Article

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Joint Specificity and Lateralization of Upper Limb Proprioceptive Perception

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Abstract

Proprioception is the sense of position and movement of body segments. The widespread distribution of proprioceptors in human anatomy raises questions about proprioceptive uniformity across different body parts. For the upper limbs, previous research, using mostly active and/or contralateral matching tasks, has suggested better proprioception of the non-preferred arm, and at the elbow rather than the wrist. Here we assessed proprioceptive perception through an ipsilateral passive matching task by comparing the elbow and wrist joints of the preferred and non-preferred arms. We hypothesized that upper limb proprioception would be better at the elbow of the non-preferred arm. We found signed errors to be less variable at the non-preferred elbow than at the preferred elbow and both wrists. Signed errors at the elbow were also more stable than at the wrist. Across individuals, signed errors at the preferred and non-preferred elbows were correlated. Also, variable signed errors at the preferred wrist, non-preferred wrist, and preferred elbow were correlated. These correlations suggest that an individual with relatively consistent matching errors at one joint may have relatively consistent matching errors at another joint. Our findings also support the view that proprioceptive perception varies across upper limb joints, meaning that a single joint assessment is insufficient to provide a general assessment of an individual's proprioception.

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Proprioception, kinesthesia, laterality, joint, upper limb

Introduction

Perceiving where are our own body segments are in space is a key element in everyday life. Such perception partly relies on proprioception, the sense of position and movement of body segments based on receptors in the muscles, tendons, joints, and skin (Cole, 2016; Elangovan et al., 2014; Fuentes & Bastian, 2010; Gandevia & Burke, 1992; Goble & Brown, 2008b; Pearson, 2001; Proske & Gandevia, 2012; Tuthill & Azim, 2018). These multiple receptors, distributed throughout the body, provide input to the central nervous system such that we perceive the state of our body parts and can exert control over their movements (Gardner & Johnson, 2013; Hall & McCloskey, 1983; Lephart & Fu, 2000; Tuthill & Azim, 2018). The role of proprioception in motor control has been well documented, notably for postural stability, motor coordination, and fine motor skills (Gandevia & Burke, 1992; Pearson, 2001; Scott, 2016). The role of proprioception with and without visual feedback has been well-illustrated by the consequences of proprioceptive loss on motor functions (Jayasinghe et al., 2021; Rothwell et al., 1982; Sarlegna et al., 2006, 2010). Considering the critical role of proprioception in the perception and control of postures and movements and considering the body's widespread proprioceptors, a key question is "Is proprioception uniform across the body?"

Several researchers have used varied methodologies to address this question by examining whether proprioception differs across upper limbs and joints. For instance, previous research investigated how proprioception at the elbow compares with that at the wrist, and better proprioceptive acuity has been found at the elbow using a movement detection threshold task (Sturnieks et al., 2007) and active matching tasks (Li & Wu, 2014; Sevrez & Bourdin, 2015). Specifically, Sevrez and Bourdin (2015) had an experimenter moving blindfolded participants' joints for them to a specific reference angle. Participants were instructed to memorize this reference angle before their joint was passively moved back to a starting position. Participants had to match their memorized reference angle with active movement of the same limb. Sevrez and Bourdin (2015) showed that active matching errors were less variable at the elbow than at the wrist, though Tripp et al. (2006), in an earlier study, had not detected significant differences in participants' errors between the wrist and elbow in a multi-joint, three-dimensional active matching task.

In this type of active matching task, the tested joint is actively or passively rotated to a specified reference angle, and the participant is asked to actively move the ipsilateral (Sevrez & Bourdin, 2015) or contralateral joint (Li & Wu, 2014) to match that reference angle. An error is then quantified as the difference between the reference angle and the participant's actual matching angle. A limitation of active matching is that it precludes distinct assessments of the underlying proprioceptive perception processes and motor control processes. Indeed, motor commands can also be used to estimate position and motion states (Desmurget & Grafton, 2000; Gandevia, 2014; Gandevia et al., 2006; Smith et al., 2009). Because such central motor control signals may contribute differently to joint position sense at the elbow and wrist (Walsh et al., 2013), passive movement tasks appear to be most suited for assessing proprioceptive perception (Carey et al., 1996; Goble & Brown, 2010: Khabie et al., 1998).

The uniformity of upper limb proprioceptive perception can be studied across joints but also across the preferred and the non-preferred limbs. Several investigators, utilizing ipsilateral active matching, reported a better joint position sense at the non-preferred thumb (Colley, 1984; Roy & MacKenzie, 1978) and elbow (Kurian et al., 1989). Similarly, others, utilizing a contralateral active matching task, reported a better joint position sense at the non-preferred elbow (Goble et al., 2006; Goble & Brown, 2007) and wrist (Adamo & Martin, 2009). Also, at the elbow, Goble and Brown (2010) used both ipsilateral and contralateral passive matching and showed better joint position sense of the non-preferred versus preferred limb. In contrast, others failed to find interlimb differences (a) at the shoulder, elbow, and wrist joints when using a contralateral active matching task (Li & Wu, 2014; Ramsay & Riddoch, 2001); (b) at the shoulder and elbow when using an ipsilateral active matching task (King et al., 2013); and (c) at the elbow (Khabie et al., 1998) and wrist (Carey et al., 1996) when using an ipsilateral passive matching task. This lack of consensus about upper limb proprioception might be related to the different research methodologies (ipsilateral/contralateral, active/passive).

One additional issue with contralateral matching is that sensory contributions (and motor contributions in active protocols) are required from both left and right body segments (Allen et al., 2007; Izumizaki et al., 2010; White & Proske, 2009). As the contributions from both the arms and the hemispheres of the brain are known to differ (Goble & Brown, 2007; Sainburg, 2014), the interpretation of the results of studies using contralateral matching tasks is not straightforward.

Our main goal in the present study was to assess proprioceptive perception at the elbow and wrist of both upper limbs across consecutive responses and determine whether proprioceptive errors vary across joints and responses. We were also interested in determining whether participants with relatively good proprioceptive perception at a specific joint also had good perception at another joint. Previous research which investigated whether proprioceptive perception is a general ability (or, in other words, is similar all over the body) or is site-specific, found only significant correlations between right and left joints of both upper and lower limbs (finger, shoulder, ankle, or knee) with no significant correlations found between ipsilateral joints such as the right shoulder and finger of the right hand (Waddington & Adams, 1999; Han et al., 2013a,b). The lack of significant correlation between data from different joints suggested that proprioception is not a global, general ability and would be better described as site-specific.

Based on prior research, we hypothesized that proprioceptive perception would be better at the elbow compared to the wrist, and at the non-preferred versus preferred limb. We tested these hypotheses using an ipsilateral passive matching task.

Method

Participants

To determine the minimum sample size required for this study, we performed a statistical power analysis using G*Power software (version 3.1.9.6; Kiel University, Kiel, Germany) and based our sample size calculation on the effect size of previous studies reporting proprioceptive differences between upper limbs (Goble & Brown, 2010; partial η^2 = .29) and between joints (Sevrez & Bourdin, 2015; partial η^2 = .189). To determine the minimum required sample size, we used the smallest partial η^2 (which corresponded to the smallest effect size) in Sevrez and Bourdin (2015). For a *F*-test, repeated measures, within factors 2 × 2 × 8 analysis of variance (ANOVA) with 32 measurements and a partial η^2 of .189 (corresponding to effect size of 0.48), the a priori power analysis indicated that for an alpha level of .05 and statistical power of .95, the minimum required sample size was estimated to be four. In the present study, we tested seven healthy adult participants (3 females, four males; *M*age = 59.3, *SD* = 7.0 years; age range = 49–67 years). None of the participants reported any neurological or musculoskeletal deficits. Participants were recruited from the University and the city of Marseille through an advertisement email. All participants showed a strong right-hand preference, quantified with the 10-item version of the Edinburgh handedness inventory (Appendix II in Oldfield, 1971). The participants' mean laterality quotient on this scale was 94.2% (*SD* = 9.7%). All participants gave their written informed consent before they participated, and no participants were compensated for their involvement. The experiment was approved by the national ethics committee CERSTAPS (IRB00012476-2020-03-06–60).

Experimental Setup

Each participant was seated in an adjustable chair with each hand grasping a handle and both forearms lightly wrapped with fabric fasteners (Velcro) to the moving levers of the apparatus (as in Sevrez & Bourdin, 2015). The setup was precisely adjusted for each participant to align its mechanical rotation axes with the elbow and wrist rotation axes. It allowed near-frictionless movement of the wrist in the sagittal plane and the elbow in the horizontal plane.

Joint rotations were recorded with precision potentiometers (linear, 10 kΩ, Vishay) mounted beneath the pivot point of the corresponding lever arms. Each potentiometer was connected to an analog-to-digital converter, and signals were sampled at 10 Hz. Data were recorded using a LabView Virtual Instrument (National Instruments Corporation, Austin, TX, USA).

During the task, all participants were blindfolded, and the experimenter moved one of the participant's upper limb body segments. The experimenter avoided reaching extreme ranges of motion and used visual feedback on a computer screen to control movement speed below 5°/s, a threshold that corresponds to the speed above which passive movement detection plateaus (Laprevotte et al., 2021).

Experimental Procedure and Conditions

Two experimenters presented the apparatus to the participants. While one joint was being tested, the others were locked. Figure 1 illustrates the ipsilateral passive matching task. For each of the seven participants, a session corresponded to eight responses collected for each of the four experimental conditions. Each session was composed as following: as in Sevrez and Bourdin (2015), one experimenter moved the body segment corresponding to the tested joint (forearm for elbow and hand for wrist) from a randomly varied starting position toward the reference angle. The reference angles were 20° of flexion for the elbow with respect to the full extension of the participant's arm in the device, and 20° of flexion for the wrist with respect to its neutral position. Once the reference angle was reached, the experimenter stabilized the joint at that angle as the participant was instructed to memorize the reference joint angle and to verbally indicate when they were ready to proceed. Participants were given the time deemed necessary to memorize the reference angle (typical time: 2–8 seconds), and the experimenter then

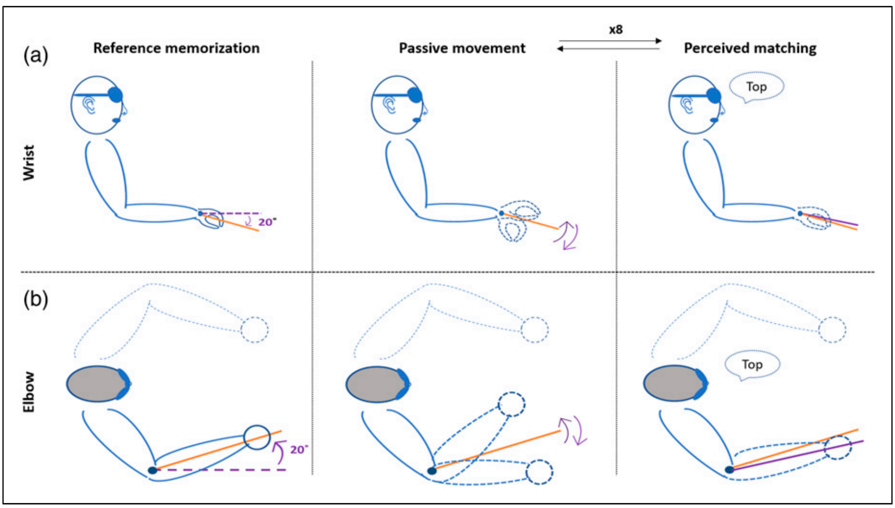

Figure 1. Illustration of the Ipsilateral Passive Matching Task. (a). Side view of the participant. (b). Top view of the participant. First (left panel), the tested joint was passively moved toward the reference angle (between the orange line and the dashed line) for memorization. Then (middle panel), it was passively and continuously moved around the reference angle. During this passive movement, participants were requested to verbally indicate (right panel) each time they detected that the current angle matched the reference angle. A session consisted of eight responses.

moved the participant's body segment cyclically around the reference angle over approximately the same range (±20° for the elbow and ±25° for the wrist) and at approximately the same speed (below 5°/s) for each participant. During the cyclic movement, participants were instructed to say "top" each time they estimated that the joint angle corresponded to the memorized reference angle. On each "top" signal, the second experimenter recorded the signaled angle value by clicking on a mouse while the experimenter continued the passive cyclic movement without interruption until eight responses were recorded, which marked the end of the session. In no cases were participants given knowledge regarding their performance, as in Goble and Brown (2010).

The first session corresponded to the right wrist, the second to the right elbow, the third to the left wrist, and the fourth to the left elbow. In order to be able to compare individual differences, we fixed the order of the sessions, as illustrated in Figure 2. However, to assess whether performance varied along the whole experiment and to assess test-retest reliability, we used a fifth session consisting of repeating the first session (performed with the right wrist) at the end of the experiment. Participants were given a short break between sessions, but they were not given any feedback about their performance during the experiment.

Data Analysis

We computed four types of errors (in degrees) as had been done in previous research (Goble & Brown, 2008b; Sevrez & Bourdin, 2015; Forestier et al., 2002) to characterize the accuracy and consistency of the matching performance:

- The signed error was calculated as the angular difference between the reported joint angle and the true reference angle (as in Goble & Brown, 2007) and was used to determine the existence of any directional bias in matching accuracy. Positive signed errors were assigned to more flexed joint angles compared to the reference, and negative signed errors were assigned to more extended joint angles.
- The variable signed error was calculated as the standard deviation around the mean of each participant's eight signed errors. It was used to assess the consistency of the directional bias.
- The absolute error was calculated as the absolute difference between the reported joint angle and the reference angle (as in Goble & Brown, 2007) and was used to

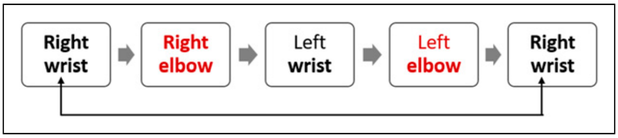

Figure 2. Order of the Experimental Sessions.

determine the extent of matching accuracy. The absolute error allowed us to focus on the magnitude of errors, irrespective of their positive or negative direction.

- The variable absolute error (Sevrez & Bourdin, 2015) was calculated as the standard deviation around the mean of each participant's eight absolute errors. It was used to assess the consistency of the extent of matching accuracy.

Eight responses were recorded for each of the five sessions, resulting in a total of 40 responses for each participant and 280 responses for all participants. We used a 2 × 2 × 8 analysis of variance (ANOVA) with repeated measures to determine the main effects of joint (wrist, elbow), laterality (right, left), and response (1–8) as well as their interactions for both signed and absolute errors. We used 2 × 2 ANOVAs with repeated measures to determine the main effects of the Joint (wrist, elbow) and Laterality (right, left) as well as their interaction for both variable signed errors and variable absolute errors.

We used linear correlation analyses to determine the relationship of the participants' errors between the two wrists, the two elbows, and the wrist and elbow of each limb; and to determine the relationship of the participants' errors with their age. Pearson correlation coefficients (r) were calculated and interpreted according to their sizes [strong (r = .7–.89), moderate (r = .5–.69), or weak (r = .1–.39), as in Schober and Schwarte (2018)].

We assessed within-day test-retest reliability, or in other words, the potential effect of test variability (due to repetition, fatigue, change of mood, etc.) when comparing data from the first and last session. We analyzed the correlations of these data and calculated the Pearson correlation coefficients (r_s). In addition, we used a 2 × 8 ANOVA with repeated measures to determine the main effects of Test (first test, last test) and Response (1–8) as well as their interaction on mean errors. We used a paired t-test to determine the effect of Test on variable errors.

All data presented a normal distribution as verified with the Kolmogorov-Smirnov method. Statistical significance was set at $p < .05$. Post hoc comparisons were performed based on Tukey's honestly significant difference method (Adamo & Martin, 2009; Goble & Brown, 2007). All ANOVA analyses and all post hoc comparisons were pre-planned. Data are available upon reasonable request.

Results

Signed Error: Differences Between Joints and Responses

Calculating the signed error allowed us to assess the direction of the error, with positive errors corresponding to perceiving the joint as more flexed than the reference angle. Figure 3 shows that signed error varied as a function of the joint and the response number. A 2 × 2 × 8 ANOVA [Joint (elbow, wrist) x Laterality (left, right) x Response (1–8)] revealed a significant joint effect (F [1,6] = 14.9, p = .008, partial η^2 = .713] on the signed error, which differed at the wrist (M = −4.7, SD = 2.5°) compared to the

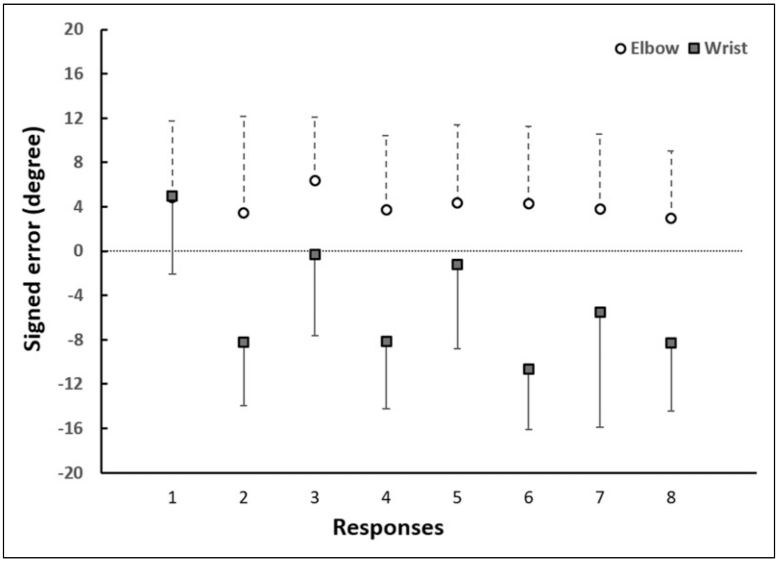

Figure 3. Signed Error at the Wrist (filled squares), and Elbow (empty circles), for Each Response. Error bars represent standard deviation around the participants' mean.

elbow ($M = 4.2$, $SD = 4.6°$). However, one cannot conclude from this analysis whether proprioceptive perception is more accurate for one joint or the other, as error magnitude was ~4.5° in both conditions. This ANOVA also revealed a significant response effect ($F\ [7,42] = 5.3$, $p < .001$, partial $\eta^2 = .473$). Tukey's *post-hoc* analysis showed that the signed error in the first response significantly differed from the second, fourth, sixth, and eighth responses, and the signed error in the sixth response also differed from that in the third response.

There was a significant joint and response interaction effect ($F\ [7,42] = 6.3$, $p < .001$, partial $\eta^2 = .511$) as shown in Figure 3, with a response effect on signed error only at the wrist and not at the elbow. An oscillatory pattern and a shift from positive to negative errors can be seen on wrist data, but the main statistical finding from *post-hoc* tests was that the first response differed from most other responses. Indeed, Tukey's *post-hoc* analysis showed that at the wrist, the signed error of the first response significantly differed from almost all the subsequent responses (i.e., responses 2, 4, 6, 7, and 8). From the second response to the last one, participants responded when their wrist was slightly less flexed than the reference angle. The second response differed from the third and the fifth. The third differed from the fourth, sixth and eighth. The fourth differed from the fifth and the fifth differed from the sixth and eighth. In contrast, at the elbow, there was no significant difference between responses which were consistently biased toward a slight flexion compared to the reference angle. There was no significant laterality effect ($F\ [1,6] = 1.1$, $p = .34$, partial $\eta^2 = .152$), and there were no other significant interactions [Laterality × Joint (F [1,6] = .01, p = .91, partial η^2 = .002), Laterality x Response (F [7,42] = .3, p = .96, partial η^2 = .041), double interaction (F [7,42] = .7, p = .70, partial η^2 = .101)].

Variable Signed Error: Differences Between Upper Limbs and Joints

A 2 × 2 ANOVA on the variable signed error revealed a significant joint effect (F [1,6] = 34.6, p = .001, partial η^2 = .853), as the variable signed error at the elbow (M = 5.1. SD = 1.7°) was significantly smaller than at the wrist (M = 7.9, SD = 1.9°). A significant laterality effect (F [1,6] = 17.4, p = .006, partial η^2 = .743) was associated with a smaller variable signed error at the left arm (M = 5.7, SD = 1.5°) compared to the right (M = 7.3, SD = 1.9°). There was also a significant interaction effect of laterality and joint (F [1,6] = 10.3, p = .018, partial η^2 = .633), illustrated in Figure 4, showing that the variable signed error was smaller at the left elbow (M = 3.7, SD = 1.4°) compared to the right elbow (M = 6.4, SD = 2.1°, p = .008), the left wrist (M = 7.8, SD = 2.0°, p = .001), and the right wrist (M = 8.1, SD = 1.8°, p < .001). There were no significant differences between the variable signed error at the left and right wrists (p = 0.94), the right elbow and the right wrist (p = .08), and the right elbow and the left wrist (p = .17). In summary

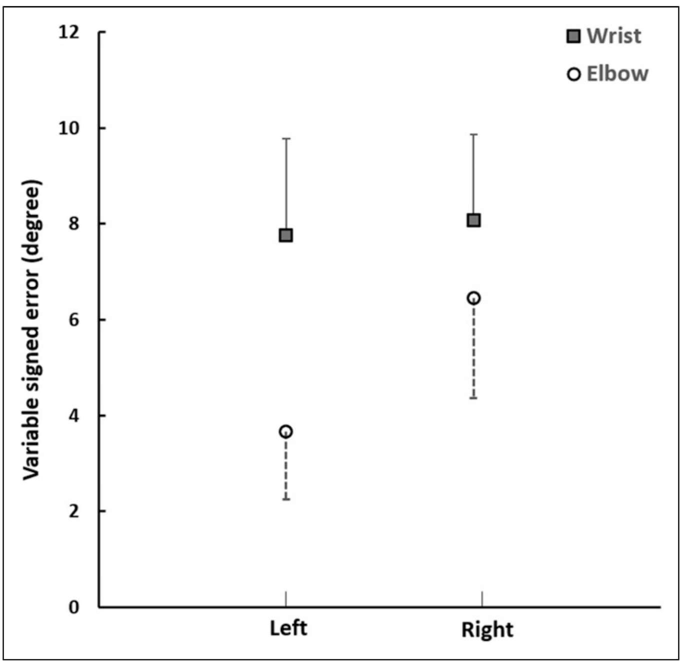

Figure 4. Variable Signed Error at the Wrist (filled squares), and Elbow (empty circles), for Each Response. Error bars represent standard deviation around the participants' mean.

for this analysis, the smallest variable signed error was found at the left elbow compared to the right elbow and both wrists.

Absolute Error: No Significant Differences Between Limbs, Joints, or Responses

A 2 × 2 × 8 ANOVA on mean absolute error revealed only a significant interaction effect of joint and response (F [7,42] = 4.2, p = .001, partial η^2 = .409), but *post-hoc* analysis showed no significant pairwise differences. Overall, there were no significant main effects for laterality (F [1,6] = 1.2, p = .32, partial η^2 = .163), joint (F [1,6] = 3.1, p = .12, partial η^2 = .342), and response (F [7,42] = .5, p = .81, partial η^2 = .081) and no other significant interactions for laterality and joint (F [1,6] = .5, p = .50, partial η^2 = .080), laterality and response (F [7,42] = .5, p = .86, partial η^2 = .071), or double interaction (F [7,42] = .4, p = .88, partial η^2 = .067). Overall, participants' absolute error averaged 5.6 (SD = 2.7°) at the left elbow, 6.8 (SD = 3.3°) at the right elbow, 7.7 (SD = 1.6°) at the left wrist and 7.9 (SD = 2.5°) at the right wrist.

Variable Absolute Error: Differences Between Limbs and Joints

Consistent with the statistical analysis of the variable signed error, a 2 × 2 ANOVA on the variable absolute error revealed significant main effects of joint (F [1,6] = 7.4, p = .03, partial η^2 = .554) and laterality (F [1,6] = 11.8, p = .01, partial η^2 = .663). Figure 5 shows that the variable absolute error at the elbow (M = 4.1, SD = 1.7°) was smaller than at the wrist (M = 5.3, SD = 1.2°). Also, the variable absolute error at the left limb (M = 4.0, SD = .9°) was smaller than at the right limb (M =5.3, SD = 1.8°). Group means

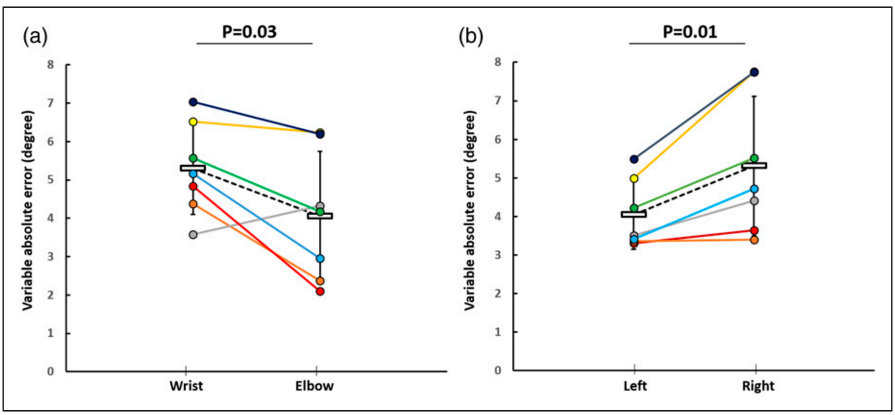

Figure 5. Variable Absolute Error for each Participant (colored dots) and Group Means (empty rectangles). Error bars represent the standard deviation around the participant's mean. (a) Joint effect. (b) Laterality effect.

and individual data are reported in Figure 5 to highlight the systematic nature of the results. There was no significant interaction effect for laterality and joint ($F\ [1,6] = 1.7$, $p = .24$, partial $\eta^2 = .220$). In summary, the variable absolute error was smaller at the elbow compared to the wrist, and at the left limb compared to the right limb.

Correlations Between Errors Across Participants

Correlations were used to determine whether participants with smaller or greater errors for a specific condition tended to have smaller or greater errors for another condition. For the signed error, we found a strong linear, positive correlation between errors at the left and right elbows across participants (right elbow = .8 × left elbow +1.3, $r = .79$, $p = .03$). This is shown in Figure 6 in which, for instance, one participant (blue dot) had the largest signed error at the right elbow and at the left elbow. No other significant correlations were found between errors at the left and right wrists ($r = -.03$, $p = .94$), left wrist and left elbow ($r = -.72$, $p = .07$), nor right wrist and right elbow ($r = -.33$, $p = .47$).

For the variable signed error, we found strong positive correlations between errors at the right wrist and the right elbow (right elbow = 1.0 × right wrist - 1.3, $r = .83$, $p = .01$) and at the right and left wrists (left wrist = 1.0 × right wrist +0.02, $r = .86$, $p = .006$). As shown in Figure 7, one participant (yellow dot) presented the highest variable signed error at both the right elbow and wrist (left panel), and the second higher variable signed error at the left wrist (right panel). Another participant (light blue dot) had the least variable signed error at the right elbow (left panel) and the left wrist (right panel) while having the second least variable signed error at the right wrist. There was also a strong correlation between errors at the right elbow and left wrist (right elbow = .9 × left wrist +0.4, $r = .83$, $p = .01$). No significant correlations were found between errors at the left wrist and left elbow ($r = .35$, $p = .39$), nor at the left and right elbows ($r = .58$, $p = .13$).

For the absolute error, no significant linear correlations were found [left wrist and left elbow ($r = -.08$, $p = .86$), right wrist and right elbow ($r = .57$, $p = .18$), left and right wrists ($r = .41$, $p = .36$), left and right elbows ($r = .58$, $p = .17$)]. For the variable absolute error, no significant linear correlations were found [left wrist and left elbow ($r = .33$, $p = .47$), right wrist and right elbow ($r = .42$, $p = .35$), left and right wrists ($r = .48$, $p = .28$), left and right elbows ($r = .63$, $p = .13$)]. For the absolute errors as well as all other errors, there were no significant correlations with participants' ages (all $p > .35$).

Test-Retest Reliability

The right wrist was tested at the beginning and at the end of the experiment. Strong significant correlations were found between the first and the last tests for the signed error (right wrist last = .8 × right wrist first +0.5, $r = .80$, $p = .03$) and the absolute error (right wrist last = 1.2 × right wrist first – 1.8, $r = .85$, $p = .01$), as shown in Figure 8. No other significant correlations were found for the variable signed error ($r = .37$, $p = .4$) nor the variable absolute error ($r = .01$, $p = .8$).

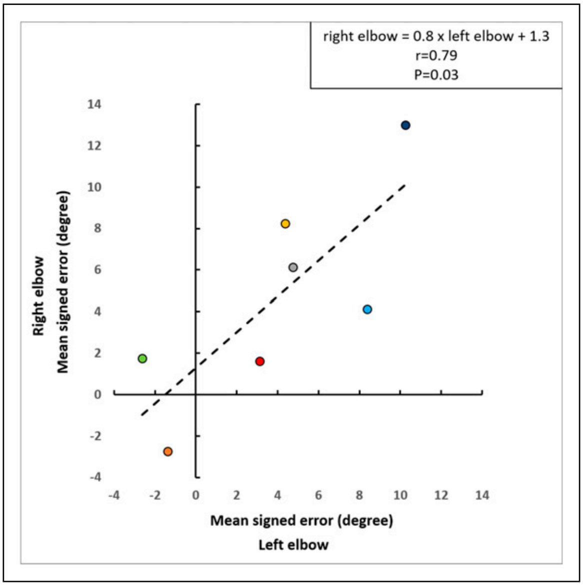

Figure 6. Relationship Between Mean Signed Errors at the Left and Right Elbows, for Each Participant (according to the same color code as in Figure 5). The linear regression (dashed line) is displayed to aid visualization.

A 2 × 8 ANOVA [Test (First, Last) × Response (1–8)] on the signed error revealed no significant main test effect (F [1,6] = 3.7, p = .10, partial η^2 = .383). However, there was a significant response effect (F [7,42] = 3.5, p = .005, partial η^2 = .365) and a significant interaction effect of test and response (F [7,42] = 2.4, p = .04, partial η^2 =0 .287), as shown in Figure 9. While for the first test, some responses significantly differed from others (response one differed from response 2, 4, 6, and 8; and response three significantly differed from response 6), no significant differences were found between responses for the last test.

For the absolute error, there was no significant main effect of test (F [1,6] = .3, p = .63, partial η^2 = .042), nor response (F [7,42] = .8, p = .63, partial η^2 = .117), nor was there a significant interaction (F [7,42] = 1.9, p = .08, partial η^2 = .247). Also, paired *t*-tests revealed no significant test effect for the variable signed error (t [6] = .2, p = .86; Cohen's d = .07) and the variable absolute error (t [6] = 1.0, p = .38; Cohen's d = .36).

Discussion

This study sought to test the hypotheses that upper limb proprioception assessed through a passive matching task would be better at the elbow than at the wrist and at the non-preferred versus preferred arm. In general, our findings are consistent with both hypotheses (at least in this small sample of right-handers). We found that

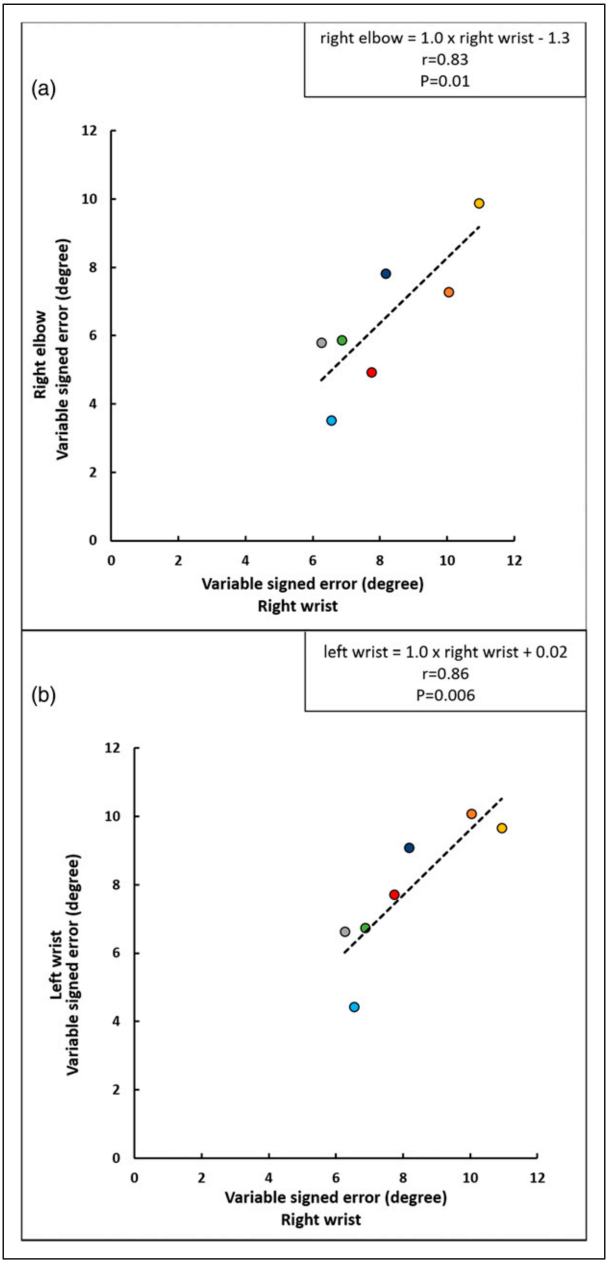

Figure 7. Relationship Between Variable Signed Errors of Each Participant (according to the same color code as in Figures 5 and 6). Each linear regression (dashed line) is displayed to aid visualization. (a) Right wrist and right elbow. (b) Right and left wrists.

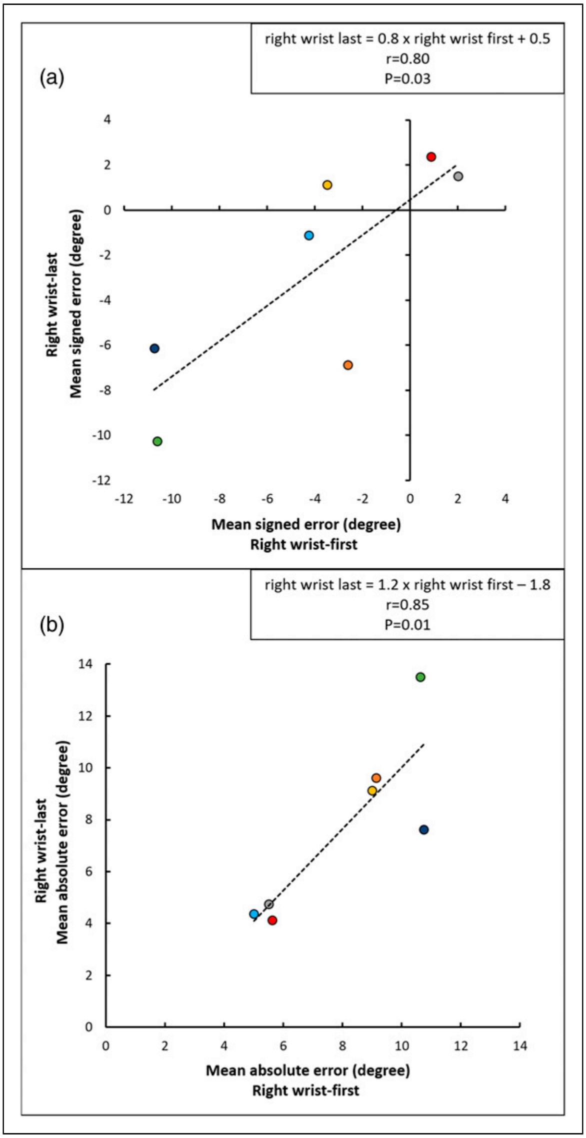

Figure 8. Relationship Between Errors in the First and Last Tests for the Right Wrist of Each Participant (according to the same color code as in Figures 5–7). Each linear regression (dashed line) is displayed to aid visualization. (a) Mean signed error of each participant. (b) Mean absolute error of each participant.

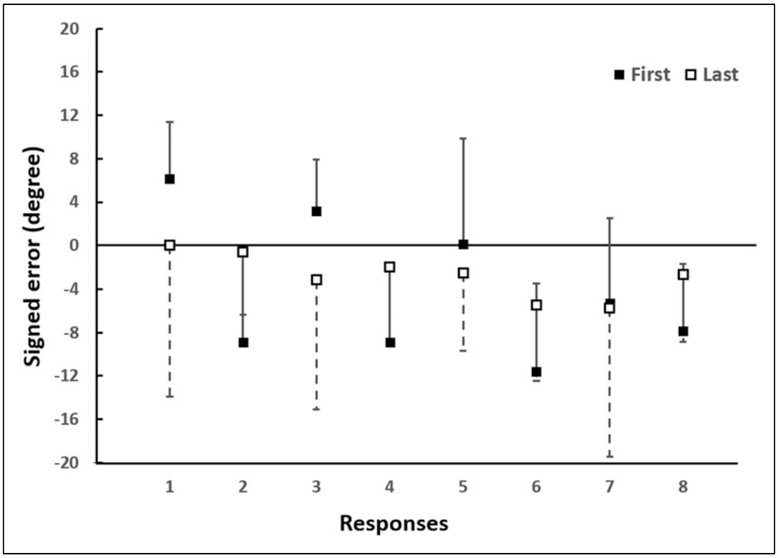

Figure 9. Right Wrist's Signed Errors for Each Response of the first (filled squares) and the Last (empty squares) Test Performed During the Experiment. Error bars represent the standard deviation around the participants' mean.

proprioception was more precise at the elbow than at the wrist as revealed by the small variable errors at the elbow. This was associated with better stability of the responses at the elbow. We also found that proprioception at the left limb was less variable than at the right limb. We now further discuss these findings.

Proprioceptive Perception is More Precise at the Elbow Compared to the Wrist

Proprioception at the elbow was less variable than at the wrist, and this was especially clear for the non-preferred arm, for both signed and absolute errors. This finding concurs with findings from Li and Wu, (2014), and Sevrez and Bourdin (2015) whose studies showed that perceiving unseen passive positions and motions at the elbow joint was more accurate than at the wrist. Similarly, Hall and McCloskey (1983) found that proprioceptive acuity was higher at upper limb joints more proximal to the brain (shoulder and elbow) than a more peripheral joint (middle finger's most distal joint). The better proprioceptive perception at proximal joints may reflect the important role these joints play in determining the location of the endpoint (Scott & Loeb, 1994). Proprioceptive differences between the elbow and wrist joints may also be associated with the larger spindle counts found at the muscles crossing the elbow compared to those crossing the wrist (Scott & Loeb, 1994). Muscle spindles are known to provide most of the afferent information for proprioception (Gandevia & Burke, 1992; Tuthill & Azim, 2018) by detecting the change in fascicle length per degree of joint rotation with great sensitivity (Hall & McCloskey, 1983). The distribution of spindles among and within individual muscles is highly specific and constant among individuals (Banks & Stacey, 1988; Matthews, 1972, 1988). The heterogeneous distribution of spindles would appear to benefit the elbow over the wrist.

It is possible that the reference angle and movement plane differentially influenced proprioceptive perception at the elbow, compared to the wrist. Goble and Brown (2010) previously showed that larger reference angles induced larger proprioceptive errors at the elbow, although Marini et al. (2017) failed to find an angle effect on the wrist in flexion-extension degree of freedom. The reference angle for the elbow was approximately in the middle of the elbow's range of motion, while the reference angle for the wrist corresponded approximately to the third of the wrist's range of motion (from a fully flexed position). Moreover, the elbow was moved in the horizontal plane while the wrist was moved in the vertical plane. While Sturnieks et al. (2007) found no significant difference in detection thresholds for wrist movements in the two planes, Darling and Hondzinski (1999) suggested that the gravitational vertical axis could be one of the preferred axes for proprioceptive perception. Therefore, movement plane, and/or gravity, may have influenced matching errors in the present study. Further research is needed to compare proprioceptive perception between joints in the same movement plane and using the same reference angle with respect to the range of motion.

Proprioceptive Perception is More Precise at the Non-Preferred Upper Limb

Our study provided additional evidence of a proprioceptive advantage at the non-preferred upper limb. Indeed, our results showed that proprioceptive variability was smaller for the non-preferred arm, particularly for the non-preferred elbow. These results confirm and extend previous results, supporting the view of lateralization of proprioceptive function. More specifically, our findings are consistent with previous studies which showed a non-preferred limb advantage at the thumb (Colley, 1984; Roy & MacKenzie, 1978) and elbow (Goble & Brown, 2010; Kurian et al., 1989) using active/passive matching tasks; and at the shoulders and fingers using an active movement extent discrimination task (Han et al., 2013b). Han et al. (2013b) found that for multiple joints (fingers, shoulders, ankles, and knees), proprioceptive performance at the non-preferred left limb was significantly better than at the preferred right limb. A laterality effect was thus found with both an active method (Han et al., 2013b) and a passive method in the present study. Overall, these findings support the view of a non-preferred limb advantage in proprioception.

Even though we obtained evidence that proprioceptive perception is lateralized, we found strong, positive correlations between signed errors at the preferred and non-preferred elbows. We also found strong, positive correlations between variable signed errors at the preferred and non-preferred wrists. These findings support previous research which reported, using an active movement extent discrimination task, significant correlations between left and right joints at the upper limbs (finger and shoulder; Han et al., 2013b) and significant correlations between left and right joints at the lower limbs (ankle and knee; Waddington & Adams, 1999), but not between ipsilateral joints. Altogether, these results suggest that proprioceptive errors may be smaller for the non-preferred upper limb compared to the preferred upper limb but also that proprioceptive errors may be correlated between right and left upper limbs. It thus would appear that an individual with relatively small proprioceptive errors at one joint also has relatively small proprioceptive errors at the contralateral joint.

Lateralization of proprioception may, to a certain extent, be associated with the functional roles of each upper limb. The postural and motor control of the non-preferred arm may rely more on proprioceptive information than the preferred arm (Sainburg, 2014). Goble and Brown (2008a) found a proprioceptive advantage at the non-preferred arm in the proprioceptive condition during an active elbow matching task. They reported that both mean absolute errors and variable absolute errors were smaller for the non-preferred elbow. One working hypothesis is that the non-preferred arm relies more on proprioceptive information compared to the preferred arm which can be controlled based on efficient feedforward and visual feedback mechanisms for several tasks.

Another possible explanation for the asymmetric proprioceptive perception found here and elsewhere in the literature is a hemispheric lateralization of proprioceptive processing. The better proprioceptive perception for the non-preferred arm of right-handers would be associated with a right hemisphere specialization for processing proprioceptive signals, a hypothesis that has been further supported by neuroimaging studies. For instance, Naito et al. (2004, 2007) investigated brain regions responsible for processing signals from muscle spindle proprioceptors using tendon vibration and these researchers provided evidence for right hemisphere dominance for processing proprioceptive signals. This hemispheric specialization would suggest that individuals with right hemisphere damage would be more prone to proprioceptive deficits. This was reported by Goble et al. (2009) who tested children with hemiplegic cerebral palsy in an ipsilateral elbow active matching task (see also Leonard and Milner, 1995).

Our results of interlimb differences in proprioceptive perception contrast with those of other studies that found no significant laterality effect when using ipsilateral active matching tasks at the elbow (Goble et al., 2006; Goble & Brown, 2007) and wrist (Adamo & Martin, 2009) of right-handed participants, or when using an ipsilateral passive matching task at the wrist (Carey et al., 1996) and elbow (Khabie et al., 1998). However, these studies did not assess variable errors that are considered important to characterize proprioceptive performance. Also, some of these studies reported a better accuracy of the non-preferred limb during contralateral active matching tasks (Adamo & Martin, 2009; Goble et al., 2006; Goble & Brown, 2007). Moreover, Goble and Brown (2010) reported better proprioceptive perception at the non-preferred elbow in a passive detection task. While elbow proprioception does appear to be better at the non-preferred limb, further research with active and passive and with contralateral and ipsilateral matching is necessary to clarify the issue of lateralization of proprioceptive perception.

Limitations and Directions for Further Study

This study has some limitations requiring our findings to be interpreted carefully. Our participant sample size was limited to seven. Although this number is sufficient for detecting statistically significant differences, increasing the sample size and further varying participant ages would allow more generalizability of these findings. Also, we did not control for potentially confounding factors such as participants' working memory, physical activity (see for instance Goble et al., 2012 and Ribeiro & Oliveira, 2007) and muscle thixotropy. Muscle thixotropy describes the fact that resistance of muscles is temporarily reduced during movement, whether due to externally applied or internally generated forces. Even though our data were collected during a continuous movement, it is possible that muscle thixotropy, during the static state of reference memorization, influenced the ensuing responses, as muscle thixotropy is maximum in stationary conditions and is known to influence proprioception (Proske et al., 2014; Lakie & Campbell, 2019). Future work should consider muscle thixotropy when designing protocols to evaluate proprioception. Finally, we used a continuous movement task that may have influenced the reported errors by introducing a response delay between the "top" of the participant and the mouse click of the experimenter. Even though we did our best to minimize the potential influence of the delay on our measures by using a low movement speed and the same experimenter in all conditions, further work should rely on direct, automated measures. The continuous passive motion was imposed manually, and this would be better controlled with a robotic device.

Conclusion

Overall, proprioceptive perception appears to be more consistent at the non-preferred arm compared to the preferred arm, and more consistent at the elbow compared to the wrist. Our findings thus suggest that the precision of proprioception, as reflected by the variability of our measures, differs across joints and limbs. The joint specificity and lateralization of proprioceptive measures suggest that assessing proprioception at a single joint is not representative of a general assessment of an individual's proprioception. Multiple joint testing may be necessary to screen for possible proprioceptive deficits. Our findings may also be considered when designing rehabilitation protocols, as it remains unclear whether proprioceptive training at one joint will generalize to another joint, on the same or opposite limb. To conclude, the present study suggests that signed errors and variable signed errors may be the most discriminative measures when assessing the influence of laterality and joint differences on upper limb proprioception. Our findings thus highlight the importance of analyzing variable errors when assessing proprioceptive perception.

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Author contributions

FS and PC designed research. NR and FS performed research. NAC, NR, and FS analyzed data. NAC wrote the first draft of the paper. FS, NR, CB, PC, and FS edited the paper.

Declaration of Conflicting Interests

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