous studies suggested that congenitally blind humans, by default, localize touch based on skin-based information and refrain from automatic spatial integration. Accordingly, task context should not affect blind participants' tactile localization performance in tasks that do not require external coding. Here, sighted and congenitally blind participants localized tactile targets on the palm or back of one hand, while ignoring simultaneous tactile distractors at congruent or incongruent locations on the other hand. Hand posture was varied either blockwise or trial-by-trial, to probe the interplay of anatomical and external location codes for spatial congruency effects: either both palms faced down, or one faced down and one up. In the latter posture, externally congruent target and distractor locations were anatomically incongruent. 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 better for anatomically congruent than incongruent target-distractor pairs. In contrast, under external instructions, performance was best when target-distractor pairs were externally congruent. These modulations were comparable in sighted and blind individuals, even if effects were smaller in the latter. Whether posture was changed blockwise or trial-by-trial did not significantly modulate congruency effects. These results suggest that blind individuals, like the sighted, automatically integrate anatomical and external information during tactile localization, and that integration is modulated by top-down information – here, task instruction. Thus, the integration of anatomical and external spatial information in tactile processing is flexibly adapted to current task demands even in the absence of developmental vision.

Keywords congenital blindness; tactile reference frames; tactile remapping.

1. Introduction

The brain continuously integrates information from multiple sensory channels (Alais & Burr, 2004; Angelaki, Gu, & DeAngelis, 2009; Ernst & Banks, 2002; Körding & Wolpert, 2004; Landy, Maloney, Johnston, & Young, 1995; Sober & Sabes, 2005; Trommershäuser, Körding, & Landy, 2011). Tactile localization, too, involves the integration of several information sources, such as cutaneous, visual, and proprioceptive information, and has therefore been investigated in the context of information integration within and across the senses. We have suggested that tactile localization involves at least two cortical processing steps (Badde & Heed, in press). When tactile information first arrives in the cortex, it is initially encoded relative to the skin in an anatomical reference frame, reflected in the homuncular organization of the somatosensory cortex (Penfield & Boldrey, 1937). This information is consecutively remapped into an external reference frame. By merging anatomical skin-based spatial information with proprioceptive, visual, and vestibular signals, the brain derives an external spatial location, a process usually referred to as tactile remapping (Clemens, Vrijer, Selen, Gisbergen, & Medendorp, 2011; Driver & Spence, 1998; Heed, Buchholz, Engel, & Röder,

2015; Holmes & Spence, 2004; Maravita, Spence, & Driver, 2003). The term ‚external', in this context, denotes a spatial code that abstracts from the original location, but may nevertheless be egocentric, and, as such, be anchored to eyes, head, or torso (Heed, Buchholz, et al., 2015). In a second step, information of the two reference frames is integrated, presumably to derive an superior tactile location estimate(Badde & Heed, in press). For sighted individuals, this integration of different tactile codes appears to be mandatory (Azañón, Camacho, & Soto-Faraco, 2010; Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001). Yet, the relative weight of each code is subject to change depending on current task demands: external spatial information is weighted more strongly when task instructions emphasize external spatial aspects (Badde & Heed, in press; Badde, Heed, et al., 2015; Badde, Röder, et al., 2015), in the context of movement (Gherri & Forster, 2012a, 2012b; Heed, Möller, & Röder, 2015; Hermosillo, Ritterband-Rosenbaum, & van Donkelaar, 2011; Mueller & Fiehler, 2014a, 2014b; Pritchett, Carnevale, & Harris, 2012), and in the context of frequent posture changes (Azañón, Stenner, Cardini, & Haggard, 2015). Thus, the tactile localization estimate depends on flexibly weighted integration of spatial reference frames.

Moreover, tactile localization critically depends on visual input from birth. Anatomical and external spatial reference frames can be experimentally misaligned by crossing the hands over the midline, so that the left hand occupies the right external space and vice versa. Such manipulations reportedly impair tactile localization compared to an uncrossed hands posture in sighted, but not in congenitally blind individuals (Collignon, Charbonneau, Lassonde, & Lepore, 2009; Röder, Rösler, & Spence, 2004). Similarly, hand crossing has been found to attenuate spatial attention effects on somatosensory event-related potentials (ERP) between approximately 100 and 250 ms poststimulus in sighted, but not in congenitally blind individuals (Röder, Föcker, Hötting, & Spence, 2008). Together, these previous studies indicate that, contrary to sighted individuals, congenitally blind may not by default integrate external information with anatomical skin-based information. Yet, recent studies have cast doubt on the generality of this conclusion. For instance, it has been demonstrated that congenitally blind individuals used external along with anatomical coding when tactile stimuli had to be localized while making bimanual movements (Heed, Möller, et al., 2015). In addition to tactile localization tasks, evidence from a bimanual coordination task, too, indicates that congenitally blind individuals use external spatial information: when they moved their fingers symmetrically, this symmetry appeared to be encoded relative to external space rather than according to anatomical parameters such as the involved muscles (Heed & Röder, 2014). Moreover, early blind individuals appear to encode time relative to external space, and this coding strategy may be related to left-right finger movements during Braille reading (Bottini, Crepaldi, Casasanto, Crollen, & Collignon, 2015). These studies imply that congenitally blind humans, like the sighted, integrate spatial information coded in different reference frames according to a weighting scheme (Badde & Heed, in press). Furthermore, although weighting preferences appear to differ between these two groups, movement contexts appear to induce stronger weighting of external spatial information in both sighted and congenitally blind individuals.

Besides movement context, task demands, too, are a factor that can modulate the weighting of spatial information in tactile localization of sighted individuals. For instance, tactile temporal order judgments (TOJ), that is, the decision which of two tactile locations was stimulated first, are sensitive to a conflict between anatomical and external locations that arises when stimuli are applied to crossed hands. These crossing effects, indicative of the weighting of the two tactile codes, were modulated when a secondary task accentuated anatomical versus external space (Badde, Röder, et al., 2015). Another possibility to study spatial tactile processing is to test how task-irrelevant distractors interfere with tactile localization

(Spence, Pavani, Maravita, & Holmes, 2004). For instance, elevation judgements of tactile stimuli on the hands are faster and more accurate when a visual distractor is simultaneously presented at a congruent than at an incongruent elevation (Spence, Pavani, & Driver, 2000). Similarly, tactile distractors presented to one hand interfere with elevation judgements about simultaneously presented tactile target stimuli presented at incongruent locations of the other hand (Gallace, Soto-Faraco, Dalton, Kreukniet, & Spence, 2008; Soto-Faraco, Ronald, & Spence, 2004). In such tasks, one can define spatial congruency in two ways: congruency in an anatomical reference frame, that is, both stimuli occur at corresponding skin locations, and congruency in an external reference frame, that is, both stimuli occur at corresponding elevations. If both hands are held in the same posture, for instance, with both palms facing down, anatomical and external congruency correspond. However, when the palm of one hand faces up and the other down, two tactile stimuli presented at upper locations in external space will be located at different anatomical skin locations and, thus, anatomical and external congruency are incongruent. A comparison of congruency effects between these postures provides a measure of the weighting of anatomical and external tactile codes. This weighting has been shown to be subject to task context effects as well: When task instructions required participants to report tactile elevation relative to their external rather than to their anatomical location spatial congruency modulated performance in an external reference frame (Gallace et al., 2008). Yet, whether congruency effects were encoded relative to anatomical or relative to external space was modifiable by both task instructions and response modalities (Gallace et al., 2008). This suggests that the weighting of anatomical and external spatial information in the tactile congruency task was flexible, and was modulated by task requirements.

In congenitally blind humans, evidence as to whether task instructions modulate spatial tactile integration in a similar way as in sighted individuals is currently indirect. Two very similar studies have investigated tactile spatial coding in early (Eardley & van Velzen, 2011) and in congenitally blind humans (Röder et al., 2008) by examining somatosensory ERPs elicited by tactile stimulation in different hand postures. Both studies asked participants to report infrequent tactile target stimuli on a pre-cued hand, but observed contradicting results: One study reported an attenuation of spatial attention-related somatosensory ERPs between 140 and 300 ms poststimulus to non-target stimuli with crossed compared to uncrossed hands (Eardley & van Velzen, 2011), suggesting that external location had affected tactile spatial processing in early blind participants. The other study (Röder et al., 2008), in contrast, did not observe any modulation of spatial attention-related somatosensory ERPs by hand posture and concluded that congenitally blind humans do not, by default, use external spatial information for tactile localization. The two studies differed in how participants were instructed about the to-be-monitored location. In the first study, a the pitch of an auditory cue indicated the task-relevant side relative to external space in each trial (Eardley & van Velzen, 2011). In the second study, in contrast, the pitch of a cuing sound referred to the task-relevant hand, independent of hand location in external space (Röder et al., 2008). Thus, one may hypothesize that task instructions modulate how anatomical and external information is weighted in congenitally blind individuals as they do in the sighted.

Here, we investigated the weighting of anatomical and external reference frames by means of an adapted version of the tactile congruency task (Gallace et al., 2008; Soto-Faraco et al., 2004). Sighted and congenitally blind participants localized vibro-tactile target stimuli, presented randomly on the palm or back of one hand, while ignoring a vibro-tactile distractor on the palm or back of the other hand. Thus, the distractor could appear at an anatomically congruent or incongruent location. Hand posture was varied to allow investigation of the weighting of the involved spatial reference frames, with either both palms facing downwards, or one palm facing downwards and

the other upwards. With differently oriented hands, anatomically congruent stimuli were incongruent in external space and vice versa. Thus, misaligning spatial reference frames by placing the hands in different orientations allows investigating whether tactile congruency effects are encoded relative to anatomical or to external spatial locations.

We introduced two experimental manipulations to investigate the role of task demands on the weighting of anatomical and external spatial information. First, every participant performed the task under two different sets of instructions: In one session, responses were instructed anatomically, that is, with respect to palm or back of the hand. In a second session, responses were instructed externally, that is, with respect to upper and lower locations in space. We hypothesized that task instructions would emphasize the weighting of the corresponding reference frame. This means that with differently oriented hands (that is, when anatomical and external reference frames are misaligned) the size, or even direction, of congruency effects should depend on task instructions.

With the second manipulation, we aimed at corroborating previous results suggesting that movement planning and execution as well as frequent posture change lead to an emphasized weighting of external spatial information (Azañón et al., 2015; Gherri & Forster, 2012a, 2012b; Heed, Möller, et al., 2015; Hermosillo et al., 2011; Mueller & Fiehler, 2014a, 2014b; Pritchett et al., 2012). Accordingly, we hypothesized that frequent posture changes would increase the weight of the external reference frame in a similar way for the spatial coding of congruency in the present task. To this end, participants either held their hands in a fixed posture for an entire experimental block, or they changed their hand posture in a trial-by-trial fashion. Again, with differently oriented hands, changes in the weighting of anatomical and external spatial information would be evident in a modulation of tactile congruency effects; frequent posture changes, compared to a blockwise posture change, should induce an increased weighting of external information. This would result in a decrease of anatomical congruency effects under anatomical instructions and in an increase of external congruency effects under external instructions.

The weighting of external spatial information reportedly depends on the sensory experiences during early childhood (Ley, Bottari, Shenoy, Kekunnaya, & Röder, 2013). Studying how congenitally blind adults weight spatial information for tactile localization, thus, offers a model to investigate whether visual deprivation form birth prevents the default integration of anatomical and external spatial information or whether anatomical and external spatial information is integrated, but with altered integration weights.

2. Methods

We follow open science policies as suggested by the Open Science Framework (see https://osf.io/hadz3/wiki/home/) and report how we determined the sample size, all experimental manipulations, all exclusions of data, and all evaluated measures of the study. Data and analysis scripts are available online (see https://osf.io/ykqhd/).

2.1. Participants

The size of our experimental groups was constrained by the availability of congenitally blind volunteers; we invited every suitable participant we identified within a period of 6 months. Group size is comparable to that of previous studies that have investigated spatial coding in the context of tactile congruency. We report data from sixteen congenitally blind participants (8 female, 15 right handed, 1 ambidextrous, age: M = 37 years, SD = 11.6, range: 19 to 53) and from a matched control group of sixteen blindfolded sighted participants (8 female, all right handed, age: M = 36 years, SD = 11.5, range: 19 to 51). All sighted participants had normal or corrected-to-normal vision. Blind participants were visually deprived from birth due to anomalies in peripheral structures resulting either in total congenital blindness (n = 6) or in minimal residual light

perception (n = 10). Peripheral defects included binocular anophthalmia (n = 1), retinopathy of prematurity (n = 4), Leber's congenital amaurosis (n = 1), congenital optical nerve atrophy (n = 2), and genetic defects that were not further specified (n = 8). All participants gave informed written consent and received course credit or monetary compensation for their participation. The study was approved by the ethical board of the German Psychological Society (TB 122010) and conducted in accordance with the standards laid down in the Declaration of Helsinki.

Of twenty originally tested congenitally blind participants, one did not complete the experiment, and three were unable to discriminate between target and distractor stimuli. We recruited 45 sighted participants to establish a group of 16 control participants. We had developed and tested the task at the beginning in a young, sighted student population (first 12 participants). We then tested the blind group before recruiting matched controls from the population of Hamburg via online and newspaper advertisement. For many older sighted participants above the age of 30 years, discriminating target and distractor stimuli proved too difficult, resulting in localization performance near chance level. Accordingly, 23 sighted participants either decided to quit, or were not invited for the second experimental session because their performance in the first session had been at chance. Moreover, technical failure during data acquisition prevented the use of data from two additional participants.

2.2. Apparatus

Participants sat in a chair with a small lap table on their legs. They placed their hands in a parallel posture in front of them, with either both palms facing down (termed "same orientation") or with one hand flipped palm down and the other palm up (termed "different orientation"). Whether the left or the right hand was flipped palm up in the different orientation condition was counterbalanced across participants. Distance between index fingers of the hands was approximately 20 cm measured while holding both palms down. For reasons of comfort, and to avoid stimulators touching the table, the hands were supported by small foam cubes. Custom built vibro-tactile stimulators were attached to the back and to the palm of both hands midway between the root of the little finger and the wrist (Fig. 1). Participants wore earplugs and heard white noise via headphones to mask any sound produced by the stimulators. Hand posture was monitored using a movement tracking system (Visualeyez II VZ4000v PTI; Phoenix Technologies Incorporated, Burnaby, Canada), with LED markers attached to the palm and back of the hands. The experiment was controlled using Presentation (version 16.2; Neurobehavioral Systems, Albany, CA, USA), which interfaced with Matlab (The Mathworks, Natick, MA, USA) and tracker control software the VZSoft (PhoeniX Technologies Incorporated, Burnaby, Canada).

2.3. Stimuli

The experiment comprised two kinds of tactile stimuli, namely, targets, to which participants had to respond, and distractors, which participants had to ignore. Target stimuli consisted of 200 Hz stimulation for 235 ms. Distractor stimuli had the same frequency, but included two gaps of 65 ms, resulting in three short bursts of 35ms each. To address our older sighted participants' difficulty with stimulus discrimination, we adjusted the distractor stimulus pattern for the last seven recruited control participants if they could not discriminate our original stimuli during a pre-experimental screening; such adjustments were necessary for three of these last seven participants, for the four other participants no adjustments were made. In a first step, we increased the distractor's gap length to 75 ms, resulting in shorter bursts of 25 ms (1 participant). If the participant was still not able to discriminate between target and distractor, we set the distractor pattern to 50 ms "on", 100 ms "off", 5 ms "on", 45 ms "off", and 35 ms

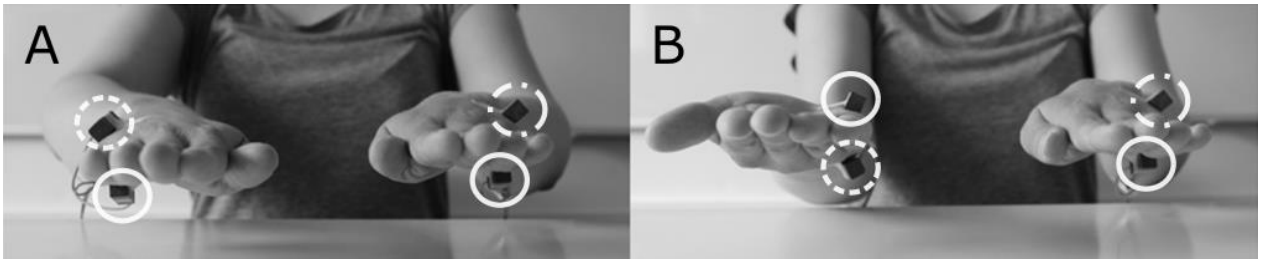

Figure 1. Experimental setup. Four vibro-tactile stimulators were attached to the palm and back of the hands (marked with white circles). The hands were either held in the same orientation with both palms facing downwards (A) or in different orientations with one hand flipped upside-down (B). In each trial, a target stimulus was randomly presented to one of the four locations. Simultaneously, a distractor stimulus was presented randomly at one of the stimulator locations on the other hand. Target and distractor stimuli differed with respect to their vibration pattern. Participants were asked to localize the target stimulus as quickly and accurately as possible. For statistical analysis and figures, stimulus pairs presented to the same anatomical locations were defined as congruent, as illustrated by dashed (target) and dashed-dotted (distractor) circles, which both point to the back of the hand here. Note that with differently oriented hands (B) anatomically congruent locations are incongruent in external space and vice versa.

"on" (2 participants). Note that, while these distractor stimulus adjustments made discrimination easier, they did not affect target localization per se. More importantly, they were the same for all experimental conditions. Yet, to ascertain that statistical results were not driven by these three control participants, we ran all analyses both with and without their data. The overall result pattern was unaffected, and we thus report results of the full matched control group.

2.4. Procedure

The experiment was divided into four large parts according to the combination of the two experimental factors Instruction (anatomical, external) and Movement Context (static vs. dynamic context, that is, blockwise vs. frequent posture changes). The order of these four conditions was counterbalanced across participants. Participants completed both Movement Context conditions in a counterbalanced order, that is, the static and the dynamic part, under the first instruction within one session, and under the second instruction in a another session, which took part on another day. Participants completed four blocks of 48 trials for each combination of Instruction and Movement Context. Trials in which participants responded too fast (RT < 100 ms), or not at all, were repeated at the end of the block.

2.5. Manipulation of instruction

Under external instructions, participants had to report whether the target stimulus was located "up" or "down" in external space and ignore the distractor stimulus. They had to respond as fast and accurately as possible by means of a foot pedal placed underneath one foot (left and right counterbalanced across participants). Participants responded by lifting the toes for target stimuli located "up" and by lifting the heel for target stimuli located "down". Under anatomical instructions, participants reported whether the target was presented to the palm or back of the hand by lifting the toes and the heel, respectively.

2.6. Manipulation of movement context

Under each set of instructions, participants performed the entire task once with a constant hand posture for entire experimental blocks (static condition), and once with hand posture varying from trial to trial (dynamic condition).

2.6.1. Static movement context

In the static context, posture was instructed verbally at the beginning of each block. A tone (1000 Hz sine, 100 ms) presented via loudspeakers placed approximately 1 m behind the participants signaled the beginning of a trial. After 1520 - 1700 ms (square distribution) a

tactile target stimulus was presented randomly to one of the four locations. Simultaneously, a tactile distractor stimulus was presented to one of the two locations on the other hand. Hand posture was changed after completion of the second of four blocks. Start posture was counterbalanced across participants.

2.6.2. Dynamic movement context

In the dynamic context, an auditory cue at the beginning of each trial instructed participants either to retain (one beep, 1000 Hz sine, 100 ms) or to change (two beeps, 900 Hz sine, 100 ms each) the posture of the left or right hand (constant throughout the experiment, but counterbalanced across participants). After this cue onset, the trial continued only when the corresponding motion tracking markers attached to the hand surfaces had been continuously visible from above for 500 ms. If markers were not visible 5000 ms after cue onset, the trial was aborted and repeated at the end of the block. An error sound reminded the participant to adopt the correct posture. Tactile targets occurred equally often at each hand, so that targets and distracters, respectively, occurred half of the time on the moved, and half of the time on the unmoved, hand. The order of trials in which posture changed and trials in which posture remained unchanged, was pseudo-randomized in a way to assure equal amounts of trials for both conditions. This was done, for the entire experimental group, by drawing 10,000 samples from all possible trial orders; the number of trials in each condition was calculated for each permutation, and permutations which contained the same number of trials for each condition were selected. An individual trial order was randomly assigned to each participant.

2.7. Practice

Before data acquisition, participants familiarized themselves with the stimuli by completing one block in which each trial contained only the target or the distractor, and participants reported which of the two had been presented. Next, participants localized 23 target stimuli without the presence of a distractor stimulus to practice the current task rules (i.e., anatomical vs. external instructions). Finally, participants practiced five blocks of 18 regular trials, two with the hands in the same orientation, and three with the hands in different orientations. Auditory feedback was provided following incorrect responses during practice, but not during the subsequent experiment.

2.8. Data analysis

Data were analyzed and visualized in R (version 3.2.2; R Core Team, 2015) using the R packages lme4 (v1.1-9; Bates, Maechler, Bolker, & Walker, 2014), afex (v0.14.2; Singmann, Bolker, & Westfall, 2015), lsmeans (v2.20-2; Lenth & Hervé, 2015), dplyr (v0.4.3; Wickham & Francois, 2015), and ggplot2 (v1.0.1; Wickham, 2009). Trials with reaction times longer than 2000 ms were excluded from further analysis (5.58 % of all trials). Reaction times were analyzed for trials with correct responses only.
It has been suggested that using an ANOVA to analyze categorical data is inappropriate (Jaeger, 2008). Therefore, we used generalized linear mixed models (GLMM) with a binomial link function to analyze accuracy (Bolker et al., 2009). We analyzed reaction times with linear mixed models (LMM). To prevent that the fitted model's residuals violated normality and homoscedasticity assumptions, reaction times were box-cox transformed (Box & Cox, 1964) with lambda = -0.06. Random intercepts and slopes per participants were estimated for each main effect, but not for interactions, as some (G)LMMs did not converge when the latter were included. Significance of fixed effects was assessed with likelihood ratio tests comparing the model with the maximal fixed effects structure and a reduced model without the fixed effect of interest (Pinheiro & Bates, 2000). These comparisons were calculated using the afex package (Singmann et al., 2015), and employed Type III sums of squares and sum-to-zero contrasts. Fixed effects were considered significant at $p < 0.05$. Post-hoc comparisons of significant interactions were conducted using

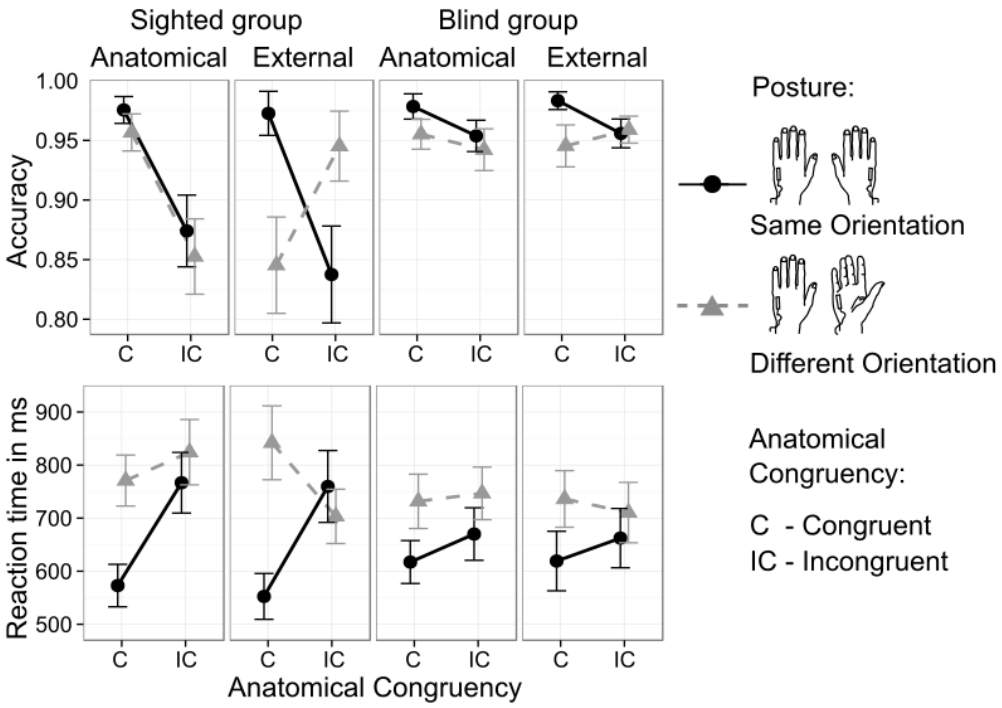

Figure 2. Accuracy (top panel) and reaction times (bottom panel) in the tactile congruency task collapsed over static and dynamic movement conditions. Sighted (2 left columns) and congenitally blind participants (2 right columns) were instructed to localize tactile targets either relative to their anatomical (first and third column) or relative to their external spatial location (second and forth column). Hands were placed in the same (black circles) and in different orientations (grey triangles). Tactile distractors were presented to anatomically congruent (C) and incongruent (IC) locations of the other hand and had to be ignored. Congruency is defined in anatomical terms (see Fig. 1). Accordingly, with differently oriented hands, anatomically congruent stimulus pairs are incongruent in external space and vice versa. Whiskers represent the standard error of the mean. Although accuracy was analyzed with a log-link GLMM, we present untransformed percentage-correct values to allow a comparison to previous studies (see methods for details).

approximate z-tests on the estimated least square means (LSM, lsmeans package; Lenth & Hervé, 2015). The resulting p-values were corrected for multiple comparisons following the procedure proposed by Holm (1979). To assess whether the overall result pattern differed between groups, we fitted a (G)LMM with the fixed between-subject factor Group (sighted, blind) and fixed within-subjects factors Instruction (anatomic, external), Posture (same, different), Congruency (congruent, incongruent), and Movement Context (static, dynamic). Congruency was defined relative to anatomical locations for statistical analysis and figures. Subsequently, to reduce (G)LMM complexity and to ease interpretability, we conducted separate analyses for each participant group including the same within-subject fixed effects as before.

3. Results

We assessed how task instructions and movement context modulate the weighting of anatomically and externally coded spatial information in a tactile-spatial congruency task performed by sighted and congenitally blind individuals. Such weight changes should become evident in a modulation of congruency effects within hand postures that induce misalignment between these different reference frames. With differently oriented hands, stimulus pairs presented to anatomically congruent locations are incongruent in external space and vice versa, whereas the two coding schemes agree when the hands are in the same orientation. Thus, a modulation of reference frame weighting by task instructions would be evident in an interaction of Instruction, Posture, and Congruency. Furthermore, a modulation of

weights by the movement context would be evident in an interaction of Movement Context, Posture, and Congruency.

Accuracy and reaction times of sighted and congenitally blind groups are illustrated in Figure 2. A GLMM on accuracy (Table 1) with fixed effect factors Group, Instruction, Posture, Congruency, and Movement Context revealed a four-way interaction of Group, Instruction, Posture, and Congruency ($\chi^2(1) = 13.83$, $p < 0.001$) and a main effect of Movement Context ($\chi^2(1) = 4.54$, $p = 0.033$). Furthermore, there was a trend towards significance for the two-way interaction of Group and Movement Context ($\chi^2(1) = 3.47$, $p = 0.063$). An LMM of reaction times (Table 2) with fixed effects Group, Instruction, Posture, Congruency, and Movement Context revealed four-way interactions between Group, Instruction, Posture, and Congruency ($\chi^2(1) = 13.67$, $p < 0.001$) and between Group, Instruction, Posture, and Movement Context ($\chi^2(1) = 20.51$, $p < 0.001$).

Successively, we separately analyzed accuracy and reaction times for each group.

3.1. Sighted group: Manipulation of task instruction

Accuracy

The GLMM for the sighted group (Table 1) revealed a three-way interaction between Instruction, Posture, and Congruency ($\chi^2(1) = 81.43$, $p < 0.001$), suggesting that congruency effects differed in dependence of Instruction and Posture. Indeed, post-hoc comparisons revealed a two-way interaction between Posture and Congruency under external ($z = 14.80$, $p < 0.001$), but not under anatomical instructions ($z = 1.50$, $p = 0.133$).

When the hands were in the same orientation, congruency matched for anatomical and external reference frames, and participants responded more accurately following (anatomically and externally) congruent than incongruent stimulation (Fig. 2, 1st and 2nd column, top, black circles). This effect was present for anatomical ($z = 8.36$, $p < 0.001$) and external instructions ($z = 10.26$, $p < 0.001$).

When the hands were oriented differently (Fig. 2, gray triangles), stimulus pairs were always congruent anatomically when they were incongruent externally, and vice versa. An anatomical congruency effect was present under anatomical instructions ($z = 7.87$, $p < 0.001$). Importantly, the congruency effect was reversed under external instructions, with more correct performance for externally congruent stimulus pairs (anatomically incongruent stimulus pairs in Figure 2) ($z = -7.32$, $p < 0.001$). Thus, the direction of the tactile congruency effect depended on the instructions.

Reaction times

The result pattern of sighted participants' reaction times was qualitatively similar to that of the accuracy results. The LMM (Table 2) showed a three-way interaction between Instruction, Posture, and Congruency ($\chi^2(1) = 52.98$, $p < 0.001$), indicating that instructions affected the congruency effect. Post-hoc comparisons yielded a two-way interaction between Posture and Congruency under anatomical ($z = 9.99$, $p < 0.001$) and external instructions ($z = 20.25$, $p < 0.001$).

With both hands in the same orientation (Fig. 2, black circles), sighted participants responded faster to (anatomically and externally) congruent stimulus pairs than to incongruent stimulus pairs, regardless of instruction (external instruction: $z = 10.47$, $p < 0.001$; anatomical: $z = 10.37$, $p < 0.001$).

With differently oriented hands (Fig. 2, gray triangles), an anatomical congruency effect emerged under anatomical instructions ($z = 2.14$, $p = 0.034$), though this effect was smaller than in the same orientation conditions. In contrast, an externally coded congruency effect emerged under external instructions ($z = -6.23$, $p < 0.001$).

In sum, analyses of accuracy and reaction times consistently reflected performance modulations that were consistent with the instructed spatial coding – anatomical or external – in sighted participants.

Table 1. Statistical results from accuracy analysis. Summary of the fixed effects in the GLMM of the sighted group, of the blind group, and of the combined analysis. Coefficients are logit units. Bold values indicate significance at $p < 0.05$. Italic values indicate a trend for significance at $p < 0.1$. Test statistics are $\chi 2$ -distributed with 1 degree of freedom.

Predictor	Estimate	SE	χ^2	*p*
Sighted group				
(Intercept)	3.061	0.293		
Instruction	0.036	0.107	0.11	0.741
Posture	-0.137	0.064	3.46	*0.063*
Congruency	0.512	0.067	25.15	**< .001**
Context	0.049	0.075	0.44	0.507
Instruction X Posture	-0.011	0.043	0.06	0.808
Instruction X Congruency	0.306	0.043	49.48	**< .001**
Posture X Congruency	-0.482	0.043	138.31	**< .001**
Instruction X Context	0.046	0.043	1.12	0.290
Posture X Context	-0.052	0.042	1.50	0.221
Congruency X Context	0.057	0.042	1.76	0.184
Instruction X Posture X Congruency	0.391	0.042	81.43	**< .001**
Instruction X Posture X Context	0.002	0.042	0.00	0.953
Instruction X Congruency X Context	0.009	0.042	0.04	0.833
Posture X Congruency X Context	-0.028	0.042	0.45	0.500
Instruction X Posture X Congruency X Context	-0.04	0.042	0.88	0.347
Blind group				
(Intercept)	3.579	0.176		
Instruction	-0.031	0.117	0.07	0.794
Posture	-0.267	0.07	11.78	**0.001**
Congruency	0.179	0.068	5.61	**0.018**
Context	-0.153	0.07	3.92	**0.048**
Instruction X Posture	0.058	0.057	1.01	0.315
Instruction X Congruency	0.053	0.057	0.85	0.357
Posture X Congruency	-0.253	0.054	22.37	**< .001**
Instruction X Context	-0.041	0.056	0.50	0.479
Posture X Context	-0.029	0.054	0.28	0.598
Congruency X Context	0.012	0.054	0.05	0.823
Instruction X Posture X Congruency	0.131	0.053	6.00	**0.014**
Instruction X Posture X Context	-0.104	0.053	3.75	*0.053*
Instruction X Congruency X Context	0.027	0.053	0.25	0.620
Posture X Congruency X Context	0.033	0.053	0.37	0.544
Instruction X Posture X Congruency X Context	-0.043	0.053	0.63	0.427
Both groups				
(Intercept)	3.313	0.168		
Group	-0.282	0.168	2.69	0.101
Instruction	0.000	0.078	0.00	0.998
Posture	-0.211	0.038	20.48	**<.001**
Congruency	0.352	0.04	40.33	**<.001**
Context	-0.099	0.043	4.54	**0.033**
Group X Instruction	0.034	0.078	0.19	0.662
Group X Posture	0.046	0.039	1.43	0.232
Instruction X Posture	0.027	0.034	0.63	0.428
Group X Congruency	0.147	0.04	12.09	**0.001**
Instruction X Congruency	0.169	0.034	23.35	**<.001**
Posture X Congruency	-0.365	0.034	120.5	**<.001**
Group X Context	0.08	0.043	3.47	*0.063*
Instruction X Context	-0.004	0.034	0.02	0.901
Posture X Context	-0.038	0.034	1.20	0.273
Congruency X Context	0.035	0.034	1.06	0.304
Group X Instruction X Posture	-0.047	0.034	1.85	0.174
Group X Instruction X Congruency	0.145	0.034	17.57	**<.001**
Group X Posture X Congruency	-0.113	0.034	10.75	**0.001**
Instruction X Posture X Congruency	0.26	0.034	58.31	**<.001**
Group X Instruction X Context	0.044	0.034	1.64	0.201
Group X Posture X Context	-0.022	0.034	0.42	0.519
Instruction X Posture X Context	-0.051	0.034	2.20	0.138
Group X Congruency X Context	0.023	0.034	0.47	0.493
Instruction X Congruency X Context	0.018	0.034	0.27	0.605
Posture X Congruency X Context	0.004	0.034	0.01	0.915
Group X Instruction X Posture X Congruency	0.129	0.034	13.83	**<.001**
Group X Instruction X Posture X Context	0.054	0.034	2.46	0.117
Group X Instruction X Congruency X Context	-0.01	0.034	0.09	0.766
Group X Posture X Congruency X Context	-0.03	0.034	0.77	0.380
Instruction X Posture X Congruency X Context	-0.043	0.034	1.62	0.203
Group X Instruction X Posture X Congruency X Context	0.000	0.034	0.00	0.993

Table 2. Statistical results from reaction time analysis. Summary of the fixed effects in the LMM of the sighted group, of the blind group, and of the combined analysis. Bold values indicate significance at p < 0.05. Italic values indicate a trend for significance at p < 0.1. Test statistics are χ2 -distributed with 1 degree of freedom.

Predictor	Estimate	SE	χ^2	*p*
Sighted group				
(Intercept)	5.327	0.046		
Instruction	0.017	0.014	1.34	0.247
Posture	0.058	0.005	33.84	**< .001**
Congruency	-0.033	0.007	14.39	**< .001**
Context	0.029	0.009	7.60	**0.006**
Instruction X Posture	0.003	0.002	1.58	0.209
Instruction X Congruency	-0.016	0.002	50.23	**< .001**
Posture X Congruency	0.049	0.002	447.97	**< .001**
Instruction X Context	0.004	0.002	2.77	*0.096*
Posture X Context	0.000	0.002	0.04	0.834
Congruency X Context	0.003	0.002	1.56	0.212
Instruction X Posture X Congruency	-0.017	0.002	52.98	**< .001**
Instruction X Posture X Context	-0.004	0.002	3.49	*0.062*
Instruction X Congruency X Context	0.001	0.002	0.32	0.574
Posture X Congruency X Context	-0.001	0.002	0.28	0.598
Instruction X Posture X Congruency X Context	0.002	0.002	0.74	0.389
Blind group				
(Intercept)	5.316	0.042		
Instruction	0.006	0.015	0.17	0.678
Posture	0.049	0.006	26.58	**< .001**
Congruency	-0.011	0.004	5.17	**0.023**
Context	0.027	0.01	5.50	**0.019**
Instruction X Posture	-0.001	0.002	0.54	0.462
Instruction X Congruency	-0.006	0.002	8.63	**0.003**
Posture X Congruency	0.013	0.002	44.35	**< .001**
Instruction X Context	-0.005	0.002	7.47	**0.006**
Posture X Context	-0.013	0.002	43.44	**< .001**
Congruency X Context	0.008	0.002	17.92	**< .001**
Instruction X Posture X Congruency	-0.005	0.002	7.26	**0.007**
Instruction X Posture X Context	0.009	0.002	22.23	**< .001**
Instruction X Congruency X Context	0.001	0.002	0.12	0.724
Posture X Congruency X Context	-0.001	0.002	0.22	0.641
Instruction X Posture X Congruency X Context	0.000	0.002	0.05	0.830
Both groups				
(Intercept)	5.321	0.031		
Group	0.006	0.031	0.03	0.852
Instruction	0.012	0.01	1.24	0.265
Posture	0.054	0.004	60.45	**< .001**
Congruency	-0.022	0.004	20.76	**< .001**
Context	0.028	0.007	12.88	**< .001**
Group X Instruction	0.005	0.01	0.28	0.594
Group X Posture	0.004	0.004	1.13	0.287
Instruction X Posture	0.001	0.002	0.20	0.658
Group X Congruency	-0.011	0.004	6.71	**0.010**
Instruction X Congruency	-0.011	0.002	53.05	**< .001**
Posture X Congruency	0.031	0.002	417.83	**< .001**
Group X Context	0.001	0.007	0.03	0.868
Instruction X Context	-0.001	0.002	0.30	0.581
Posture X Context	-0.007	0.002	20.52	**< .001**
Congruency X Context	0.006	0.002	14.08	**< .001**
Group X Instruction X Posture	0.002	0.002	1.95	0.162
Group X Instruction X Congruency	-0.005	0.002	11.45	**0.001**
Group X Posture X Congruency	0.018	0.002	136.92	**< .001**
Instruction X Posture X Congruency	-0.011	0.002	52.72	**< .001**
Group X Instruction X Context	0.005	0.002	9.47	**0.002**
Group X Posture X Context	0.006	0.002	17.73	**< .001**
Instruction X Posture X Context	0.003	0.002	2.93	*0.087*
Group X Congruency X Context	-0.003	0.002	3.49	*0.062*
Instruction X Congruency X Context	0.001	0.002	0.43	0.513
Posture X Congruency X Context	-0.001	0.002	0.50	0.479
Group X Instruction X Posture X Congruency	-0.006	0.002	13.67	**< .001**
Group X Instruction X Posture X Context	-0.007	0.002	20.51	**< .001**
Group X Instruction X Congruency X Context	0.000	0.002	0.04	0.849
Group X Posture X Congruency X Context	0.000	0.002	0.01	0.927
Instruction X Posture X Congruency X Context	0.001	0.002	0.25	0.618
Group X Instruction X Posture X Congruency X Context	0.001	0.002	0.59	0.444

3.2 Sighted group: Manipulation of movement context

Accuracy

In contrast to the effects of task instructions, neither the effect of Movement Context (see Fig. 3 left, Fig. 4 top) nor the interactions of Movement Context and any other variable were significant in the GLMM on accuracy (all $\chi^2(1) \leq 1.50$, $p \geq 0.221$). To demonstrate that these null effects were not due simply to high variance or a few outliers, Fig. 4 illustrates individual participants' performance.

Reaction times

For reaction times, the LMM revealed a main effect of Movement Context ($\chi^2(1) = 7.60$, $p = 0.005$), indicating that sighted participants responded overall faster in the static than in the dynamic movement context. In addition, there was a trend for a three-way interaction between Instruction, Posture, and Movement Context ($\chi^2(1) = 3.49$, $p = 0.062$), due to a larger reaction time gain under anatomical than under external instructions, but only when the hands were in the same orientation: in this latter case, the two-way interaction of Instruction and Movement Context was significant ($z = 2.51$, $p = 0.024$); participants responded faster in the static than in the dynamic condition under anatomical instructions ($z = 3.72$, $p = 0.008$), and this effect was reduced under external instructions ($z = 2.12$, $p = 0.034$). With the hands in different orientations, the two-way interaction between Instruction and Movement was not significant ($z = -0.14$, $p = 0.886$). Thus, an effect of Movement Context was evident in all conditions, and the marginal three-way interaction of Instruction, Posture, and Movement Context suggested that it was mainly due to the instruction effects for the same orientation condition.

In sum, although frequent movement generally slowed reaction times, movement context did not affect the congruency effect in either of the present study's dependent measures, accuracy or reaction times.

3.3. Congenitally blind group: Manipulation of task instruction

Accuracy

The GLMM on blind participants' accuracy revealed a significant three-way interaction between Instruction, Posture, and Congruency ($\chi^2(1) = 6.00$, $p = 0.014$), suggesting that task instructions modulated the congruency effect. Post-hoc comparisons revealed a two-way interaction between Posture and Congruency under external instructions ($z = 4.91$, $p < 0.001$) and a trend for a two-way interaction under anatomical instructions ($z = 1.66$, $p = 0.097$).

With the hands in the same orientation, participants responded more accurately following (anatomically and externally) congruent than incongruent stimulation (Fig. 2, 3rd and 4th column, top, black circles), regardless of whether they were instructed anatomically ($z = 2.92$, $p = 0.011$) or externally ($z = 3.75$, $p = 0.001$).

With differently oriented hands (Fig. 2, 3rd and 4th column, top, gray triangles), performance was not significantly affected by congruency under anatomical instructions ($z = 1.06$, $p = 0.290$). In contrast, under external instructions, the effect of congruency showed a reversed pattern than with the hands in the same orientation, with more accurate responses when stimulus pairs were externally congruent (but anatomically incongruent) than when they were externally incongruent (but anatomically congruent, $z = -2.56$, $p = 0.021$).

Reaction times

Reaction time analysis corroborated accuracy results. The LMM on blind participants' reaction times revealed a three-way interaction between Instruction, Posture, and Congruency ($\chi^2(1) = 7.26$, $p = 0.007$; see Fig. 2, 3rd and 4th column, bottom). Post-hoc comparisons revealed a two-way interaction between Posture and Congruency under anatomical ($z = 2.79$, $p = 0.005$) and external instructions ($z = 6.65$, $p < 0.001$).

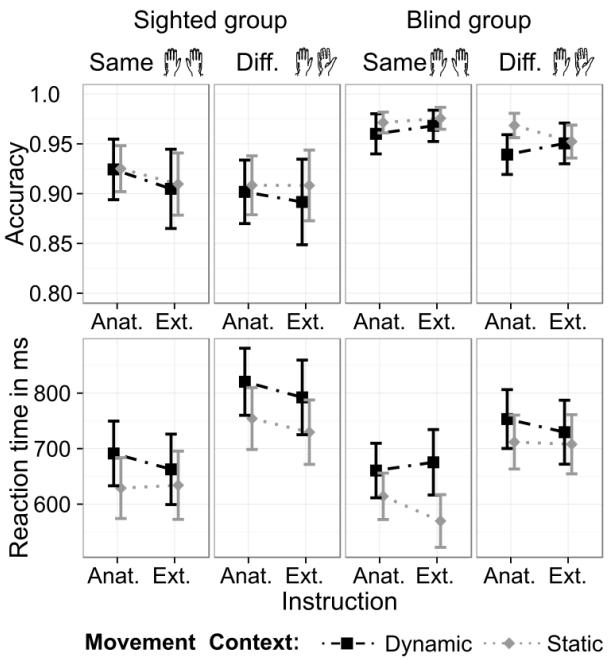

Figure 3. Effect of Movement Context on accuracy and reaction times, collapsed over congruency conditions. Participants localized tactile targets with hands in the same (first and third column) and in different orientations (second and fourth column), under anatomical ("Anat.") and under external instructions ("Ext."), in the context of static blockwise posture changes (gray diamonds) and in the context of frequent trial-by-trial posture changes (black squares). Error bars show standard errors of the mean.

With hands held in the same orientation, blind participants responded significantly faster to (anatomically and externally) congruent than incongruent stimulus pairs under anatomical ($z = 4.41$, $p < 0.001$) and under external instructions ($z = 4.26$, $p < 0.001$).

With differently oriented hands, no significant congruency effect was observed under anatomical instructions ($z = 1.55$, $p = 0.120$). The congruency effect was reversed under external instructions relative to the congruency effect when the hands were held in the same orientation, with faster responses to externally congruent (but anatomically incongruent) than externally incongruent (but anatomically congruent) stimulus pairs ($z = -2.48$, $p = 0.026$).

In sum, both accuracy and reaction times of blind participants reflected an influence of task instructions on tactile-spatial congruency coding.

3.4 Congenitally blind group: Manipulation of movement context

Accuracy

The GLMM on blind participants' accuracy showed a main effect of Movement Context (Fig.3, 3rd and 4th column; $\chi^2(1) = 3.92$, $p = 0.048$), with more accurate responses in the static than in the dynamic context. Moreover, there was a trend for a three-way interaction between Instruction, Posture, and Movement Context ($\chi^2(1) = 3.75$, $p = 0.053$). Following up on this trend, post-hoc comparisons yielded a trend for a two-way interaction between Instruction and Movement Context with hands in different orientations ($z = -2.15$, $p = 0.063$), but not with hands in the same orientation ($z = 0.73$, $p = 0.465$).

Following up on the two-way interaction between Instruction by Movement Context revealed that static and dynamic conditions did not significantly differ under either instruction when the hands were in the same orientation, (anatomical: $z = 0.50$, $p = 0.618$; external: $z = 1.36$, $p = 0.173$). With differently oriented hands, participants responded more accurately in the static than in the dynamic condition under anatomical ($z = 3.09$, $p = 0.004$), but not under external instructions ($z = 0.37$, $p = 0.713$). Thus, the performance pattern was suggestive of some selective effects of task instructions on accuracy, but the statistical results were only marginal.

We had hypothesized that frequent posture changes would emphasize the weighting of external spatial information. Such an effect would be evident in a modulation of congruency effects emerging with the hands in different postures. The corresponding interaction in the GLMM, the four-way interaction of Instruction, Posture, Congruency, and Movement Context, was not significant ($\chi^2(1) = 0.63$, $p = 0.427$). Yet, visual inspection of Fig. 4 suggested that an effect may be present, but remained non-significant due to lack of power of a GLMM with several factors. Therefore, we performed hypothesis-based post-hoc tests for conditions with differently oriented hands. In the static condition, no significant congruency effect was

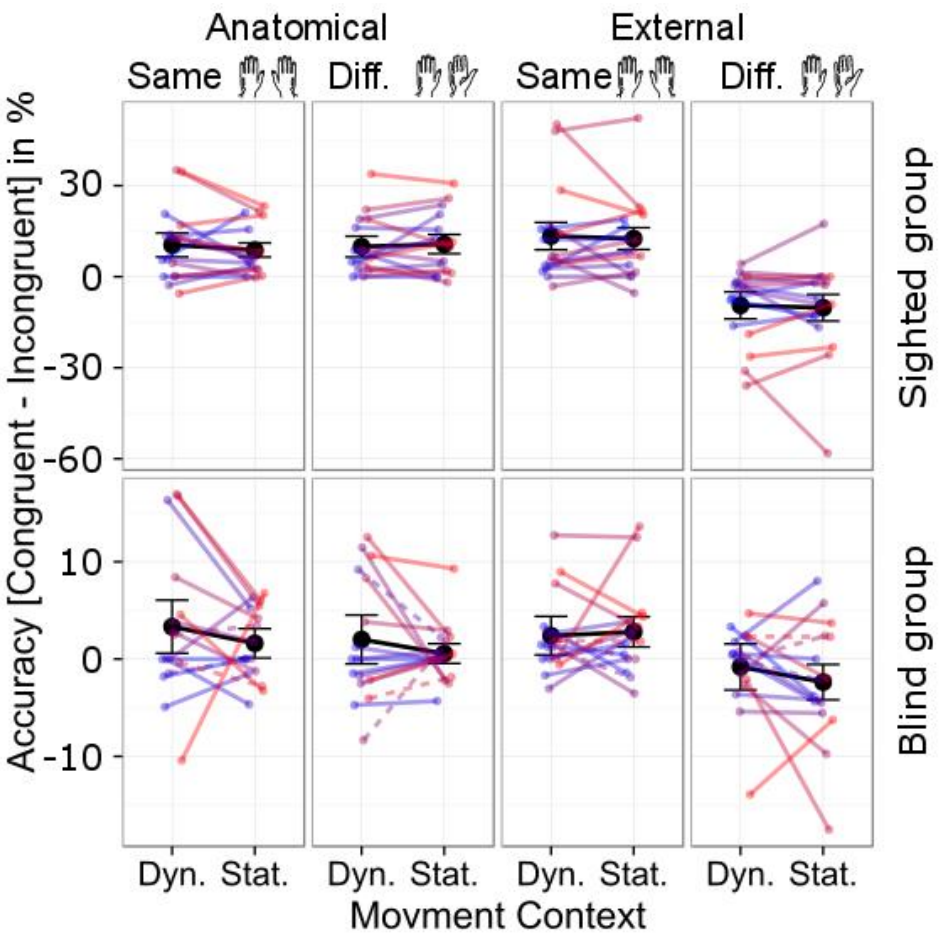

Figure 4. Individual participants' tactile congruency effects in accuracy. Responses from anatomically incongruent trials were subtracted from responses in congruent trials. Congruency effects are plotted for dynamic ("Dyn.") and static ("Stat.") contexts with hands in the same (1st and 3rd column) and in different orientations (2nd and 4th column) under anatomical (1st and 2nd column) and external instructions (3rd and 4th column) in the sighted (top row) and in the congenitally blind group (bottom row). Note that scales differ between groups because congruency effects in the blind group were smaller than in the sighted group. Mean congruency effects for each condition are plotted in black, whiskers represent SEM. Each color represents one participant.

present under anatomical instructions ($z = 0.52$, $p = 0.605$), but a trend for a congruency effect was observed under external instructions ($z = -2.34$, $p = 0.078$). In the dynamic condition, no significant congruency effect was present under anatomical instructions ($z = 1.15$, $p = 0.252$) and external instructions ($z = -1.48$, $p = 0.138$). Thus, even when directly comparing movement conditions while ignoring other experimental conditions, the hypothesis that a dynamic context modulates spatial integration in tactile congruency coding of congenitally blind humans did not receive any substantial support.

Reaction times

The LMM on reaction times revealed a three-way interaction between Instruction, Posture, and Movement Context ($\chi^2(1) = 22.23$, $p < 0.001$), suggesting a modulation of the congruency effect on reaction times by Movement Context. Following up on the three-way interaction, post-hoc comparisons yielded a two-way interaction between Instruction and Movement Context with the hands in the same ($z = -5.30$, $p < 0.001$), but not in different orientations ($z = 1.39$, $p = 0.163$).

Blind participants responded significantly faster in the static than in the dynamic condition with hands in the same orientation under external instructions ($z = 5.01$, $p < 0.001$), but only marginally faster under anatomical instructions ($z = 2.27$, $p = 0.069$). No significant difference

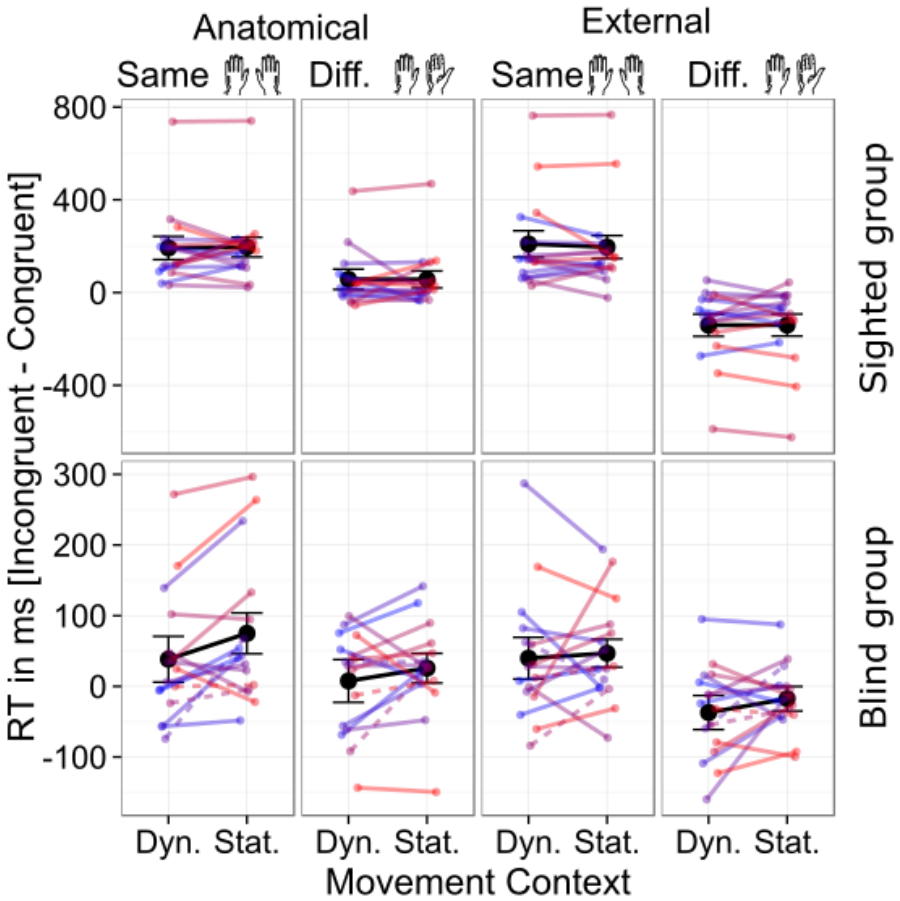

Figure 5. Individual participants' tactile congruency effects in reaction times. Responses from anatomically incongruent trials were subtracted from responses in congruent trials. Congruency effects are plotted for dynamic ("Dyn.") and static ("Stat.") contexts with hands in the same (1st and 3rd column) and in different orientations (2nd and 4th column) under anatomical (1st and 2nd column) and external instructions (3rd and 4th column) in the sighted (top row) and in the congenitally blind group (bottom row). Note that scales differ between groups because congruency effects in the blind group were smaller than in the sighted group. Mean congruency effects for each condition are plotted in black, whiskers represent SEM. Each color represents one participant.

between conditions was observed with differently oriented hands under either instruction (anatomical: $z = 1.58$, $p = 0.113$; external: $z = 0.85$, $p = 0.391$).

An influence of frequent posture changes on the weighting of external spatial information should be evident in a modulation of congruency effects with the hands oriented differently rather than in the same posture. Just like for accuracy, the corresponding four-way interaction of Instruction, Posture, Congruency, and Movement Context was not significant for reaction times ($\chi^2(1) = 0.05$, $p = 0.830$). Although there was a two-way interaction of Congruency and Movement Context ($\chi^2(1) = 17.92$, $p < 0.001$) with a congruency effect in the static ($z = 4.02$, $p < 0.001$), but not in the dynamic condition ($z = 0.47$, $p = 0.635$), this interaction does not differentiate between instructions and postures. As had been the case with accuracy, visual inspection of the reaction times result pattern (Fig. 5, bottom) suggested that – as hypothesized – posture may have modulated the congruency effect in the expected direction, but a lack of power may have prevented statistical significance. Therefore, we conducted hypothesis-driven post-hoc tests of the relevant conditions (i.e., conditions with differently oriented hands). Under anatomical instructions, a congruency effect was present in the static movement context ($z = 2.06$, $p = 0.047$), but not

in the dynamic movement context (z= 0.13, p = 0.900). Under external instructions, a significant congruency effect was not evident in the static (z = -0.96, p = 0.335), but in the dynamic context (z = -3.06, p = 0.009), with faster responses for externally congruent (but anatomically incongruent) than externally incongruent (but anatomically congruent) stimulus pairs. These comparisons imply that an anatomical congruency effect was present under anatomical instructions only in the static context, and an external congruency effect under external instruction only in the dynamic context. While the presence of these partial instruction-related effects are in line with our hypotheses, the lack of a significant higher-order interaction precludes any strong interpretation of these direct statistical tests. Specifically, congruency effects decreased numerically in all instruction and posture conditions (see Fig. 5, bottom), an effect that does not comply with our hypothesis about an effect of the movement context. Furthermore, congruency effects were quite variable across blind participants, as evident in individual modulations of congruency effects (see Fig. 5), further corroborating the conclusion that reliable modulations of congruency by movement context were not present on the group level.

3.5. Comparison of the congruency effect between sighted and congenitally blind participants

Visual inspection of Figure 2 suggests that congruency effects on accuracy and on reaction times were overall larger in the sighted than in the blind group. For accuracy, this difference seems to stem from the blind participants outperforming sighted participants when responding to stimulus pairs that were

Table 3. A, Interaction between Group and Congruency for each instruction and posture

	anatomical instruction		external instruction	
	same posture	different posture	same posture	different posture
Accuracy	z = 3.65, *p* < 0.001	z = 4.81, *p* < 0.001	z = 2.99, *p* = 0.003	z = -3.88, *p* < 0.001
Reaction times	z = -5.89, *p* < 0.001	z = -0.82, *p* = 0.412	z = -6.10, *p* < 0.001	z = 3.65, *p* < 0.001

B, Comparison between groups for each combination of Instruction, Posture, and Congruency

Accuracy				
	anatomical instruction		external instruction	
	same posture	different posture	same posture	different posture
Congruent	z = -0.13, *p* = 0.895	z = -0.29, *p* = 0.774	z = 0.73, *p* = 0.465	z = 2.40, *p* = 0.016
Incongruent	z = 2.67, *p* = 0.008	z = 2.85, *p* = 0.004	z = 3.35, *p* < 0.001	z = -0.09, *p* = 0.932
Reaction times				
Congruent	z = 0.75, *p* = 0.454	z = -0.47, *p* = 0.641	z = 0.86, *p* = 0.385	z = -0.58, *p* = 0.564
Incongruent	z = -1.05, *p* = 0.296	z = -0.71, *p* = 0.475	z = -0.74, *p* = 0.459	z = 0.42, *p* = 0.678

incongruent relative to the instructed reference frame (i.e., anatomically incongruent under anatomical instructions and externally incongruent under external instructions). For statistical testing, we accordingly followed up on the significant four-way interaction between Group, Instruction, Posture, and Congruency for both accuracy and reaction times (see Tables 1 & 2) with post-hoc comparisons for each combination of Instruction and Posture. Indeed, there were significant two-way interactions between Group and Congruency, with larger congruency effects in the sighted than in the blind group for almost all combinations of Instruction and Posture for both accuracy and reaction times (Table 3A, bold font). Moreover, blind participants responded more accurately than sighted participants following stimulus pairs that were anatomically incongruent under anatomical instructions and externally incongruent under external instructions (all $p \leq 0.016$, bold font in Table 3B). These advantages for the blind group were evident only in accuracy, but not in reaction times (all $p \geq 0.296$; Table 3B).

4. Discussion

The present study investigated whether congenitally blind humans integrate anatomical and external spatial information during tactile localization in a flexible manner similarly to sighted humans. By manipulating hand posture, we varied the congruency of target and distractor locations relative to anatomical and external spatial reference frames. The study comprised two contextual manipulations, both of which have been demonstrated to influence tactile localization performance in sighted humans. First, we manipulated task context by formulating task instructions with reference to anatomical vs. external spatial terms (hand surfaces vs. elevation in space). Second, we manipulated movement context by asking participants to leave the hands in the same posture for entire experimental blocks, or to change hand posture in a trial-by-trial fashion.

With the hands in the same posture, both sighted and congenitally blind participants responded faster and more accurately to (anatomically and externally) congruent than incongruent target-distractor pairs. With differently oriented hands, task instruction modulated the size and direction of congruency effects. Specifically, under anatomical instructions, sighted participants responded faster and more accurately to anatomically congruent than anatomically incongruent target-distractor pairs, whereas blind participants did not exhibit a significant congruency effect, but instead responded similarly to congruent and incongruent target-distractor pairs. In contrast, under external instructions, both sighted and congenitally blind participants responded faster and more accurately to externally congruent (but anatomically incongruent) than externally incongruent target-distractor pairs, even if these effects were smaller in blind participants. Movement context, that is, static hand positioning versus frequent posture change, did not significantly modulate congruency effects in either experimental group.

Flexible weighting of reference frames according to task instructions in both sighted and blind individuals

Auditory information coded in an external spatial reference frame is available to both sighted and congenitally blind individuals (Röder, Kusmierek, Spence, & Schicke, 2007). Yet, tactile external spatial information has long been presumed to be automatically integrated only by normally sighted and late blind, but not by congenitally blind individuals, (Collignon et al., 2009; Röder et al., 2008, 2004). In the present study, blind participants' performance should have been independent of posture and instructions if they had relied on anatomical information alone. In contrast to this assumption, blind participants' congruency effects reflected an external reference frame when the task had been instructed externally. Moreover, under anatomical instructions, a congruency effect emerged only when the hands were in the same orientation.

The flexible and strategic weighting of

anatomical and external tactile information, observed here in both sighted and blind individuals, presumably reflects top-down regulation of spatial integration (Badde & Heed, in press). In line with this proposal, anatomical and external spatial information are presumed to be available concurrently, as evident, for instance, in event-related potentials (Heed & Röder, 2010) and in oscillatory brain activity (Buchholz, Jensen, & Medendorp, 2011, 2013; Schubert et al., 2015). Furthermore, performance under reference frame conflict, for instance due to hand crossing, is modulated by a secondary task, and this modulation reflects stronger weighting of external information when the secondary task accentuates an external as compared to anatomical spatial code (Badde, Röder, et al., 2015). The present results, too, demonstrate directed, top-down mediated modulations of spatial weighting, with anatomical task instructions biasing weighting towards anatomical coding, and external instructions biasing weighting towards external coding.

Comparison with previous tactile localization studies in blind individuals

The present study's effect of hand posture on tactile localization in congenitally blind participants contrasts with findings from previous studies. In several experiments, blind participants' performance did not differ between hand postures, and these results have been interpreted as indicating that congenitally blind individuals do not, by default, use external spatial information for tactile localization (Collignon et al., 2009; Röder et al., 2008, 2004). Several aspects of the present study may account for the differences we observed compared to these reports. First, most studies have manipulated the congruence of anatomical and external spatial information by means of hand crossing. Here, in contrast, posture was modulated by manipulating the up-down orientation of the hands. Thus, each hand remained in its hemispace. Turning the hands upside down changes the gravitational pull on the hands between conditions. In addition, different parts of the hand (palm vs. back of the hand) rested on the table in different posture conditions, and, thus, may have provided additional external-spatial information in the vertical direction, encouraging the use of external coding. Second, distractor interference on tactile localization in the present study may have operated on a different processing level compared to previous studies, which required for tactile localization without any distractors (Collignon et al., 2009; Röder et al., 2008, 2004). Third, the context of the task may have emphasized the weighting of external spatial information in the blind group in comparison to previous studies. The present response with a foot pedal requires a spatial mapping of the target location to the location of the foot that had to be lifted. Such a spatial mapping was not required in some previous studies (Röder et al., 2008, 2004). In sum, congruency effects in the blind group changed with task instructions in a similar manner as in the sighted group; this finding suggests that flexible and strategic weighting of anatomical and external spatial information emerges even in the absence of vision from birth.

Comparison of sighted participants' susceptibility to task instruction with previous tactile localization studies

A previous study employed a similar tactile congruency task as that of the present study, though only within sighted individuals (Gallace et al., 2008). This study reported that the congruency effect always depended on the external spatial location of tactile stimuli, independent of task instructions (Gallace et al., 2008). These previous results are at odds with the present finding of performance biases that depended on the reference frame used in the task instructions. Gallace and colleagues (2008) attributed their results to the spatial stimulus-response mapping to different response locations (i.e., lifting the toes versus lifting the heel) (Gallace et al., 2008). However, the same kind of stimulus-response mapping was used in the present study. Nevertheless, the observed differences between the present and the study

by Gallace and colleagues may be explained by at least three factors. First, Gallace and colleagues (2008) presented stimuli to the tips of the index fingers and the thumbs while participants held two foam cubes. Because the to-be-grasped object needs to be encoded within the external world, the involvement of these external objects could have induced a greater weighting of external information in the previous study by Gallace and colleagues. Second, the spatial relations between two points on the palm and back of the hand, such as their absolute distance, are fixed, whereas such spatial relationships vary for the fingers. The involvement of body parts that can flexibly change their relative location may contribute, thus, to an overall stronger weighting of an external reference frame. Third, non-informative vision (Newport, Rabb, & Jackson, 2002) as well as online visual information about the crossed posture of artificial rubber hands (Azañón & Soto-Faraco, 2007) seem to evoke an emphasis of the external reference frame. Online visual information (Cadieux & Shore, 2013; Gallace et al., 2008) about the current hand posture may, thus, have led to the dominance of the external congruency effect. In contrast, in our study sighted participants were blindfolded for comparability with blind participants, so that no visual information was available during the experiment, potentially biasing weighting away from external spatial coding.

Weak evidence for an effect of movement context in blind, but not in sighted participants

Based on previous findings with other tactile localization paradigms that manipulated movement (Azañón et al., 2015; Heed, Möller, et al., 2015; Hermosillo et al., 2011; Mueller & Fiehler, 2014a, 2014b; Pritchett et al., 2012), we had expected that frequent posture change would emphasize the weighting of an external reference frame in both sighted and blind participants. Sighted participants responded faster overall in the static than in the dynamic context. However, this effect did not significantly differ across postures, instructions, and congruency conditions and, thus, appears to have been related to increased task difficulty rather than to differential weighting of spatial reference frames. The reason for the lack of a movement context effect in the present study is unclear; it may be related to the specific localization paradigm employed here, as previous reports of movement-related performance modulation were based on a hand-crossing paradigm (Azañón et al., 2015; Heed, Möller, et al., 2015; Hermosillo et al., 2011).

Enhanced vibrotactile discrimination in congenitally blind individuals

Congenitally blind participants performed more accurately compared to sighted participants when target and distractor were anatomically incongruent under anatomical instructions and externally congruent under external instructions. In addition, many sighted participants had to be excluded because they had been unable to discriminate the original distractor from the target stimulus, whereas only few blind participants had this problem. These findings suggest that blind participants had a general advantage over sighted participants in the dissociation between vibro-tactile patterns. Indeed, congenitally blind participants reportedly discriminate vibrotactile stimuli better than sighted participants when the vibration frequency ranges from 20 to 100 Hz (Wan, Wood, Reutens, & Wilson, 2010). Tactile target and distractor stimuli of the present experiment differed at an even lower frequency, with the distractors' timing pulsed at 10 Hz. This finding, thus, adds to the notion of enhanced frequency discrimination of congenitally blind individuals at low vibrotactile frequencies (Wan et al., 2010).

Summary and conclusion

In sum, we have reported that both sighted and congenitally blind individuals can flexibly adapt the weighting of anatomical and external information during the encoding of touch, evident in the dependency of tactile congruency effects on task context. However, of two tested

context manipulations, namely task instructions and movement, only the former evoked reliable modulations of tactile localization behavior. Although the movement context led to slowed responses in sighted individuals, this modulation was unrelated to the weighting of spatial information. Moreover, visually apparent evidence for an effect of the movement context on the weighting of spatial information in the blind group was statistically unreliable, precluding firm conclusions about the movement manipulation for this group. In contrast, the present study revealed strong effects of task instructions on reference frame weighting not just in sighted, but also in congenitally blind individuals. These results demonstrate that congenitally blind individuals do not rely on only a single reference frame but, instead, flexibly integrate anatomical and external spatial information, indicating that the use of external spatial information in touch does not ultimately depend on the availability of vision during development.

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