

Contribution of proprioception to determining coordinates in anatomical and external reference frames during tactile localization

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Abstract

This study examined whether humans rely on proprioception to determine the location of a tactile stimulus both on the body, represented as an anatomical reference frame (ARF) coordinate, and in external space, represented as external reference frame (ERF) coordinates. Eighteen healthy participants reached toward a target. Tactile stimulus was applied to one of four sites on the hand during reaching. After touching the target, participants moved the hand so that the stimulated site returned to the perceived spatial location of the tactile stimulus. This location was considered to represent the perceived location of the tactile stimulus in external space (ERF coordinates). Participants then verbally reported the location of the tactile stimulus on the dorsum of the hand, representing the ARF coordinate. Vibration applied to the biceps brachii produced a distal bias in the ARF coordinate when participants reached toward a target at an angle of 5, 25, or 30 degrees to the right of the anterior–posterior axis. For the ERF coordinates, the vibration induced a backward bias during reaching toward a target at an angle of 10 degrees and a forward bias during reaching toward a target at an angle of 25 degrees to the right of the anterior–posterior axis. These findings indicate that proprioception contributes differently to determining the ARF coordinate and to tactile remapping into ERF coordinates. The reaching angle-dependent effect of vibration indicates that the contribution of proprioception to ARF and ERF coordinates depends on the motor command planned for each reaching direction.

Introduction

When something contacts the body surface, humans determine which part of the body is touched and where the contact occurs in external space. The locus of the tactile stimulus is represented on a map of the body surface, called an anatomical reference frame (ARF; (Schicke & Röder, 2006; Röder et al., 2007)). Tactile stimulation of individual fingers evoked somatotopically organized activity in the primary sensory cortex (Martuzzi et al., 2014). Accordingly, the ARF coordinates are likely determined based on which region of the primary sensory cortex responds to afferent signals arising from the activated cutaneous receptors at the stimulated site.

Body representation has been suggested to contribute to tactile localization (Margolis & Longo, 2015). The implicit representation of hand size has been shown to vary with finger posture (Longo, 2015). When the hand was opened, the distance between two tactile stimuli on the hand was perceived to be greater (Longo, 2017). More specifically, several previous studies have reported that the localization of tactile stimuli depends on hand position. The perceived location of tactile stimuli on the hand surface was biased by the proprioceptively specified position of the hand (Liu & Medina, 2021). Manipulating forearm posture by placing the forearm in pronated or supinated positions shifted the perceived location of tactile stimuli on the forearm (Sadibolova et al., 2018). These findings indicate that the perceived ARF coordinate depends on hand position. Accordingly, the ARF coordinate is likely to depend on proprioception. Thus, it is hypothesized that humans rely on proprioception to determine the ARF coordinates (Hypothesis 1).

However, in those previous studies, the task did not involve active movement, and it therefore remains unclear whether Hypothesis 1 is applicable to the process of determining the ARF coordinate during movement. During movement, an efference copy of the motor command is used by an internal forward model to predict the sensory consequences of the movement and to estimate the current state of the limb (Miall et al., 1993; Miall & Wolpert, 1996). This predictive estimate is integrated with proprioceptive afferent information to determine the current limb state. Because motor cortical activity varies systematically with reaching direction (Georgopoulos et al., 1982), consistent with direction-dependent motor commands, the predicted sensory consequences of movement may also differ across reaching directions. Accordingly, the influence of proprioceptive information on ARF coordinate determination may depend on reaching direction (Hypothesis 2).

The process underlying the determination of the location of a touch in external space is called tactile localization (Heed et al., 2012, 2015). The location of the tactile stimulus in external space is represented in an external reference frame (ERF). It has been proposed that the location of a tactile stimulus in external space is determined by transforming its ARF coordinate into an ERF coordinate, a process known as tactile remapping (Azañón & Soto-Faraco, 2008; Heed et al., 2015; Schicke & Röder, 2006). This transformation critically depends on information about body posture (Heed et al., 2015), to which proprioceptive signals make an important contribution (Farrer et al., 2003; Tuthill & Azim, 2018). From this perspective, the ERF coordinate may be influenced by proprioceptive information at two stages: during ARF coordinate determination and during tactile remapping.

For the ARF coordinate, proprioception may exert its influence through a single stage: ARF coordinate determination. In contrast, the ERF coordinate may be influenced by proprioception at two stages: during ARF coordinate determination and during tactile remapping. Thus, although the determination of both ARF and ERF coordinates relies on information about body posture provided by proprioception, the underlying mechanisms may differ (Hypothesis 3). If Hypothesis 3 is correct, the influence of proprioception on the ERF coordinate should differ from that on the ARF coordinate.

To examine these hypotheses, proprioceptive information during reaching was manipulated in the present study. Microneurographic evidence has shown that group Ia muscle spindle afferents are particularly sensitive to tendon vibration (Amiez et al., 2026; Roll & Vedel, 1982). Muscle-tendon vibration induces an illusory lengthening of the vibrated muscle (Goodwin et al., 1972; Roll & Vedel, 1982). During voluntary movement, vibration of the antagonist muscle induces movement errors consistent with altered proprioceptive information from that muscle (Capaday & Cooke, 1981, 1983; Cody et al., 1990). These findings indicate that muscle vibration induces a proprioceptive illusion. Thus, in the present study, we examined the effects of vibration applied to the biceps brachii on the ARF coordinate and ERF coordinates to test these hypotheses.

Methods

(Participants)

Eighteen healthy participants (ten males and eight females), aged 23.5 ± 7.3 years, participated in this study. They had no history of neurological disease. The required sample size was estimated using G*Power 3.1.9.6. To achieve a statistical power of 0.80 with an alpha level of .05, a total of 12 participants were required to detect a medium effect ($f = 0.25$). Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). A laterality quotient (LQ) was calculated for each participant using the following formula: $[(\text{number of right-hand scores} - \text{number of left-hand scores}) / (\text{number of right-hand scores} + \text{number of left-hand scores})] \times 100$. The mean LQ was 94.0 ± 14.3 . Based on the cutoff criteria used in previous studies (Frankford et al., 2021; Harvey et al., 2021; Roup, 2011; Shin et al., 2024; Wong et al., 2008), 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.

(Apparatus)

The participants wore earmuffs to minimize extraneous auditory input. An electromagnetic sensor was attached to the dorsal side of the right index fingertip to measure its position in space (Viper Unit 8; Polhemus, USA; Fig. 1A). The signals from this sensor were sampled at 960 Hz. Four small vibration devices (Motionboard 3.4, Teknikio, Tokyo), each 8 mm in diameter, were attached to the dorsum of the right hand along the longitudinal axis of the third metacarpal at 1.5-cm intervals (Fig. 1A). Each vibration device delivered a tactile stimulus at a frequency of 100 Hz for 200 ms. The vibration devices were assigned identification numbers 1 to 4 (Device #1 to #4) in order from distal to proximal.

A vibration device (VC-100, Uchida Denshi, Tokyo) was attached to the belly of the right biceps brachii. The vibration frequency was set at 100 Hz. This was to induce an illusion of muscle lengthening (Capaday & Cooke, 1981, 1983; Cody et al., 1990). A vibration frequency of 100 Hz was selected because tendon vibration at approximately 70–115 Hz is particularly effective in eliciting kinesthetic illusions, which are mediated predominantly by group Ia muscle spindle afferents (Marasco & de Nooij, 2023).

A 5-mm-diameter marker indicating the ready position of the index fingertip was placed on the table surface (home marker; Fig. 2). A ready cue and a target cue, each consisting of a circle 10 mm in diameter, were projected onto the table surface. The locations of the ready and target cues were programmed using visual presentation software (S-15001, Takei Kiki, Japan).

(Task paradigm)

The task procedure shown in Fig. 2 was the same as that used in a previous study (Futamura et al., 2026). Before the experiment, an experimenter informed the participants of the identification numbers (Device #1 – #4) assigned to the four vibration devices attached to the dorsum of the hand. In addition, the experimenter confirmed that the participants could perceive the tactile sensation produced by each vibration device before the experiment.

The participants placed their right index fingertip on the home marker before the reaching task. A ready cue (an open circle with a black outline) appeared 9 cm in front of the home marker for 4000 ms. While the ready cue was present, the participants kept their index fingertip on the cue. When the ready cue disappeared, a target cue (an open circle with a black outline) appeared and remained visible for 100 ms. The target cue was projected onto the table surface at one of four distances from the ready cue (17.5, 20.0, 22.5, and 25.0 cm) and at one of seven reaching angles (0, 5, 10, 15, 20, 25, and 30 degrees) relative to the participant's anterior-posterior axis in each trial (Fig. 1B). In total, there were 28 target locations (4 target distances $\times$ 7 target angles), one of which was randomly selected on each trial. In response to the target cue, the participants memorized the target location, closed their eyes, and reached toward the memorized location. During reaching toward the memorized target, one of the four small vibration devices was activated for 200 ms.

After touching the memorized target on the table, participants moved their hand back to the position where they had perceived the tactile stimulus, with the activated vibration device remaining attached to the hand. After that, participants verbally reported the identification number (1–4) of the vibration device that they had perceived as being activated during reaching. The identification number of the vibration device reported by the participant was considered to represent the ARF coordinate. An experimenter verbally instructed the participants not to move too quickly. If the reaching duration was less than 700 ms, the trial was discarded and repeated. Before the experiment, the participants practiced reaching toward a memorized target at least three times (practice trials).

(Vibration to biceps brachii)

In some trials, vibration was applied to the biceps brachii during reaching (vibration condition). In the remaining trials, vibration was not applied (non-vibration condition). One of these two conditions was randomly assigned on each trial. In the vibration condition, vibration applied to the biceps brachii was initiated at the onset of the ready cue. The vibration duration was set so that vibration applied to the biceps brachii ended 300 ms after the latest offset of the tactile stimulus applied to the dorsum of the hand.

(Tactile stimulus)

Before the experimental trials, each participant performed one reaching movement toward a target to determine the timing of the tactile stimulus (calibration trial). The onset and offset of the reaching movement in the calibration trial were visually identified from the recorded movement trajectory. Movement onset was defined as the first time point at which the index finger transitioned from a stationary state to movement, whereas movement offset was defined as the first time point at which the finger became stationary again. The reaching movement duration was calculated as the interval between movement onset and offset.

Based on the reaching movement duration obtained from the calibration trial, five stimulus timings were predetermined for the experimental trials: at the temporal midpoint and 100 and 200 ms before and after

the midpoint. The tactile stimulus timing was expressed as a percentage of the reaching movement duration based on the interval from movement onset to tactile stimulus onset and was calculated as follows: Tactile stimulus timing (%) = $100 \times (\text{tactile stimulus onset} - \text{movement onset}) / \text{reaching movement duration}$. The onset of the 200-ms tactile stimulus was used to define the tactile stimulus timing. Thus, 0% corresponded to movement onset and 100% corresponded to movement offset. One of these five tactile stimulus timings was randomly assigned on each trial. If the tactile stimulus was delivered before movement onset or after movement offset, the trial was discarded and repeated.

(Conditions and number of trials)

There were 28 target locations (4 target distances $\times$ 7 target angles) for two vibration conditions. Two trials were conducted in each target for each vibration condition. Thus, a total of 112 trials were conducted.

(ARF error)

The vibration device that participants reported as being activated during reaching was considered to represent the ARF coordinate. Because Device #1 was the most distal device, a perceived location distal to Device #1 could not be represented on this response scale. Similarly, because Device #4 was the most proximal device, a perceived location proximal to Device #4 could not be represented. Including trials in which Device #1 or #4 was stimulated would therefore have introduced one-sided boundary effects. Accordingly, only trials in which Device #2 or #3 was stimulated were included in the analysis. The error in the perceived ARF coordinate (ARF error) was defined as the signed distance between the location of the device reported by the participant and that of the actually activated device. A positive value of ARF error indicated a distal bias of the ARF coordinate.

(TS and TP)

The mean coordinates of the electromagnetic sensor during tactile stimulation were calculated (TS; Fig. 3). In addition, the mean coordinates of the sensor while the participants held their hand at the location where they had perceived the stimulus at the end of each trial were calculated (TP). The location of the sensor and the site of the tactile stimulus were not identical; the sensor was attached to the dorsum of the index fingertip, whereas the tactile stimulus was delivered to the dorsum 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 coordinate. To confirm that displacement of the sensor represented displacement of the stimulated site, we conducted a preliminary validation experiment in one 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 $\times$ 5 grid was positioned

such that its center coincided with one of the seven target locations used in the main experiment, each located 25 cm from the ready cue at an angle of 0, 5, 10, 15, 20, 25, or 30 degrees (Fig. 1B). The grid was oriented such that one axis was parallel to the reaching direction and the other was perpendicular to it. In each trial, the participant placed the right index fingertip on each of the 25 grid points. The coordinates of both sensors were recorded at each grid point. The displacement of each sensor relative to the grid center was calculated. Thus, for each grid point, two displacement measures were obtained: one from the fingertip sensor (Sensor #1) and one from the hand sensor (Sensor #2). This procedure yielded 700 displacement observations (4 stimulation sites $\times$ 7 reaching angles $\times$ 25 grid points). To determine whether fingertip displacement was equivalent to hand displacement, the differences between the two sensors across the 25 grid points for each combination of stimulation site and reaching angle were analyzed using the two one-sided tests (TOST) procedure for paired samples.

Example plots of the displacement measured by Sensor #2 against that measured by Sensor #1 for Devices #1 and #4 are shown in Fig. 4. The equivalence bounds were set at ± 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 indicated statistical equivalence between the two sensors within the predefined bounds in all datasets ($p < .05$). In addition, large positive correlations were observed in all cases ($r = 0.80\text{--}0.99$, mean $r = 0.90$). These results were consistent with those of a preliminary validation experiment reported in a previous study, in which the same configuration of the sensor and vibration devices was set (Futamura et al., 2026). These findings demonstrate that displacement measured at the index fingertip closely matched displacement measured at the stimulated locations on the hand. Therefore, it is reasonable to assume that the fingertip sensor provides a valid measure of the displacement of the tactile stimulus site in the main experiment.

(ERF error)

The error in the ERF coordinate (ERF error) was defined as the signed distance between TP and TS (Fig. 5A). The Euclidean distance between TP and TS was first calculated. To determine the sign of this distance, the anterior–posterior coordinate of TS was subtracted from that of TP. When this difference was negative, the ERF error was assigned a negative value; when the difference was positive, it was assigned a positive value. Thus, a positive ERF error indicated a forward deviation of the perceived tactile stimulus locus in external space, whereas a negative ERF error indicated a backward deviation of that.

The spatial offset between the sensor and the stimulated site differed across trials because the stimulus was delivered at one of four different sites on the dorsum of the hand in each trial. Both TS and TP were derived from the same sensor within each trial. Because the ERF error was calculated from the difference between TS and TP, the spatial offset between the sensor and the stimulated site was eliminated by this subtraction. This remained true despite differences in the sensor-to-stimulus offset

across trials. Therefore, the ERF error was independent of the spatial offset between the sensor and the stimulated site. This relationship is illustrated in Fig. 5B.

(Data analysis)

The onset and offset of each reaching movement in the experimental trials were identified offline using an algorithm. The maximum anterior–posterior coordinate value during the 1-s interval preceding the offset of the ready cue was identified and used as the reference value for movement onset. Movement onset was defined as the first frame in which the anterior–posterior coordinate exceeded this reference value after the onset of the target cue. The frame-to-frame difference in the anterior–posterior coordinate was then calculated as a measure of anterior–posterior velocity. Starting 300 frames after movement onset, movement offset was defined as the first frame at which the absolute value of the velocity fell below 0.001 cm/frame. The algorithmically determined movement onsets and offsets were visually reviewed, and erroneous detections were corrected on the basis of the anterior–posterior displacement traces. The duration of the reaching movement was defined as the interval between movement onset and offset.

The tactile stimulus timing was expressed as the interval from movement onset to tactile stimulus onset as a percentage of the reaching movement duration. The scatter plot suggested a negative relationship between the ERF error and tactile stimulus timing, and this finding was consistent with a previous finding by Futamura and colleagues (2026) (Fig. 6A). The correlation coefficients between the ERF error and tactile stimulus timing were significantly less than zero (one-sample t-test, $t(17) = -20.10$, $p < 0.001$, $d = -4.74$; Fig. 6B). Given this relationship, we conducted a repeated-measures two-way analysis of covariance (ANCOVA), with tactile stimulus timing included as a covariate. The within-participant factors were reaching angle (seven levels: 0, 5, 10, 15, 20, 25, and 30 degrees) and vibration applied to the biceps brachii (two levels: vibration, and non-vibration). The alpha level was set at 0.05. Statistical analyses were performed using R (version 4.5.3; R Core Team, Vienna, Austria). The results were expressed as adjusted means and their standard errors.

Results

(ARF error)

The mean ARF errors are shown in Fig. 7. The adjusted mean error directed distally (positive value) across the conditions. The covariate (tactile stimulus timing) was not significant [$F(1, 58.396) = 0.282$, $p = 0.598$, $\eta^2 p = 0.005$]. The main effect of the vibration applied to the biceps brachii was significant [$F(1, 221.440) = 12.330$, $p = 0.001$, $\eta^2 p = 0.05$]. The main effect of the reaching angle was significant [$F(6, 222.123) = 2.881$, $p = 0.010$, $\eta^2 p = 0.07$]. There was a significant interaction between the main effect of the vibration and that of the reaching angle [$F(6, 221.988) = 3.018$, $p = 0.007$, $\eta^2 p = 0.08$]. The test of simple main effect revealed that vibration applied to the biceps brachii significantly deviated distally at

the reaching angle of 5 degrees [$t(222) = -2.22, p = 0.028, d = -0.52$], 25 degrees [$t(222) = -3.76, p < 0.001, d = -0.89$], and 30 degrees [$t(225) = -3.15, p = 0.002, d = -0.74$].

(ERF error)

The mean ERF errors are shown in Fig. 8. The covariate was significant [$F(1, 236.97) = 196.97, p < 0.001, \eta^2 p = 0.45$]. Main effect of the vibration was significant [$F(1, 220.17) = 5.58, p = 0.019, \eta^2 p = 0.025$]. Main effect of the reaching angle was significant [$F(6, 220.37) = 2.24, p = 0.040, \eta^2 p = 0.06$]. There was a significant interaction between main effect of vibration and that of the reaching angle [$F(6, 220.45) = 3.72, p = 0.002, \eta^2 p = 0.092$] (Fig. 8). Test of simple main effect revealed that the vibration significantly deviated the ERF coordinates backward at the reaching angle of 10 degrees [$t(220) = 2.363, p = 0.019, d = 0.56$], but deviated forward at the reaching angle of 25 degrees [$t(220) = -4.16, p < 0.001, d = -0.98$].

Discussion

(ARF coordinate)

In the present study, vibration applied to the biceps brachii induced a distal bias in the ARF coordinate when participants reached toward a target at reaching angles of 5, 25, or 30 degrees to the right of the anterior–posterior axis. Muscle-tendon vibration induces an illusion of movement in the direction that would lengthen the vibrated muscle (Goodwin et al., 1972; Keyser et al., 2019). This vibration-induced proprioceptive illusion is thought to arise from activation of muscle spindle afferents caused by cyclic mechanical stretching of the muscle–tendon complex (Amiez et al., 2026; Hagbarth et al., 1976; Roll & Vedel, 1982). Because of this mechanism, during voluntary movement, vibration of the lengthening antagonist muscle produces systematic movement errors consistent with altered proprioceptive information from that muscle (Capaday & Cooke, 1981, 1983; Cody et al., 1990). Accordingly, the distal bias of the ARF coordinate induced by vibration applied to the biceps brachii may be caused by the illusory lengthening of the biceps brachii, the antagonist muscle during the reaching movement.

Tactile sensation is initially encoded in skin coordinates in Brodmann area 3b, whereas proprioceptive information is encoded in area 3a, and these two sources of information are subsequently integrated in area 5 (Kaas, 1983). Based on this, the present finding may reflect the influence of proprioception on the localization of tactile stimuli on the body surface (i.e., the ARF coordinate), arising from the integration of tactile and proprioceptive information in this area. Several previous findings demonstrating a contribution of proprioception to ARF coordinate determination support this view. For example, the perceived ARF coordinate on the dorsum of the hand depended on hand position (Liu & Medina, 2021). Overvliet et al. (2011) manipulated the relative positions of the fingers by having participants keep them together, spread them apart, or interweave the fingers of the two hands. They found that the accuracy of identifying which fingertip was stimulated depended on finger configuration. This indicates that proprioceptive information about relative finger position contributes to identifying the stimulated finger. Based on these previous findings, the present finding may be explained by the contribution of

proprioceptive information about body posture to the determination of the perceived location of a tactile stimulus on the body surface during movement (i.e., the ARF coordinate). Thus, Hypothesis 1 was supported.

Body representation has been suggested to contribute to ARF coordinate determination (Margolis & Longo, 2015). Spreading the fingers increased the implicit representation of hand size (Longo, 2015). When the fingers were splayed, the perceived distance between two tactile stimuli on the surface of the hand increased (Longo, 2017). These findings indicate that the representation of hand size is influenced by hand posture. Based on these findings, ARF coordinates on the hand may be influenced by posture-dependent changes in the perceived size of the hand. In accordance with this view, the present finding may reflect a vibration-induced change in proprioceptive information about the limb, which may alter the representation of hand size and thereby produce a distal bias in the ARF coordinate.

Another possibility is that a forward bias of the ERF coordinate may contribute to the distal bias of the ARF coordinate. The perceived location of tactile stimuli on the hand surface was biased by the proprioceptively specified position of the hand (Liu & Medina, 2021). Sadibolova et al. (2018) manipulated forearm posture by placing the forearm in pronated or supinated positions and found that the perceived location of tactile stimuli on the forearm shifted with the position of the forearm, indicating that tactile localization is influenced by the body posture. Accordingly, at least under static conditions, ARF coordinates depend on body posture. In the present study, participants performed reaching movements. During reaching, the elbow underwent continuous extension. During this period, the biceps brachii, an antagonist of elbow extension, would have been lengthened. During voluntary movement, vibration of the lengthening antagonist muscle produces systematic movement errors consistent with altered proprioceptive information from that muscle (Capaday & Cooke, 1981, 1983; Cody et al., 1990). Vibration applied to an antagonist muscle can induce an illusion of further movement in the direction that would lengthen the vibrated muscle (Goodwin et al., 1972; Roll & Vedel, 1982). Thus, vibration applied to the biceps brachii during elbow extension would be expected to induce an illusion of greater elbow extension in the present study. Elbow extension during reaching displaces the hand forward. Accordingly, the distal bias of the ARF coordinate observed at reaching directions of 5°, 25°, and 30° to the right of the anterior–posterior axis may be related to an illusory forward shift in the perceived spatial location of the hand receiving the tactile stimulus induced by vibration applied to the biceps brachii.

(ERF coordinates)

The location of a tactile stimulus in external space (i.e., the ERF coordinate) is thought to be determined through tactile remapping, during which information about the ARF coordinate derived from the location of activated cutaneous receptors is integrated with proprioceptive information (Heed et al., 2015; Kitazawa, 2002). As described above, elbow extension displaces the hand forward during reaching. Therefore, an illusion of greater elbow extension induced by vibration applied to the biceps brachii during reaching would be expected to shift the perceived spatial location of the hand forward. Accordingly, this illusory forward shift of the hand might be expected to result in a forward bias in the perceived location

of the tactile stimulus in external space (i.e., the ERF coordinate). However, the present findings did not support this view because vibration applied to the biceps brachii did not consistently induce a forward bias in the ERF error; rather, its effect depended on reaching angle. Vibration applied to the biceps brachii produced a backward bias in the ERF error when participants reached toward a target at a reaching angle of 10 degrees to the right of the anterior–posterior axis, whereas it induced a forward bias at a reaching angle of 25 degrees to the right of the anterior–posterior axis.

If the effect of altered proprioceptive information on the ARF coordinate were simply carried over to the ERF coordinate through tactile remapping, similar reaching-angle dependencies of the vibration effect would be expected for the ARF and ERF errors. However, this was not the case. Vibration applied to the biceps brachii produced a distal bias in the ARF error at reaching angles of 5, 25, and 30 degrees, whereas it produced a backward bias in the ERF error at 10 degrees and a forward bias at 25 degrees. Thus, the effect of altered proprioceptive information on the ERF coordinate cannot be explained solely by the propagation of its effect on the ARF coordinate. Rather, proprioceptive information may provide an additional influence to the process of tactile remapping. These findings therefore suggest that proprioceptive information contributes differently to ARF coordinate determination and tactile remapping, supporting Hypothesis 3.

Reaching movements in different directions require different motor commands (Georgopoulos et al., 1982). During movement, an efference copy of the motor command is used by an internal forward model to predict the sensory consequences of the movement and thereby provide an estimate of the current limb state despite delays in sensory feedback (Miall et al., 1993; Miall & Wolpert, 1996). Because the motor command varies with reaching direction, this predictive estimate of limb state may also differ across reaching directions. Vibration applied to the biceps brachii alters proprioceptive information related to limb state, and responses to muscle vibration during reaching can depend on movement direction and task demands (Keyser et al., 2019). Therefore, the influence of vibration on limb-state estimation may depend on the interaction between the vibration-induced proprioceptive signal and the direction-specific predictive estimate. Such stage-dependent integration of predictive limb-state estimates and proprioceptive information could account for the different reaching-direction dependencies of the vibration effects on determination of ARF coordinate and ERF coordinates. Thus, Hypothesis 2 was supported.

Conclusions

Altered proprioceptive information induced by vibration of the antagonist muscle during reaching affected both the ARF and ERF coordinates. Vibration applied to the biceps brachii produced a distal bias in the ARF coordinate when participants reached toward a target at reaching angles of 5, 25, and 30 degrees to the right of the anterior–posterior axis. This indicates that humans rely on proprioception to determine the ARF coordinates. For the ERF coordinate, vibration applied to the biceps brachii produced a backward bias when participants reached toward a target at a reaching angle of 10 degrees and a forward bias at a reaching angle of 25 degrees to the right of the anterior–posterior axis. These findings

indicate that proprioceptive information is used differently for ARF coordinate determination and tactile remapping during movement. Stage-dependent integration of predictive limb-state estimates and proprioceptive information could account for the different reaching-direction dependencies of the vibration effects on ARF coordinate determination and tactile remapping. Contribution process of proprioception to ARF coordinate and ERF coordinates is dependent on motor command planned for each direction of reaching movement.

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. conducted experiments. M.F. and K.H. conducted data analysis. M.F. and K.H. wrote the manuscript.

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Figures

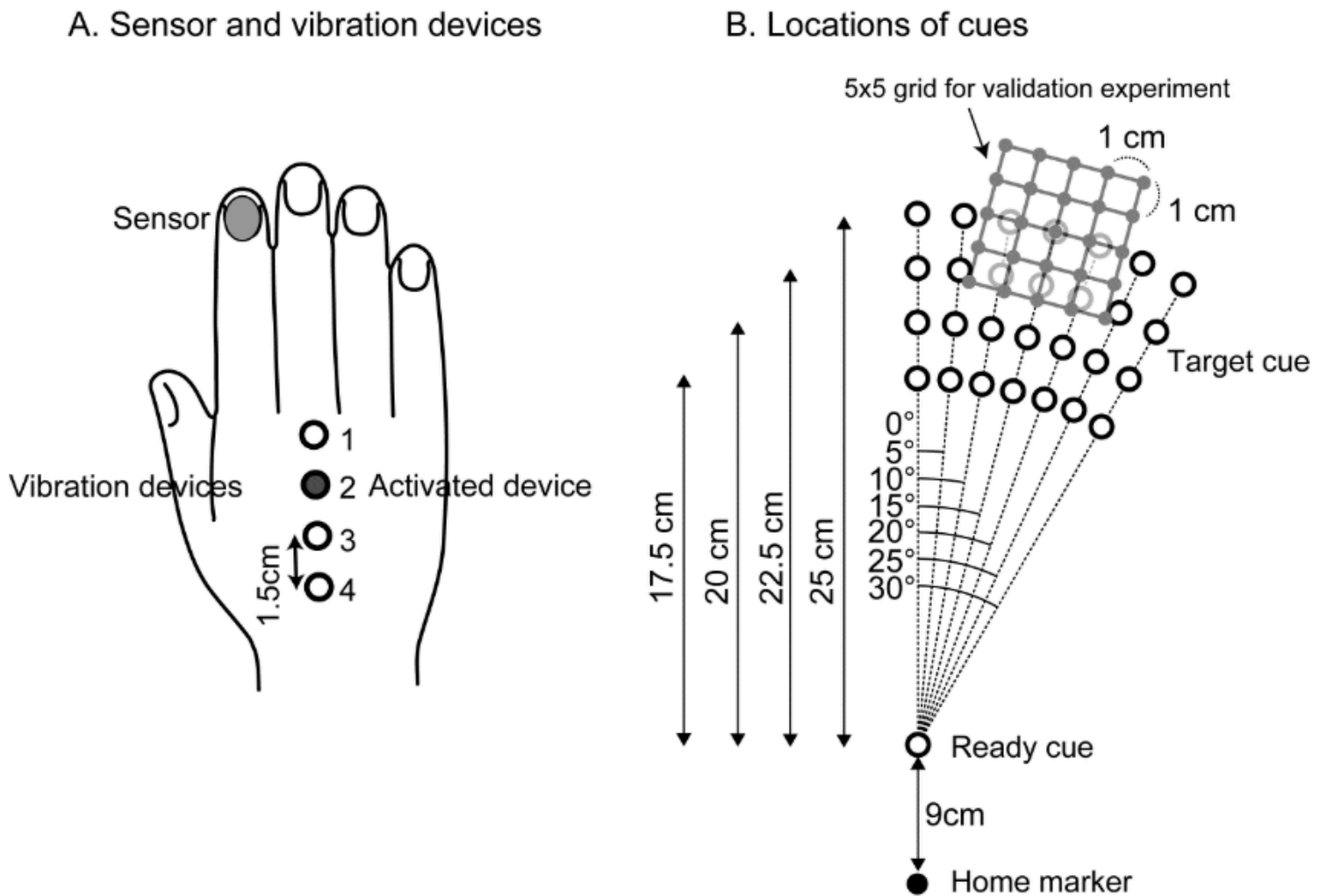


Figure 1

The experimental set up and targets. (A) Four small vibration devices were attached to the dorsum of the hand at 1.5-cm intervals, and an electromagnetic sensor was placed on the index fingertip. The filled circle indicated the activated device in a trial. (B) The targets, cues, and markers were presented on a table. The home marker was located 9 cm behind the ready cue. Each target had one of seven angles relative to the ready cue (0, 5, 10, 15, 20, 25, and 30 degrees) and four distances relative to the ready cue (17.5, 20.0, 22.5, and 25.0 cm). In the preliminary validation experiment, the center of the 5 × 5 grid (1-cm spacing) was positioned at the target. The grid was oriented such that one axis was parallel to the reaching direction and the other was perpendicular to it.

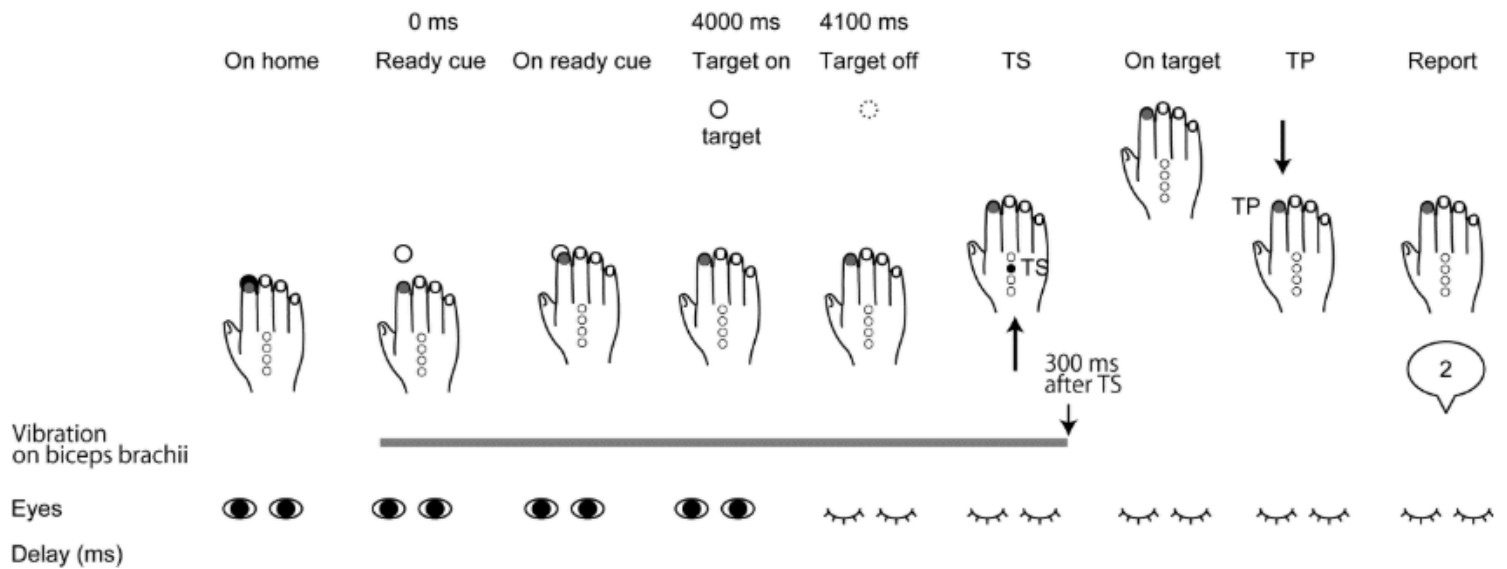


Figure 2

Task paradigm. Participants placed the index fingertip on a home marker. A ready cue appeared for 4000 ms in front of the home marker. As long as the ready cue was presented, participants placed their index fingertip on this cue. A target cue appeared for 100 ms at the end of the ready-cue period. As soon as this cue appeared, they memorized the location of the target and closed their eyes. Then, they reached toward the memorized target. While they were reaching toward the target, one of four vibration devices was activated for 200 ms. In the vibration condition, vibration to the biceps brachii was provided in the time window from the onset of the ready cue until 300 ms after the latest offset of the tactile stimulus. After completing the reach to the memorized target, they placed the stimulated hand at the location where they had perceived the tactile stimulus (TP). Finally, they verbally reported the number of the device that they perceived to have been activated.

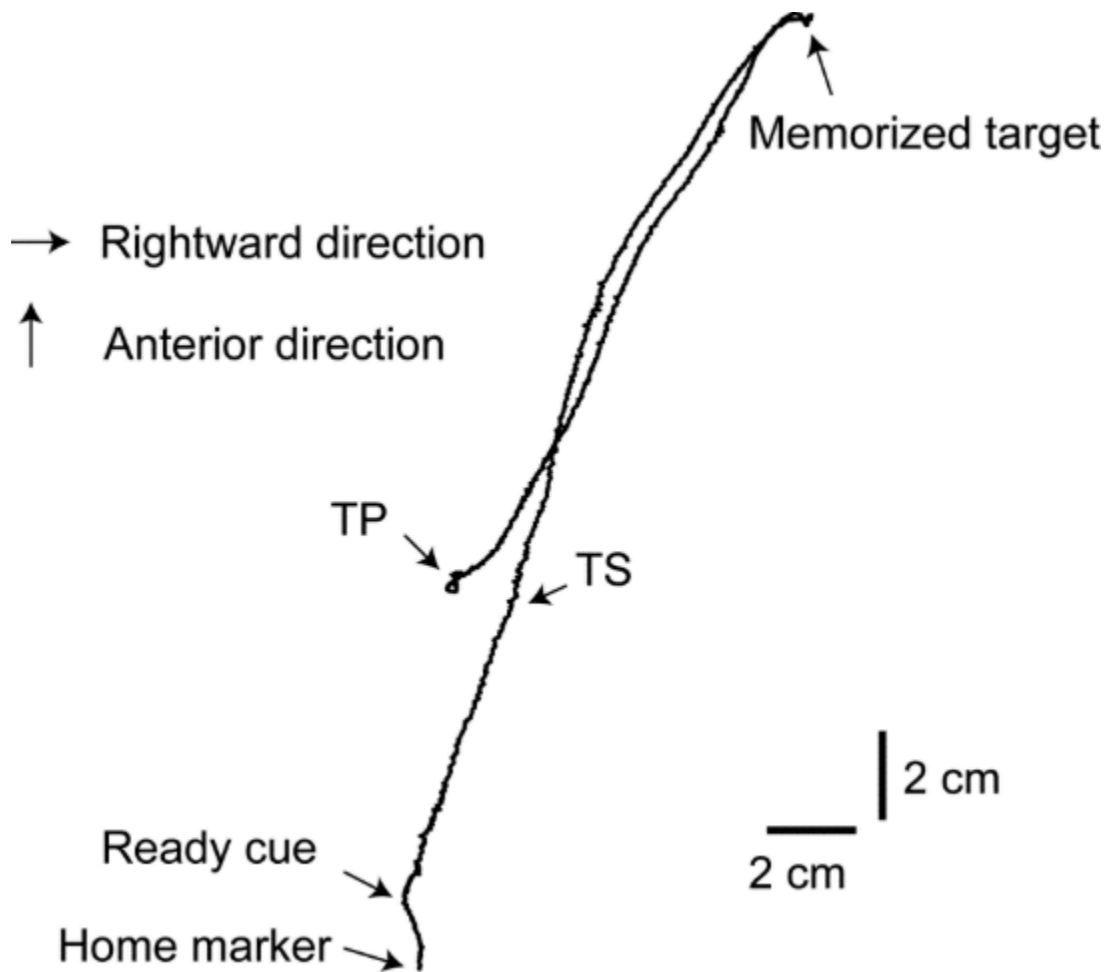


Figure 3

An example of the raw trajectory of the sensor during a reaching movement. TS indicates the mean coordinates of the electromagnetic sensor during tactile stimulation. TP indicates the location of the index fingertip when participants moved the hand back to where they perceived the tactile stimulus.

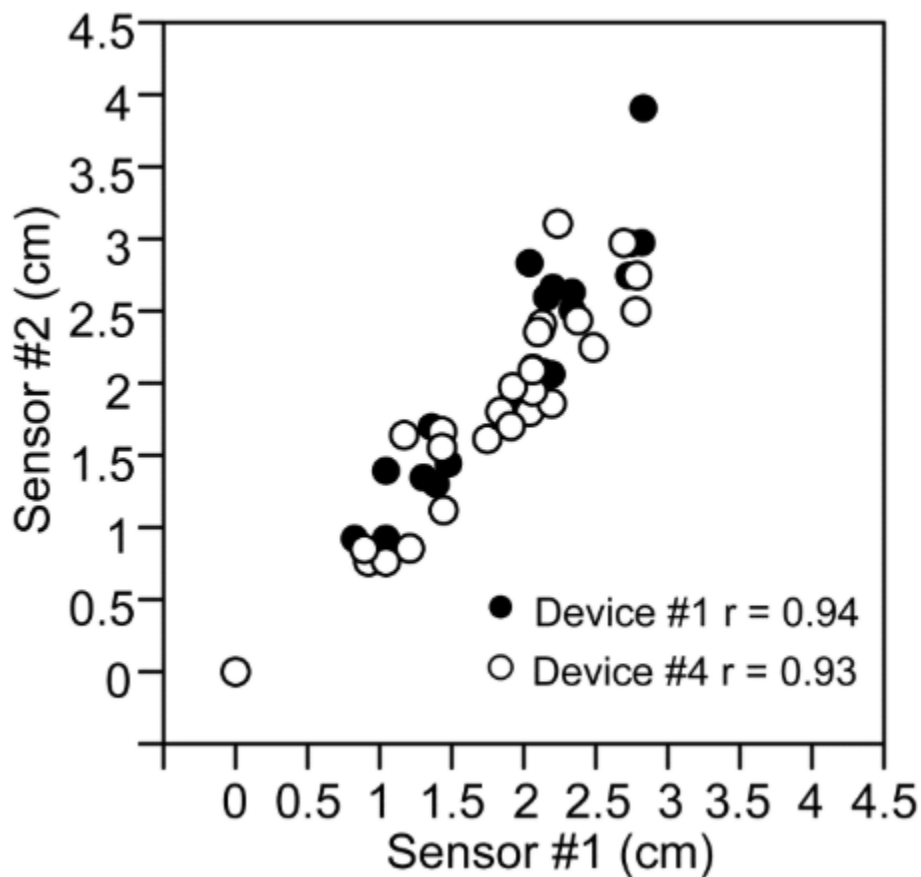


Figure 4

Displacement measurements from two electromagnetic sensors recorded in the preliminary validation experiment. For a target positioned 20 degrees to the right of the ready cue, the displacement of Sensor #2 was plotted against that of Sensor #1 across 25 grid points, illustrating the positive and linear relationship between the two sensors. Filled and open circles indicate measurements for Devices #1 and #4, respectively. The r values indicate Pearson's correlation coefficients.

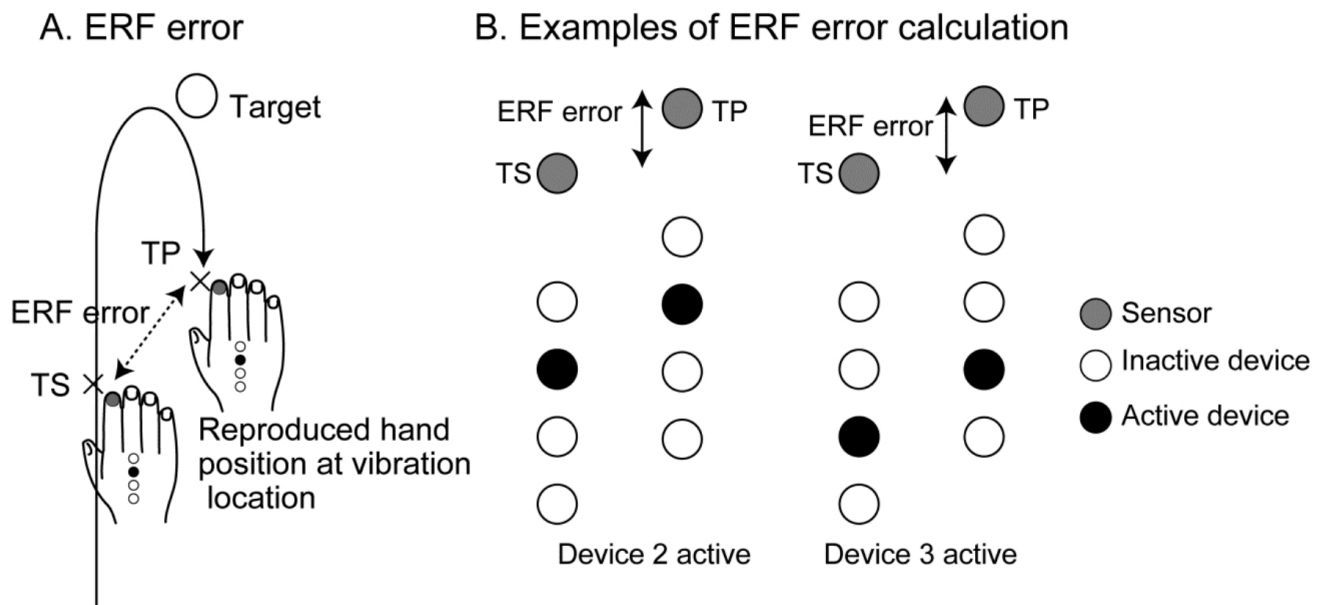


Figure 5

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 mean coordinates of the electromagnetic sensor attached to the dorsum of the index fingertip were calculated during the 200-ms tactile stimulation period (TS). At the end of each trial, participants reproduced the perceived location of the tactile stimulus, and the mean coordinates of the sensor during this reproduction phase were calculated (TP). The ERF error was defined as the signed spatial distance between TS and TP with positive values indicating errors in the forward direction. (B) Rationale for using the sensor position to quantify the ERF error. The tactile stimulus was delivered to the hand, whereas the sensor was attached to the index fingertip. Therefore, the spatial offset between the sensor and the stimulated site varied across the trials. However, both TS and TP were obtained from the same sensor within each trial. Because ERF error was computed as the difference between these two sensor-based positions, any constant spatial offset between the sensor and the stimulated site was cancelled out.

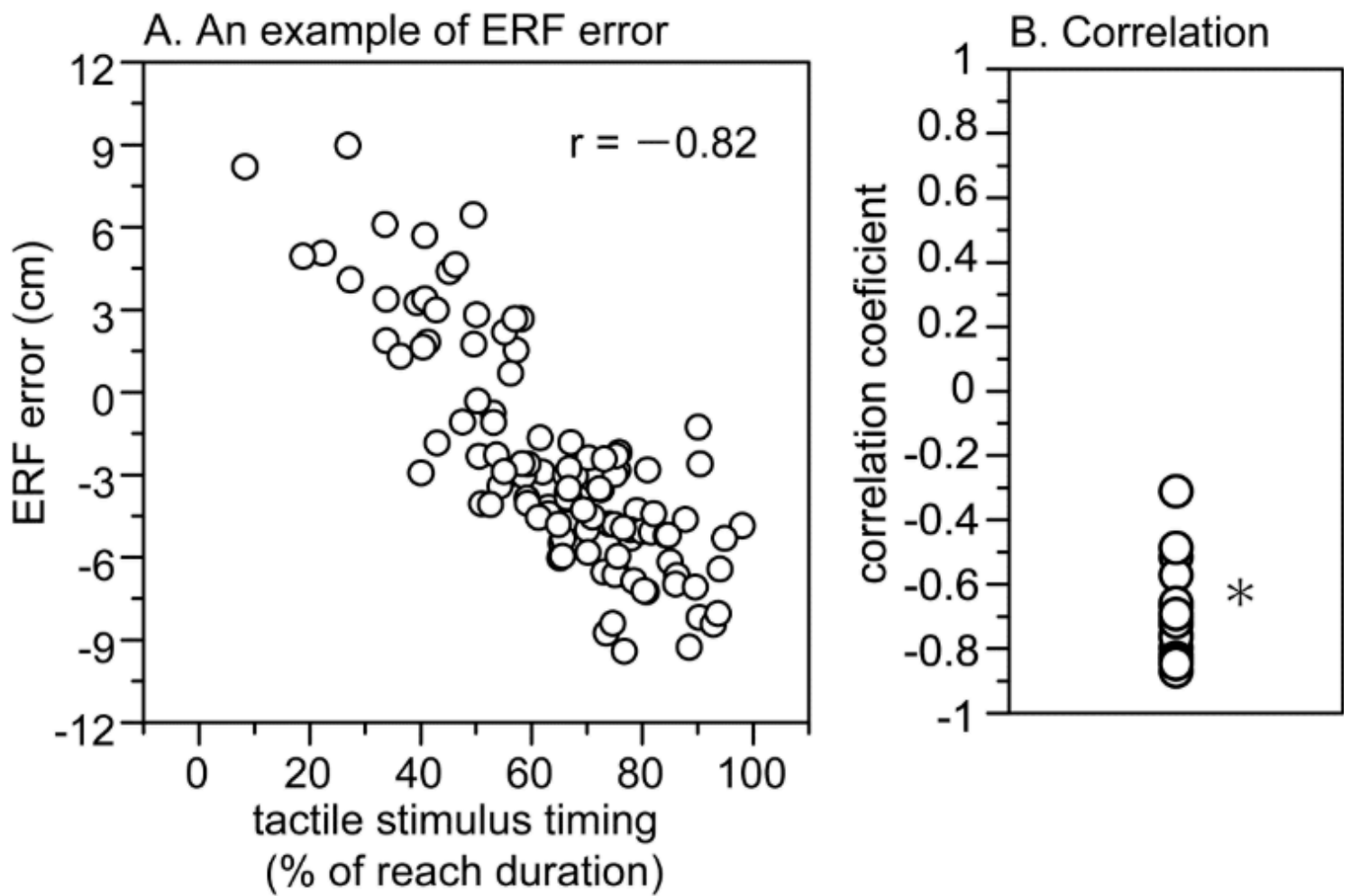


Figure 6

Relationship between tactile stimulus timing and ERF error. (A) An example scatter plot showing the relationship between ERF error and tactile stimulus timing, expressed as a percentage of the reaching duration. A strong negative correlation was observed. (B) Correlation coefficients between ERF error and tactile stimulus timing in all participants. An asterisk indicates a significant difference from zero ($p < 0.001$, one-sample t-test).

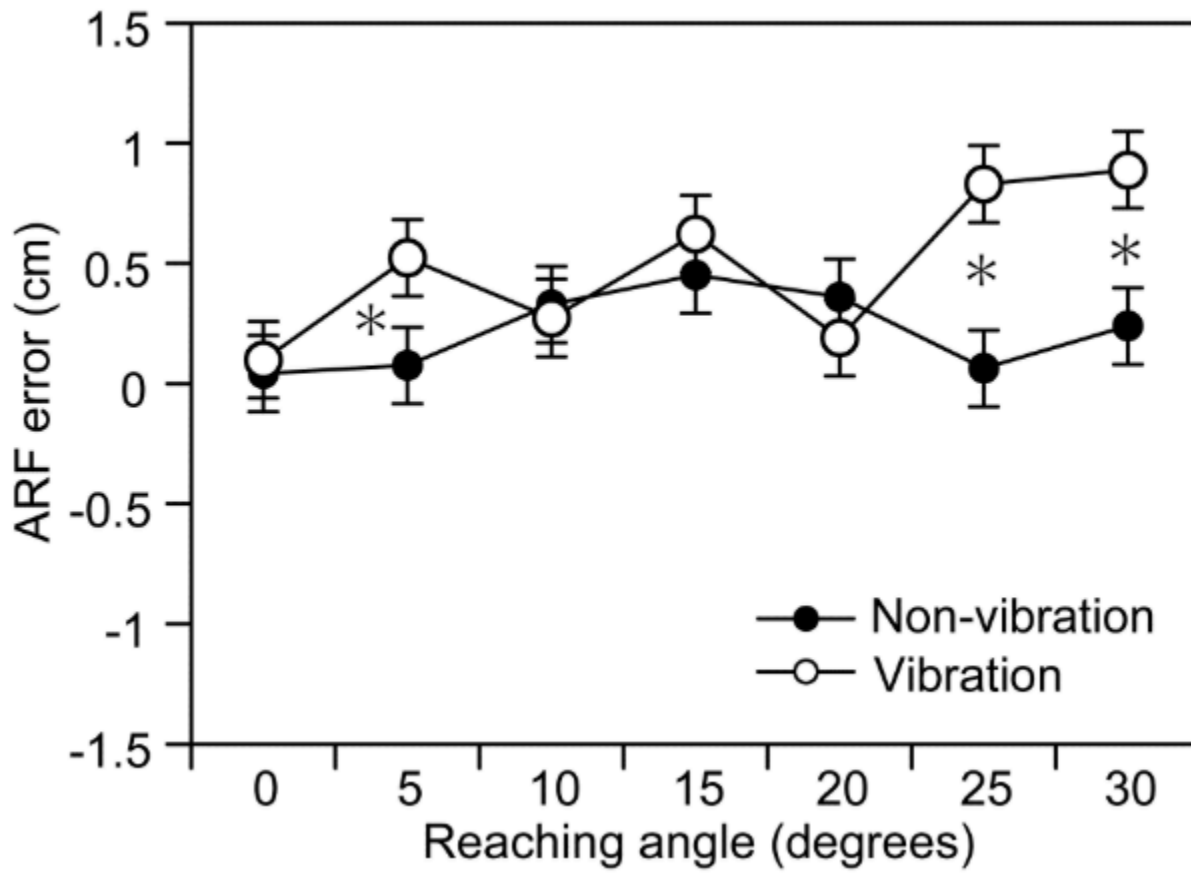


Figure 7

The simple main effects of the vibration applied to the biceps brachii on the ARF error in each reaching angle. Points indicate the adjusted means and error bars indicate the standard error of the adjusted mean. Asterisks indicate significant simple main effects ($p < 0.05$).

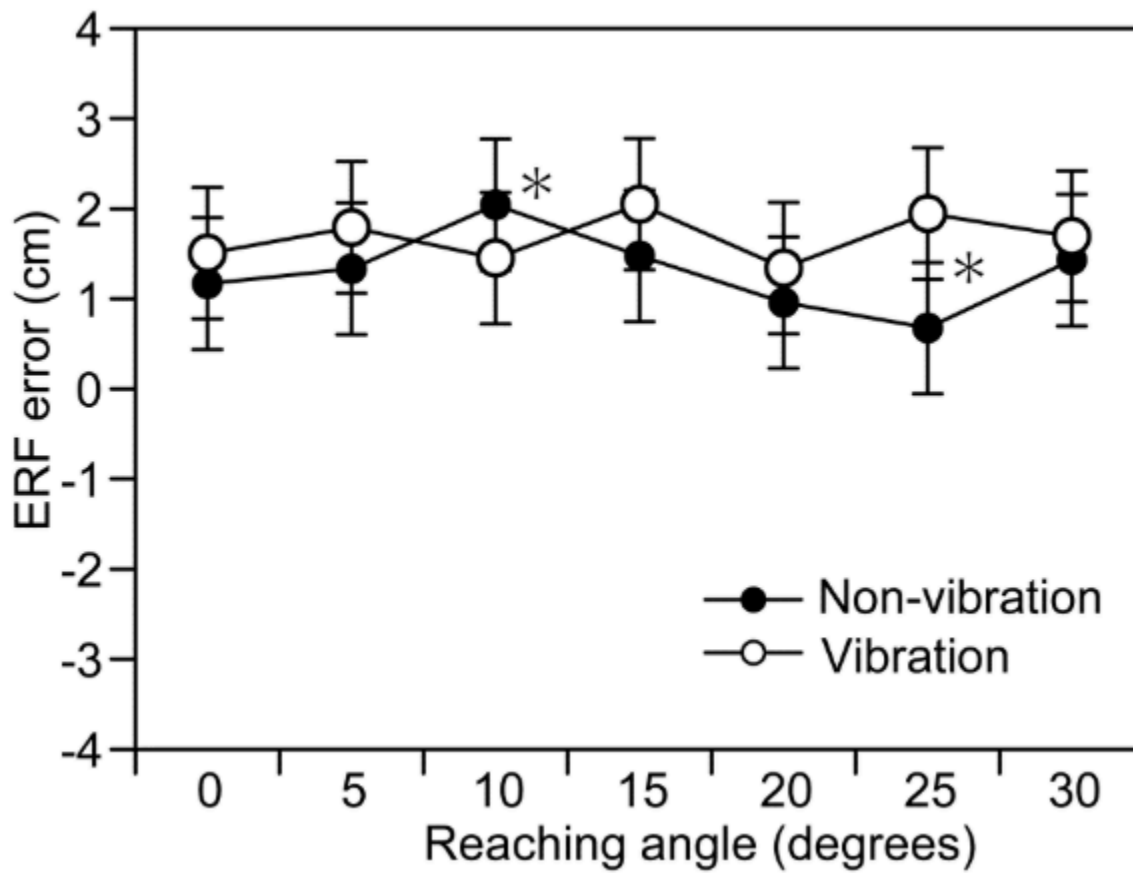


Figure 8

The simple main effects of the vibration applied to the biceps brachii on the ERF error. Points indicate the adjusted means and error bars indicate the standard error of the adjusted mean. Asterisks indicate significant simple main effects ($p < 0.05$).