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Effect of Spatial Attention on Anatomical and External Reference Frames in Tactile Localization

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Abstract

This study examined whether spatial attention contributes to anatomical and external reference frames for tactile localization during reaching movements. Nineteen right-handed participants reached toward a target in the left or right spatial hemifield with the left or right index finger. During the reach, a tactile stimulus was delivered to the reaching hand. After reaching, participants repositioned the stimulated hand to the location where the tactile stimulus had been delivered. They then verbally reported the perceived location of the tactile stimulus on the hand. The error in the anatomical reference frame for the left hand showed a more distal deviation than that for the right hand when participants reached into the left spatial hemifield, whereas no such difference was observed when they reached into the right spatial hemifield. This finding suggests that the proximal deviation of the perceived tactile stimulus locus in the anatomical reference frame is cancelled when tactile perception interacts with spatial attention processes within the left hemisphere. In the external reference frame, the error for the right hand showed a distal deviation relative to the left hand when reaching to a target in the left spatial hemifield. Conversely, the error for the left hand showed a distal deviation relative to the right hand when reaching to a target in the right spatial hemifield. These results indicate that conflict between the anatomical and external reference frames weakens the influence of spatial attention, resulting in a distal bias in perceived tactile location in external space.

Introduction

Humans determine which part of their body is touched and where the touch occurs in space. The process underlying the determination of touch location in space is called tactile localization (Heed & Azañón, 2014; Heed et al., 2015). Two reference frames have been considered to play a role in tactile localization. Initially, a tactile stimulus on a body part is mapped onto the skin-based reference frame (Disbrow et al., 2000; Yang et al., 1993), which is referred to as the coordinates of the anatomical reference frame (ARF; Badde et al., 2014; Röder et al., 2007; Röder et al., 2008). These coordinates are then transformed into an external reference frame (ERF) representing the spatial location of the tactile stimulus; this process is referred to as tactile remapping (Driver & Spence, 1998a; Heed & Azañón, 2014, Heed et al., 2015).

In a tactile spatial discrimination task, responses to tactile targets were faster when they appeared on the same side as a preceding tactile cue (Spence & McGlone, 2001). This indicates that exogenous spatial attention enhances tactile processing. There are cross-modal links in spatial attention (Butter et al., 1989; Driver & Spence, 1998b; Spence et al., 1998). For example, when a salient event is presented in one modality, processing in another modality is facilitated at the same spatial location. Cross-modal links in spatial attention indicate that spatial attention operates across sensory modalities (Driver & Spence, 1998a, 1998b). However, it remains unclear whether such spatial attention to the cross-modal links in perception influences higher-level spatial processes such as tactile localization. Thus, in the present study, a visual target for the reaching movement was used as a salient event, and the contribution of spatial attention induced by the visual target to tactile localization was examined.

To examine the contribution of spatial attention to tactile localization, we leveraged the hemispheric asymmetry of spatial attention. Tactile spatial discrimination predominantly engages the right cortical hemisphere, particularly the right supramarginal gyrus (Loayza et al., 2011). Importantly, this right-hemisphere dominance was observed for stimulation of both hands, indicating that it reflects hemispheric specialization for spatial processing rather than contralateral somatosensory representation. The right hemisphere contributes to attention to both the left and right spatial hemifield, whereas the left hemisphere contributes only to the right spatial hemifield (Mesulam, 1999; Pouget & Driver, 2000). The right temporoparietal junction responded to invalid targets in both hemifields, whereas the left temporoparietal junction responded selectively to invalid targets in the right hemifield, providing direct support for the Mesulam model of hemispheric asymmetry in spatial attention (Dragone et al., 2015). Computational and neurophysiological accounts suggest that spatial representations in the right parietal cortex cover both sides of space, whereas those in the left hemisphere are largely contralateral (Pouget & Driver, 2000). In humans, alpha activity in the right parietal cortex decreased following both left- and right-sided visual warning stimuli, whereas alpha activity in the left parietal cortex decreased primarily when the stimulus was presented on the right spatial hemisphere (Heilman & Van Den Abell, 1980). When attention was directed to the stimulus, right parietal cortex showed reduced contralateral bias—reflecting increased ipsilateral visual-field representation—whereas left parietal cortex maintained a strongly contralateral representation (Sheremata & Silver, 2015). Based on this, tactile localization processes may differ for stimuli presented in the left versus right spatial hemifield (Hypothesis 1) because of the asymmetrical contribution of the cortical hemispheres to spatial attention across hemifields. To test Hypothesis 1, we examined whether the coordinates of the ARF and ERF differ between leftward and rightward reaching.

The laterality of the cortical response to right-hand tactile stimulation was present, but such laterality was weaker when the left hand was stimulated (Jin et al., 2020). The primary somatosensory cortex is larger in the left hemisphere than in the right, and the N20 component of the somatosensory-evoked potential was greater in the left hemisphere than in the right (Jung et al., 2003), indicating that the left hemisphere plays a dominant role in somatosensory processing. Accordingly, we hypothesized that the ARF would be lateralized in a manner that reflects this asymmetry in tactile processing (Hypothesis 2).

The present study therefore investigated whether spatial attention influences tactile localization with respect to the ARF and ERF during reaching movements. By manipulating reaching direction (left vs. right spatial hemifield) and the responding hand (left vs. right), we examined whether spatial attention differentially modulates the coordinates of the ARF and ERF.

Methods

(Participants)

Nineteen young healthy adults (eleven males and eight females; mean age = 23.3 ± 7.1 years) participated in this study. They had no history of neurological disease. A priori power analysis using

G*Power 3.1.9.6 indicated that a total of 12 participants were required to achieve a statistical power of 0.80 with an alpha level of .05 to detect a medium effect (f = 0.25). According to the Edinburgh Handedness Inventory (Oldfield, 1971), all participants were right-handed. All participants provided informed consent prior to participation. The study was approved by the Ethics Committee of Osaka Metropolitan University (approval number: 2024 − 104).

(Apparatus)

Participants wore earmuffs to minimize extraneous auditory input. An electromagnetic sensor, measuring the locus of the index fingertip in space, was attached to the dorsal side of the index fingertip (Viper; Polhemus, VT, USA; Fig. 1A). Four small vibration devices with an 8-mm diameter (MotionBoard 3.4, Teknikio, Tokyo) were attached to the dorsal surface of the participant's hand. The vibration frequency of the activated device was 100 Hz, and the duration was 200 ms. The devices were attached to the skin over the third metacarpal bone at 1.5 cm intervals. All vibration devices were numbered sequentially from distal to proximal (i.e., 1–4) along the long axis of the hand. Before conducting the experiment, we confirmed that participants perceived the tactile sensation when each of the four devices was activated individually.

A table was placed in front of participants. A marker with a diameter of 5 mm, indicating the position of the index fingertip before the ready cue was presented (home marker), was placed on the table surface (Fig. 1B). The home marker was positioned 12 cm to the left of the midline when participants reached with the left index finger, and 12 cm to the right of the midline when they reached with the right index finger. A target and a ready cue, circles with a diameter of 10 mm, were projected onto the table surface by a projector (PJWX4152, Ricoh, Tokyo, Japan). The locations and timing of the presentation of the ready and target cues were programmed using Visual Presentation Program software (S-15001, Takei Kiki, Japan).

(Task paradigm)

The task paradigm is shown in Fig. 2. Participants placed the index fingertip on the home marker. A ready cue (open circle with a black outline) appeared for 4000 ms in front of the body midline. As long as this cue was present, participants kept their index fingertip on this cue. A target cue (open circle with a black outline) appeared for 100 ms at the offset of the ready cue. The target was presented 20 cm in front of the ready cue on the table surface. The target was projected at one of five directional angles from the midline (14 degrees, 27 degrees, 37 degrees, 45 degrees, and 51 degrees) in either the left or right spatial hemisphere. One of the ten targets was randomly presented in each trial. Participants closed their eyes and reached toward the memorized location of the target in response to the target cue.

During the reach toward the target with the eyes closed, one of the four vibration devices was activated for 200 ms. The activated vibration device was randomly selected in each trial. To determine the timing of the vibration device activation, before the experimental trials, participants performed reaching movement to a target with the index finger. The onset and offset of this reaching movement were

visually identified by an experimenter. Five stimulus timings were set within the time window between the onset and offset of the reaching movement. One stimulus timing was at the temporal midpoint of the movement. The other four stimulus timings were 100 ms and 200 ms before and after this midpoint. One of these five tactile stimulus delays was randomly assigned in each trial.

After touching the target with the index finger, participants moved their hand back to the location where they had perceived the tactile stimulus to occur. Participants then verbally reported the number of the device (1–4) that they had perceived as being activated during the reaching movement. When the duration of the reaching movement was less than 700 ms, the trial was discarded and repeated. If the tactile stimulus was delivered before the ready cue or after the index finger contacted the table near the target, the trial was discarded and repeated. Before the experiment, participants practiced reaching to a memorized target at least three times.

In each condition, two trial blocks were conducted: one performed with the left hand and the other performed with the right hand. The order of the two trial blocks was counterbalanced across participants. In each trial block, participants performed 40 trials (10 targets × 4 devices). In total, participants completed 80 experimental trials (40 trials in the left-hand reaching block and 40 trials in the right-hand reaching block).

(ARF error)

The vibration device that participants reported as being activated during the reaching movement was an indicator of the coordinates in the ARF. Anteriorly directed errors for Device 1 fell outside the measurement range because no device was located anterior to Device 1. Similarly, posteriorly directed errors for Device 4 fell outside the measurement range because no device was located posterior to Device 4. Thus, only trials in which the vibration was delivered to Device 2 or 3 were analyzed. The error in the coordinates of the ARF at which the tactile stimulus was perceived (ARF error) was defined as the distance between the coordinates of the perceived device (TP) and those of the actually activated device (TS). Because the devices were placed sequentially along the long axis of the hand, the positive value indicated the ARF error in the distal direction.

(TS and TP in ERF)

The average coordinates of the electromagnetic sensor at the dorsal side of the index fingertip, when the vibration was active (i.e., the time window between the onset and offset of the vibration for 200 ms), was calculated (TS; Fig. 3). The average coordinates of the electromagnetic sensor, when they maintained the hand at the place where they perceived the stimulus in the end of each trial, was estimated (TP). The locus of the electromagnetic sensor and the site of the vibration stimulus were not identical; the sensor was attached to the dorsal side of the index fingertip, whereas the vibration was delivered on the dorsal surface of the hand. Moreover, the stimulated site differed across trials, meaning that the spatial offset between the sensor and the stimulated site also varied across trials. Therefore, one might argue that the sensor position may not provide a valid measure of the ERF.

To confirm the view that the displacement of the sensor represented the displacement of the stimulated site, we conducted a preliminary validation experiment in a healthy participant using two electromagnetic sensors. Sensor 1 was attached to the dorsum of the right index fingertip, replicating the sensor placement used in the main experiment. Sensor 2 was attached to one of four locations on the dorsum of the right hand, corresponding to the vibration device locations used in the main experiment. A 5 × 5 grid was positioned such that its center coincided with one of the ten target locations used in the main experiment in each trial, and the grid was oriented along the reaching direction on the line between the ready cue and target (Fig. 1B).

In each trial, the participant placed the right index fingertip sequentially on each of the 25 grid points. The positions of both sensors were recorded. For each trial, we calculated the displacement of each sensor relative to the grid center. Thus, for each grid cell, two displacement measures were obtained: one from the fingertip sensor (sensor 1) and one from the hand sensor (sensor 2). This procedure yielded 1,000 displacement observations (4 stimulation sites × 5 reaching angles × 2 spatial hemifields × 25 grid points). An example plots of displacement measurements from Sensor 2 against the measurements in Sensor 2, corresponding to vibration stimulus devices 1 and 4, are shown in Fig. 4. To determine whether fingertip displacement was equivalent to hand displacement, the differences between the two sensors in 25 grid points in each stimulation site in each reach angle in each spatial hemifield were analyzed using the two one-sided tests (TOST) procedure for paired samples. The equivalence bounds were set to ± 1 cm, which was defined as the maximum difference considered practically negligible for representing the displacement of a rigid body segment. Pearson's correlation coefficients were computed between the displacements measured by the two sensors across the 25 grid points in each dataset.

The TOST results demonstrated statistical equivalence between the two sensors within the predefined bounds in all datasets ($p < .05$). In addition, Large and positive correlations were observed in all cases ($r = 0.75–0.97$, mean $r = 0.90$). Taken together, these findings demonstrate that displacement measured at the index fingertip closely matches displacement measured at the stimulated hand locations. Therefore, it is reasonable to assume that the fingertip sensor provides a valid measure for representing the displacement of the tactile stimulation site in the main experiment.

(ERF error)

The error in the coordinates of the ERF (ERF error) was defined as the distance between the coordinates of TP and those of TS (Fig. 5A). The distance between the sensor and stimulated site was different among the trials because there was four stimulus sites over the dorsal side of the hand. Both TS and TP were derived from the same sensor within each trial. Because the ERF error was calculated as the difference between TS and TP, any distance between the sensor and the stimulated site was cancelled out in this subtraction. This remained true even if the distance between the sensor and the stimulated site differed across trials. Therefore, the ERF error is independent of the distance between the sensor and the stimulated site. This view is depicted in Fig. 5B.

(Statistical analysis)

Reaching movement onset was defined as the time at which the coordinates of the index finger sensor first begun to move in the direction to the target coordinates. Reaching movement offset was defined as the time at which the coordinates of the index finger sensor first terminate to move after the movement onset. The duration of the reaching movement was defined as the difference between the reaching movement onset and offset. The tactile stimulus delay from the reaching movement onset was defined as the delay of the tactile stimulus as the percentage of the reaching movement duration. According to the scatter plot of the ERF error against the tactile stimulus delay, the ERF error was dependent on the tactile stimulus delay (Fig. 6A). There was a significant negative correlation coefficient between the ERF error and the tactile stimulus delay ($p < 0.05$, one-sample t-test; Fig. 6B).

Because of this, we conducted a repeated-measures three-way analysis of covariance (ANCOVA), and the tactile stimulus delay was considered to be the covariance. The main effects were reaching angle (five levels; 14 degrees, 27 degrees, 37 degrees, 45 degrees, 51 degrees), spatial hemifield (two levels; right spatial hemifield, left spatial hemifield), and hand used for reach (two levels; right hand, left hand). The alpha level was set to 0.05. Statistical analyses were performed using R (version 4.5.3; R Core Team, Vienna, Austria).

Results

(ARF error)

For the ARF error, the covariate was not significant [$F(1, 313.20) = 2.326$, $p = 0.128$], indicating that tactile stimulus delay did not significantly affect the main effects. There was a significant interaction between spatial hemifield and hand [$F(1, 346.01) = 4.083$, $p = 0.044$]. Based on this, tests of simple main effects were conducted for the effect of hand within each spatial hemifield and for the effect of spatial hemifield within each hand (Fig. 7A). These analyses revealed that, in the left spatial hemifield, the ARF error in the right hand was significantly smaller than that in the left hand [$F(1, 344) = 8.614$, $p = 0.004$]. By contrast, there was no significant difference in the ARF error between the hands in the right spatial hemifield [$F(1, 343) = 0.002$, $p = 0.966$]. There was no significant difference between the left and right spatial hemifields in the left hand [$F(1, 342) = 0.004$, $p = 0.947$]. In the right hand, the ARF error in the right spatial hemifield was significantly greater than that in the left spatial hemifield [$F(1, 353) = 7.541$, $p = 0.006$]. There was no significant main effect of reaching angle [$F(4, 345.28) = 0.267$, $p = 0.899$] (Fig. 7B).

(ERF error)

For the ERF error, the covariate was significant [$F(1, 354.06) = 52.48$, $p < 0.001$], indicating that tactile stimulus delay significantly affected ERF error. There was a significant three-way interaction among spatial hemifield, hand, and reaching angle [$F(4, 341.11) = 3.065$, $p = 0.017$]. Given this interaction, tests of simple main effects were conducted (Fig. 8). In the left spatial hemifield, the right hand showed significantly greater ERF error than the left hand at a reaching angle of 45 degrees [$F(1, 341) = 6.386$, $p =$

0.012] and at 51 degrees [$F(1, 342) = 5.570$, $p = 0.019$] (Fig. 8A). In the right spatial hemifield, the left hand showed significantly greater ERF error than the right hand at a reaching angle of 27 degrees [$F(1, 341) = 8.785$, $p = 0.003$], at 37 degrees [$F(1, 341) = 7.497$, $p = 0.007$], at 45 degrees [$F(1, 341) = 18.723$, $p < 0.001$], and at 51 degrees [$F(1, 341) = 21.455$, $p < 0.001$] (Fig. 8B). When reaching with the left hand, the ERF error was significantly greater in the right spatial hemifield than in the left spatial hemifield at a reaching angle of 45 degrees [$F(1, 341) = 3.897$, $p = 0.049$] and at 51 degrees [$F(1, 344) = 11.958$, $p = 0.001$] (Fig. 8C). When reaching with the right hand, the ERF error was significantly greater in the left spatial hemifield than in the right spatial hemifield at a reaching angle of 27 degrees [$F(1, 341) = 8.880$, $p = 0.003$], at 37 degrees [$F(1, 342) = 12.166$, $p = 0.001$], at 45 degrees [$F(1, 341) = 23.912$, $p < 0.001$], and at 51 degrees [$F(1, 341) = 10.439$, $p = 0.001$] (Fig. 8D).

Discussion

(ARF error)

The ARF error of the right hand (i.e., reaching with the right arm) was significantly smaller than the left hand (i.e., reaching with the left arm) when participants reached to the left spatial hemifield. The cortical response to the right hand tactile stimulus was asymmetrical, but such an asymmetry was weak in the left hand (Jin et al., 2020). The area of the primary sensory cortex, and the N20 of the somatosensory-evoked potential were asymmetrical (Jung et al., 2003). Such an asymmetrical somatosensory system between the hemispheres may lead to the asymmetrical ARF error between the stimulated hands. Based on this view, supporting Hypothesis 2, the significant hand effect on the ARF error when they reached to the left spatial hemifield may represent an asymmetrical tactile perceptual process that affects the ARF.

The difference in the ARF error between the hands disappeared when they reached to the right spatial hemifield. This means that the hand effect is dependent on the spatial hemifield to reach. The change in the arm proprioception changed the locus of the tactile stimulus (i.e., coordinates of the ARF) over the hand (Liu & Medina, 2021). The body representation was dependent on the body posture (Longo, 2015). The reaching movement to the left spatial hemifield and that to the right spatial hemifield causes different proprioception. Thus, one might argue that the spatial hemifield–dependent hand effect observed in the present study could be explained by differences in proprioception-mediated perception of body posture contributing to the ARF error between reaches to the left and right spatial hemifield. However, in the present study, the ARF error was not dependent on reaching direction, although proprioception differed across movement directions. Thus, the proprioception is not the main cause of the difference in the hand effect on the ARF error between reaching to the left spatial hemifield and that to the right spatial hemifield.

The arm crosses the body midline into the contralateral spatial hemifield when the left hand reaches into the right hemifield or when the right hand reaches into the left hemifield. On the one hand, coordinates in the ARF are mapped onto the somatotopic representation of the body. On the other hand, coordinates in the ERF are mapped onto the spatial hemifield toward which the movement is directed. Accordingly, a

conflict between the ARF and ERF arises when the arm crosses the body midline into the contralateral spatial hemifield (Badde & Heed, 2016). Indeed, crossing the arms—placing the left hand in the right side of space and the right hand in the left side of space—increased the temporal order judgment (TOJ) error (Shore et al., 2002; Yamamoto & Kitazawa, 2001). However, such a conflict between ARF and ERF does not appear to account for the spatial-hemifield–dependent hand effect observed in the present study, because the results were not symmetrical: overestimation of tactile stimulus location in the ERF occurred when the right hand reached to the left spatial hemifield, but not when the left hand reached to the right spatial hemifield.

The right hemisphere mediates attention across both left and right spatial hemifields, whereas the left hemisphere predominantly mediates attention to the right hemifield (Mesulam, 1999; Pouget & Driver, 2000). Previous work has shown that the right temporoparietal junction responds to invalid targets across both hemifields, whereas the left temporoparietal junction is preferentially engaged by invalid targets in the right hemifield (Dragone et al., 2015). Consistent with this asymmetry, spatial representations in the right parietal cortex have been proposed to encompass both sides of space, whereas representations in the left hemisphere are largely contralateral (Pouget & Driver, 2000). In line with this view, reductions in parietal alpha activity have been reported bilaterally in the right hemisphere following visual warning stimuli presented in either hemifield, whereas the left hemisphere shows a stronger decrease primarily for right-sided stimuli (Heilman & Van Den Abell, 1980). Moreover, directing attention to visual stimuli has been shown to reduce contralateral bias in the right parietal cortex—reflecting enhanced ipsilateral representation—while the left parietal cortex maintains a predominantly contralateral coding scheme (Sheremata & Silver, 2015). Thus, the dominant cortical hemisphere contributing to spatial attention is asymmetrical between the left and right spatial hemispheres.

Based on this, the contribution of spatial attention to tactile localization differs between reaching to the left and right spatial hemifields. Thus, the asymmetric hand effect across spatial hemifields is likely explained by asymmetrical contributions of spatial attention. In the present study, a hand effect was observed when participants reached to the left spatial hemifield, but not when they reached to the right spatial hemifield. Accordingly, the present findings can be explained by the view that spatial attention in the left hemisphere reduces the proximal deviation of the perceived tactile stimulus location on the right hand within the ARF.

(ERF error)

The effect of the hand and spatial hemifield on the ERF error was different from that on the ARF error. This means that the contribution of spatial attention to the ERF is different from that to the ARF. On the one hand, the tactile locus of the right hand in the ERF deviated distally to the left hand when reaching to a target in the left spatial hemifield. On the other hand, that of the left hand in the ERF deviated distally to the right hand occurred when reaching to a target in the right spatial hemifield. The arm crossed the midline when the right hand reached to the left side or the left hand reached to a target in the right spatial hemifield. Thus, the present findings suggest that the coordinates of the ERF is deviated distally

when the arm crosses the midline to reach. The symmetrical effect of the spatial hemisphere did not support Hypothesis 1.

When the arm crossing occurs, the conflict between the ARF and ERF occurs (Badde et al., 2014, Badde & Heed, 2016). When crossing the hand, the TOJ error increased (Shore et al. 2002; Yamamoto et al., 2001). This is considered to be due to the conflict between the ARF and ERF (Badde et al., 2014, Badde & Heed, 2016). Thus, one possible explanation for the present finding is that the distal deviation of the tactile stimulus locus in the space occurs when the ARF and ERF conflict.

Attentional modulation of early somatosensory processing occurs, and the magnitude of this modulation depends on whether the ARF and ERF conflict (Röder et al., 2008). In this study, participants were instructed on each trial which hand to attend to, and they detected rare double-touch deviants at the attended hand. In sighted adults, attention effects on early event-related potential (P1, Nd1, Nd2) were robust when the hands were uncrossed but were reduced when the hands were crossed, indicating that ARF–ERF conflict disrupts spatial attentional processing. Accordingly, the distal deviation of the coordinates of the ERF when crossing the arm in the present study is possibly explained by the attenuated spatial attention due to the conflict between the ARF and ERF.

(Spatial attention contributing to ERF)

We must consider previous findings that are difficult to reconcile with the present findings. After a salient tactile event on the hand, visually evoked event-related potentials to stimuli presented in the same hemispace were enhanced, and this cross-modal facilitation shifted in external space when the hands were crossed (Eimer & Driver, 2001). Accordingly, cross-modal spatial attention was suggested to be tied to the location of the hand in external space rather than to the stimulated hand, consistent with the view that spatial attention operates within the ERF (Driver & Spence, 1998b). Additionally, facilitation of visual processing speed and enhanced event-related potentials at the external spatial location of the tactually cued hand suggest that cross-modal attentional orienting operates in the ERF rather than the ARF (Kennett et al., 2001). These findings suggest that the temporal dynamics of attentional reorientation and reengagement play a critical role in resolving conflicts between spatial codes in tactile processing. Based on this view, at first glance, the asymmetrical spatial-attention pattern observed in the present study, particularly within the ARF, appears inconsistent with these previous findings that support an external-reference account.

Several methodological differences between the previous and present studies may explain this discrepancy. In the previous studies, tactile events were presented while participants' eyes were open, allowing vision to provide a reliable spatial reference for localizing tactile events in external space (Eimer & Driver, 2001; Kennett et al., 2001). In contrast, participants in the present study performed the task with their eyes closed. According to reliability-weighting accounts of multisensory integration (Ernst & Banks, 2002), the relative contribution of each sensory modality depends on its reliability. Moreover, the weighting of multisensory integration is task-dependent and flexibly adjusted (Badde et al., 2015). Thus, the absence of visual input in the present study may have increased reliance on somatotopic or

anatomical representations, thereby enhancing the contribution of spatial attention primarily operates within the ARF. This interpretation remains speculative and should be directly tested in future studies.

(Limitations)

Several limitations of the present study should be acknowledged. Although the ERF error was computed as the difference between two measurements obtained from the same fingertip-mounted sensor, the tactile stimulus itself was delivered to the dorsum of the hand. While our validation experiment demonstrated statistical equivalence between fingertip and hand displacement within ± 1 cm, small deformations of the hand or skin during movement may still have introduced residual discrepancies that were not fully captured by the sensor-based subtraction.

Previous studies have shown that handedness strongly modulates hemispheric lateralization and spatial attention. For example, right-handers exhibited stronger hemispheric lateralization for spatial attention than left-handers (O'Regan & Serrien, 2018). In addition, the representation of the dominant hand in the somatosensory cortex was larger in right-handers, indicating that handedness affects somatosensory processing (Sörös et al., 1999). Importantly, the spatial extent of peripersonal space was asymmetric in right-handers (larger in left hemispace) but symmetric in left-handers, suggesting that handedness directly shapes spatial–tactile interactions (Hobeika et al., 2018). These findings indicate that the asymmetry observed in the present study may be specific to right-handed participants. Because handedness was not manipulated or systematically examined, the present cannot be generalized to left-handed individuals. Future studies directly comparing right- and left-handed participants will be necessary to clarify the role of handedness in the interaction between the ARF/ERF and spatial attention.

Because tactile stimulation occurred during ongoing reaching movements, motor-related processes—such as motor plan, motor command, or efference copy—may have interacted with tactile localization. For example, attentional resources are shared with motor plan (Long & Ma-Wyatt, 2014). The significant influence of stimulus delay on ERF error suggests that movement progression modulated tactile remapping, making it difficult to fully dissociate attentional contributions from motor-related influences. This is also limitation of the present study.

Conclusions

The present findings demonstrated a hemispace-dependent asymmetry in the ERF errors between the hands. Specifically, the left hand showed a larger distal error than the right hand when reaching to the left hemifield, whereas this asymmetry disappeared when reaching to the right hemifield. This indicates that the proximal bias of the ARF is attenuated when tactile processing interacts with spatial-attention mechanisms in the left hemisphere. Furthermore, ERF errors shifted distally in the hand contralateral to the reached hemifield: the right hand exhibited a larger distal error during left-hemifield reaching, whereas the left hand exhibited a larger distal error during right-hemifield reaching. These results suggest that when the ARF and ERF are in conflict, the contribution of spatial attention is diminished, leading to a reduction of the distal bias in perceived tactile location.

Declarations

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Data availability statement

The data that support the findings of this study are not openly available due to reasons of sensitivity and are available from the corresponding author upon reasonable request.

Conflict of interest

The authors have no conflict of interest.

Author Contribution

M.F. and K.H. made a research plan. M.F., H.G, K.H. conducted experiments. M.F. and K.H. conducted data analysis. M.F. and K.H. prepared figures 1-8. M.F. and K.H. wrote the main manuscript text. All authors reviewed the manuscript.

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Figures

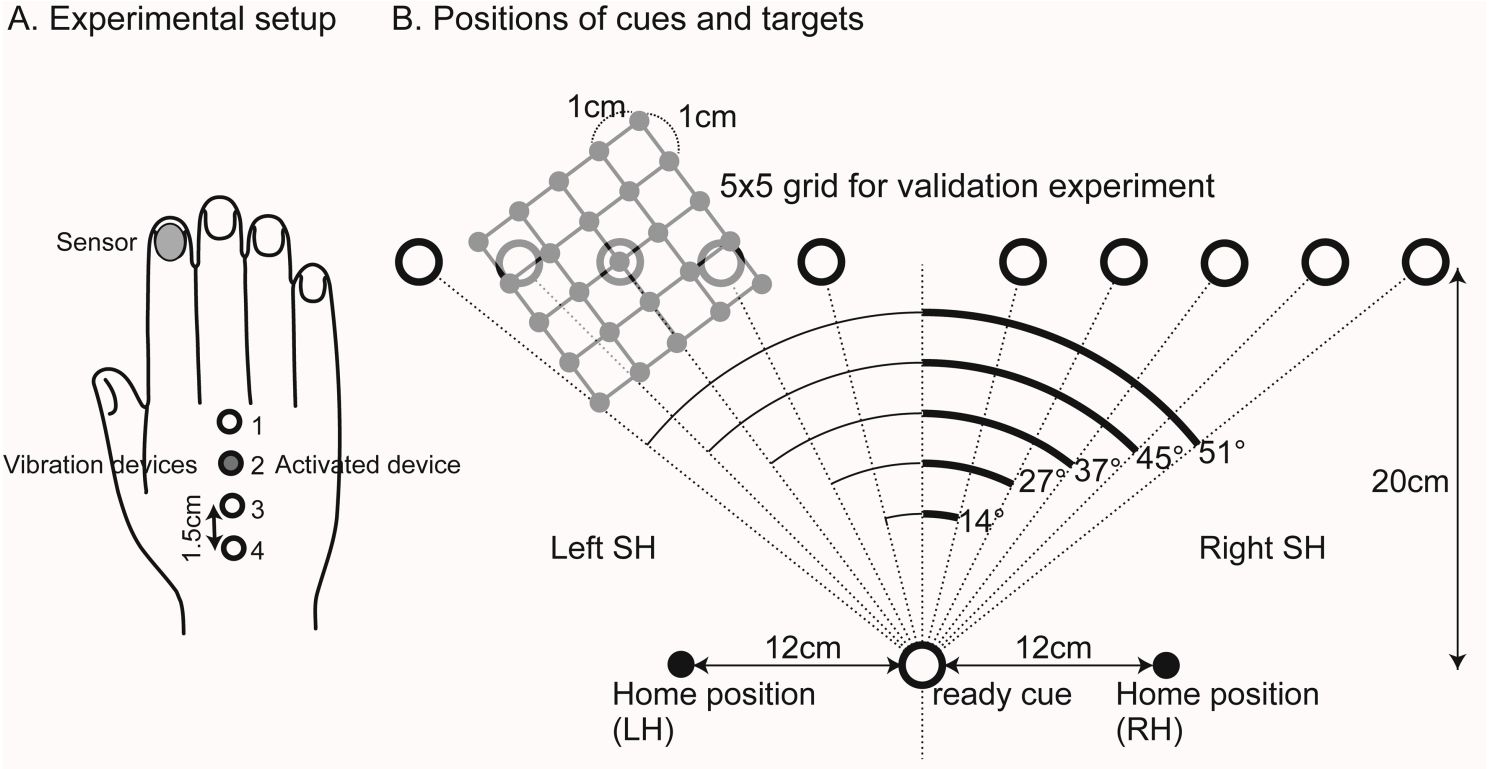


Figure 1

The experimental set up and targets. (A) Four small vibration devices are attached to the dorsum of the hand at 1.5cm interval, and an electromagnetic sensor was placed on the index fingertip. The filled circle indicates the activated device in a trial; i.e., the activated device #2. (B) The targets, cues, and markers presented on a table. The waiting position was located 12 cm lateral to the ready cue. The targets are 20 cm in front of the ready cue on the midline of the participant's body. Each target has one of five angles relative to the midline (14 degrees, 27 degrees, 37 degrees, 45 degrees, 51 degrees). The center of the 5 x 5 grid (1 cm spacing) is positioned at the target and perpendicular to the reaching direction on the line between the ready cue and target when conducting a preliminary validation experiment. SH, spatial hemisphere; LH, left hand; RH, right hand.

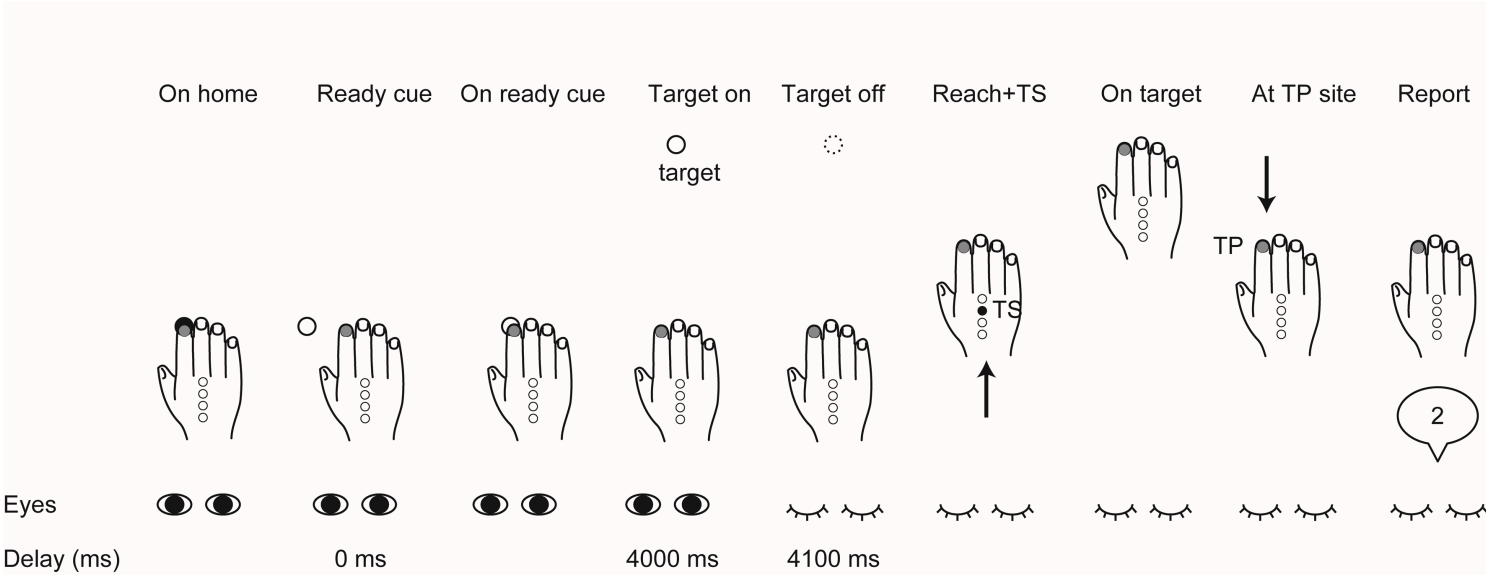


Figure 2

Task paradigm. Participants place the index fingertip on the home marker. A ready cue appears for 4000 ms in front of the midline of the body. As long as this cue is presented, participants place their index fingertip on this cue. Target cue appear at the end of the ready cue for 100 ms. They close their eyes and the memorized locus of the target. Then, they reach to the memorized target in response to the target cue. While reaching the target with the index finger, one of four vibration devices is activated (TS). After the completion of the reaching to the memorized target, they places the stimulated hand at the locus at which they perceive the location where they have perceived the tactile stimulus. Finally, they verbally report the number of the device that they have perceived as being activated during the reaching movement.

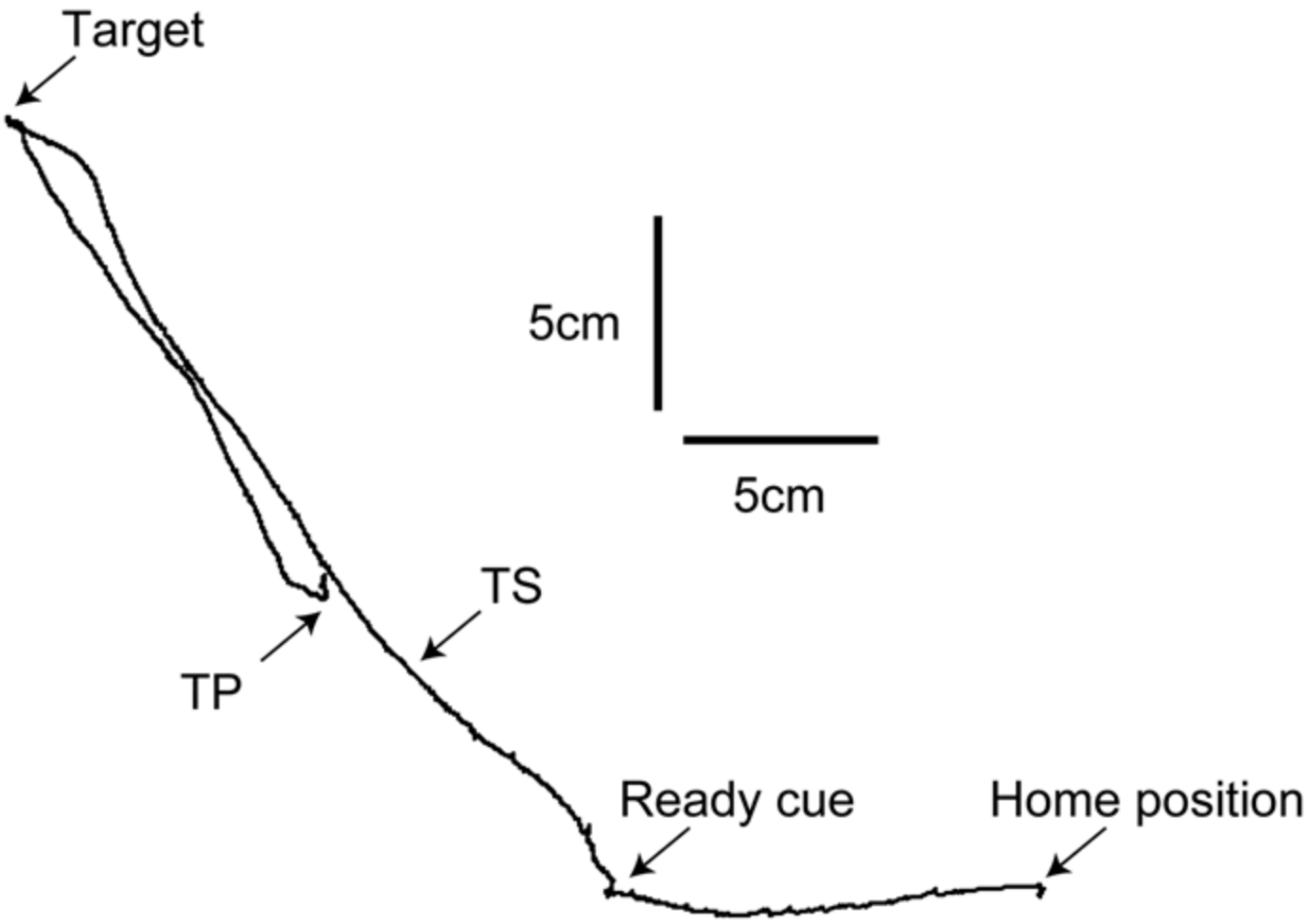


Figure 3

An example of the raw trace of the trajectory of the sensor during reaching movement. TS indicates the locus where the tactile stimulus is delivered. TP indicates the locus of the index fingertip when participants move the hand back to the locus where they perceive the tactile stimulus.

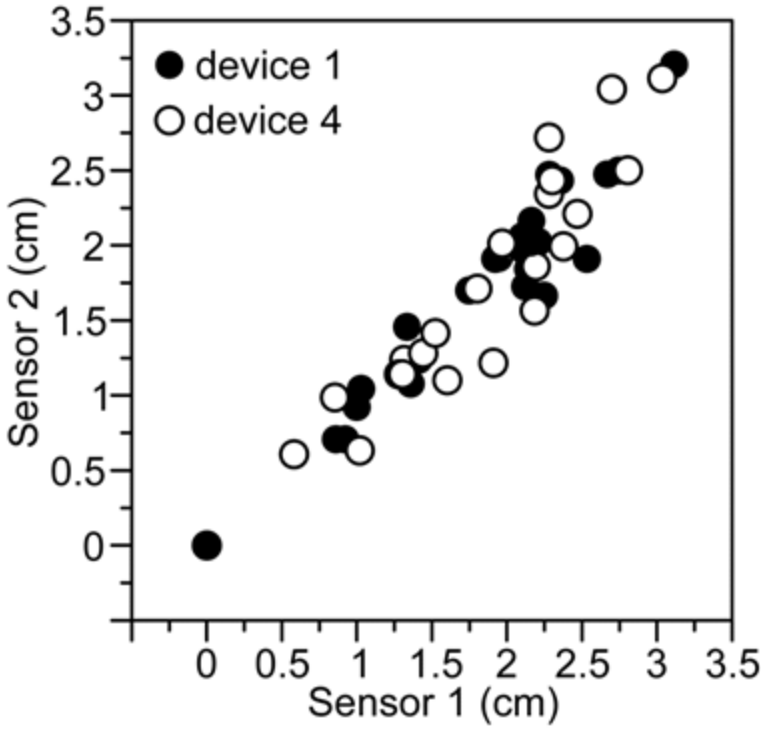


Figure 4

Displacement measurements from two electromagnetic sensors recorded in the preliminary validation experiment. For a target positioned 37° to the right of the midline, the displacement of sensor 2 is plotted against that of sensor 1 across 25 grid points, illustrating the positive and linear relationship between the two sensors.

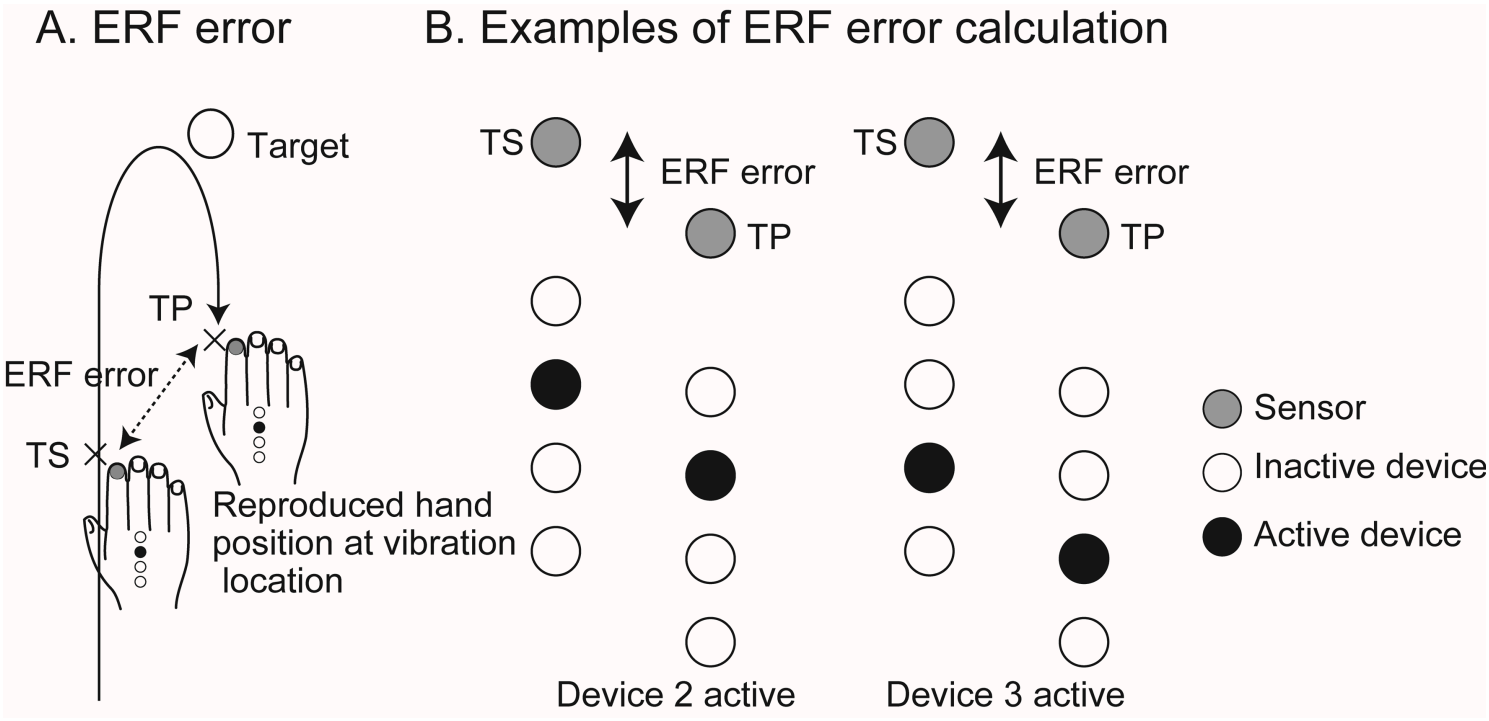


Figure 5

Calculation of ERF error and rationale for sensor-based measurement. (A) Calculation of the error in the external reference frame (ERF error). During reaching, the average position of the electromagnetic sensor attached to the dorsal side of the index fingertip is calculated during the 200-ms vibration period (TS). At the end of each trial, participants reproduced the perceived location of the tactile stimulus, and the average sensor position during this reproduction phase is calculated (TP). The ERF error is defined as the spatial distance between TS and TP. (B) Rationale for using the sensor position to quantify the ERF error. The vibration stimulus is delivered to the hand, whereas the sensor is attached to the index fingertip. Therefore, the spatial offset between the sensor and the stimulated skin site varies across the trials. However, both TS and TP are obtained from the same sensor within each trial. Because ERF error is computed as the difference between these two sensor-based positions, any constant spatial offset between the sensor and the stimulated site is cancelled out.

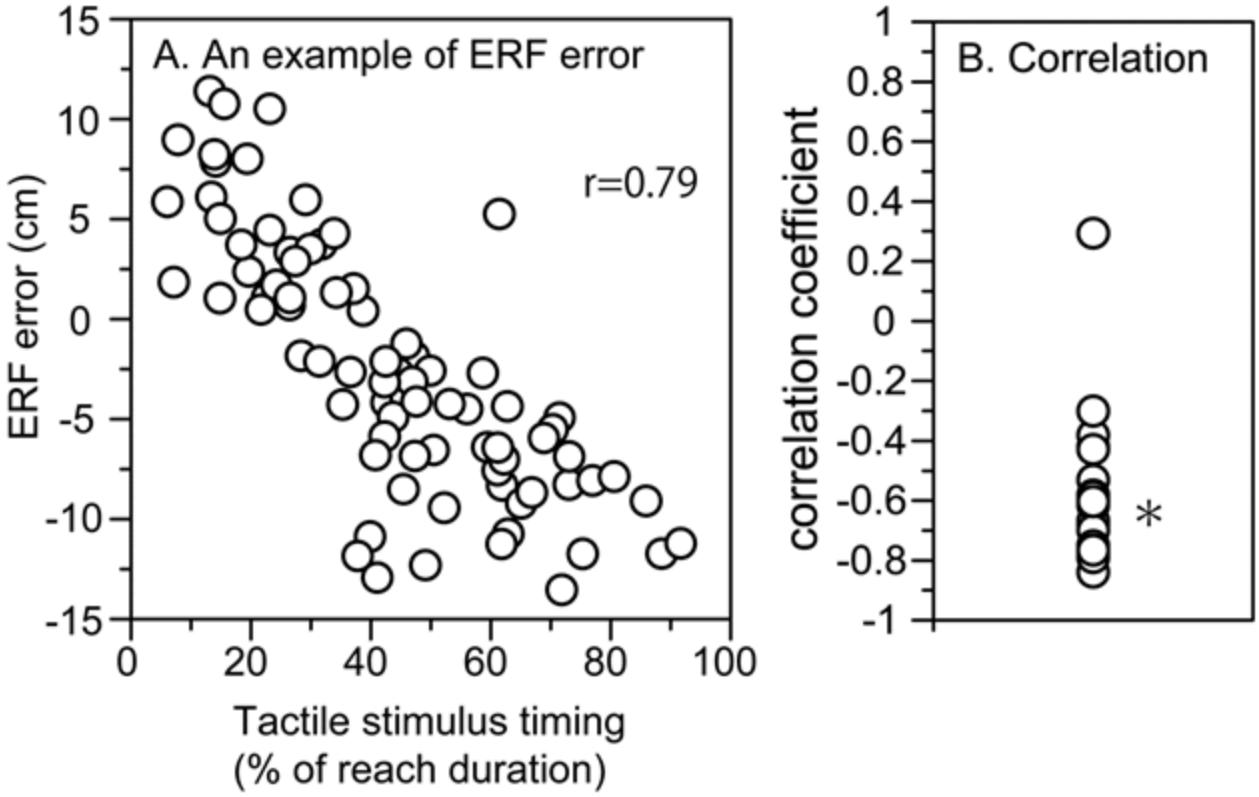


Figure 6

The influence of the tactile stimulus delay to the reaching onset. (A) An example of the scatter plots in the ERF error against the tactile stimulus delay to the reaching onset expressed as the percentage of the reaching duration. (B) Correlation coefficient between the ERF error and the tactile stimulus delay. An asterisk indicates significant difference from zero ($p < 0.001$, one-sample t-test).

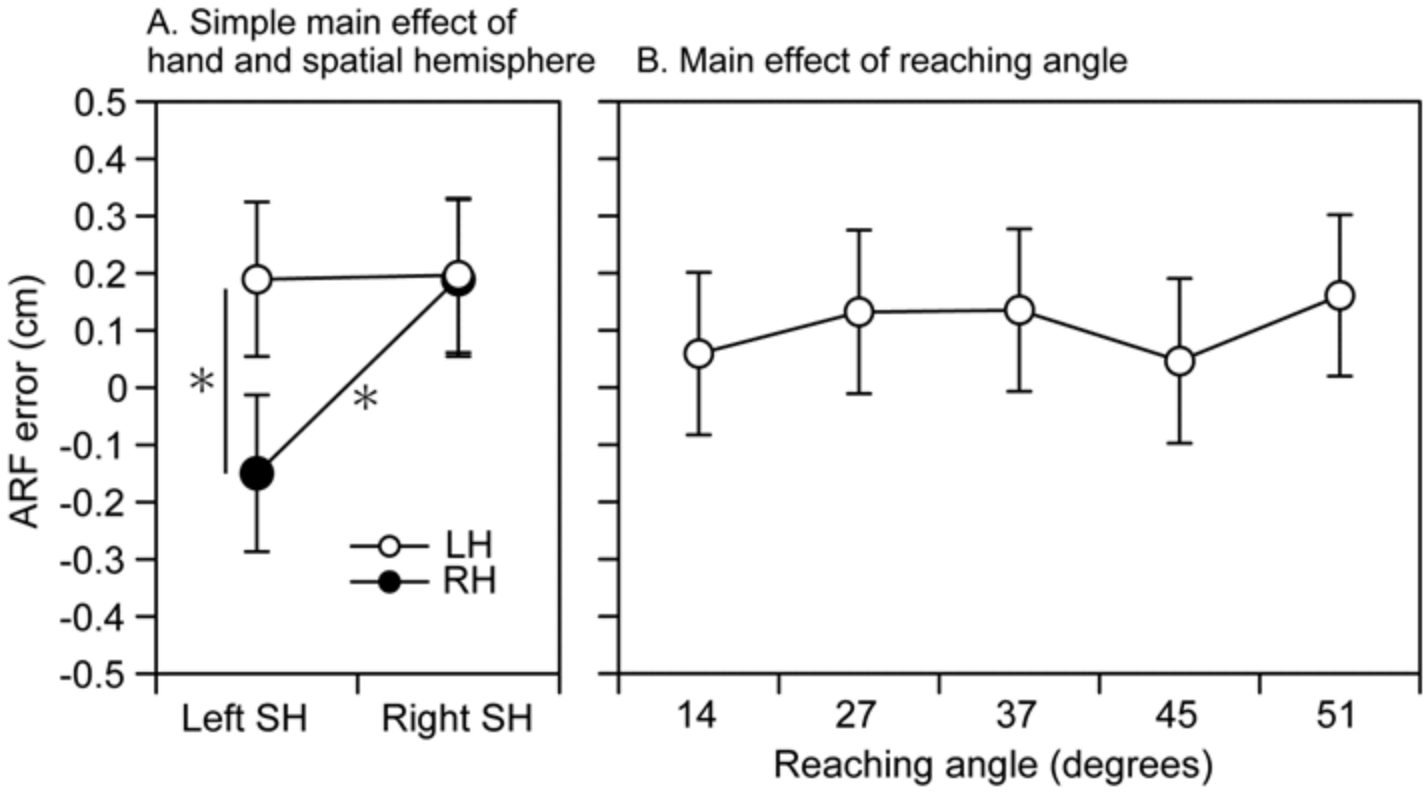


Figure 7

The ARF error. (A) The simple main effect of the hand and spatial hemifield. (B) The main effect of the reaching angle. Points indicate the means and error bars indicate the standard error of the mean. An asterisk indicates a significant simple main effect ($P < 0.05$). SH, spatial hemisphere; LH, left hand; RH, right hand.

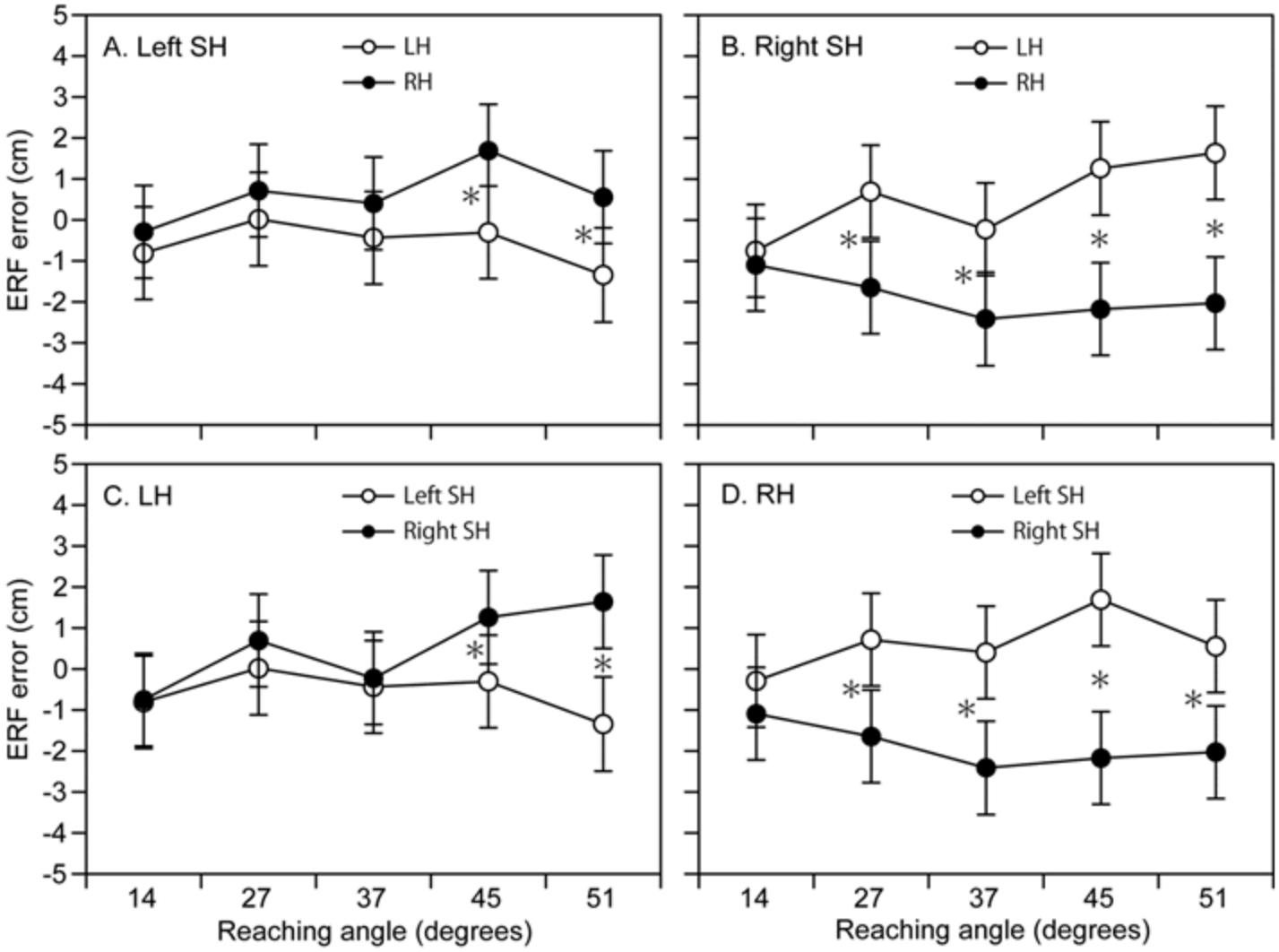


Figure 8

The simple main effects on the ERF error. Points indicate the means and error bars indicate the standard error of the mean. An asterisk indicates a significant simple main effect ($P < 0.05$). SH, spatial hemisphere; LH, left hand; RH, right hand.