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## Joint Specificity and Lateralization of Upper-Limb Proprioceptive Perception

Najib M Abi Chebel, Nadège A Roussillon, Christophe Bourdin, Pascale  
Chavet, Fabrice R Sarlegna

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21

*Abstract*

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

40 *Keywords: Proprioception – Kinesthesia – Laterality – Joint –Upper limb*

41

## Introduction

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

59 Several researchers have used varied methodologies to address this question by  
60 examining whether proprioception differs across upper limbs and joints. For instance,

61 previous research investigated how proprioception at the elbow compares with that at  
62 the wrist, and better proprioceptive acuity has been found at the elbow using a  
63 movement detection threshold task (Sturnieks et al., 2007) and active matching tasks (Li  
64 & Wu, 2014; Sevrez & Bourdin, 2015). Specifically, Sevrez and Bourdin (2015) had an  
65 experimenter moving blindfolded participants' joints for them to a specific reference  
66 angle. Participants were instructed to memorize this reference angle before their joint  
67 was passively moved back to a starting position. Participants had to match their  
68 memorized reference angle with active movement of the same limb. Sevrez and Bourdin  
69 (2015) showed that active matching errors were less variable at the elbow than at the  
70 wrist, though Tripp et al. (2006), in an earlier study, had not detected significant  
71 differences in participants' errors between the wrist and elbow in a multi-joint, three-  
72 dimensional active matching task.

73 In this type of active matching task, the tested joint is actively or passively  
74 rotated to a specified reference angle, and the participant is asked to actively move the  
75 ipsilateral (Sevrez & Bourdin, 2015) or contralateral joint (Li & Wu, 2014) to match  
76 that reference angle. An error is then quantified as the difference between the reference  
77 angle and the participant's actual matching angle. A limitation of active matching is that  
78 it precludes distinct assessments of the underlying proprioceptive perception processes  
79 and motor control processes. Indeed, motor commands can also be used to estimate  
80 position and motion states (Desmurget & Grafton, 2000; Gandevia, 2014; Gandevia et

81 al., 2006; Smith et al., 2009). Because such central motor control signals may contribute  
82 differently to joint position sense at the elbow and wrist (Walsh et al., 2013), passive  
83 movement tasks appear to be most suited for assessing proprioceptive perception (Carey  
84 et al., 1996; Goble & Brown, 2010; Khabie et al. 1998).

85         The uniformity of upper limb proprioceptive perception can be studied across  
86 joints but also across the preferred and the non-preferred limbs. Several investigators,  
87 utilizing ipsilateral active matching, reported a better joint position sense at the non-  
88 preferred thumb (Colley, 1984; Roy & MacKenzie, 1978) and elbow (Kurian et al.,  
89 1989). Similarly, others, utilizing a contralateral active matching task, reported a better  
90 joint position sense at the non-preferred elbow (Goble et al., 2006; Goble & Brown,  
91 2007) and wrist (Adamo & Martin, 2009). Also, at the elbow, Goble and Brown,  
92 (2010) used both ipsilateral and contralateral passive matching and showed better joint  
93 position sense of the non-preferred versus preferred limb. In contrast, others failed to  
94 find interlimb differences (a) at the shoulder, elbow, and wrist joints when using a  
95 contralateral active matching task (Li & Wu, 2014; Ramsay & Riddoch, 2001); (b) at  
96 the shoulder and elbow when using an ipsilateral active matching task (King et al.,  
97 2013); and (c) at the elbow (Khabie et al., 1998) and wrist (Carey et al., 1996) when  
98 using an ipsilateral passive matching task. This lack of consensus about upper limb  
99 proprioception might be related to the different research methodologies  
100 (ipsilateral/contralateral, active/passive).

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

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

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

## 123 **Method**

### 124 *Participants*

125 To determine the minimum sample size no required for this study, we performed a  
126 statistical power analysis using G\*Power software (version 3.1.9.6; Kiel University,  
127 Kiel, Germany) and based our sample size calculation on the effect size of previous  
128 studies reporting proprioceptive differences between upper limbs (Goble & Brown,  
129 2010; partial  $\eta^2=0.29$ ) and between joints (Sevrez & Bourdin, 2015; partial  $\eta^2=0.189$ ).  
130 To determine the minimum required sample size, we used the smallest partial  $\eta^2$  (which  
131 corresponded to the smallest effect size) in Sevrez & Bourdin (2015). For a F-test,  
132 repeated-measures, within factors 2x2x8 ANOVA (number of measurements=32) with a  
133 partial  $\eta^2$  of 0.189 (corresponding to effect size of 0.48), the a priori power analysis  
134 indicated that for an alpha level of 0.05 and a power of 0.95, the minimum required  
135 sample size was estimated to be four. In the present study, we tested seven healthy adult  
136 participants (3 females, 4 males;  $M_{age} = 59.3$ ,  $SD = 7.0$  years; age range = 49-67 years).  
137 None of the participants reported any neurological or musculoskeletal deficits.



138 Participants were recruited from the University and the city of Marseille through an  
139 advertisement email. All participants showed a strong right-hand preference, quantified  
140 with the 10-item version of the Edinburgh handedness inventory (Appendix A in  
141 Oldfield 1971). The participants' mean laterality quotient on this scale was 94.2% (*SD*  
142 = 9.7%). All participants gave their written informed consent before they participated,  
143 and no participants were compensated for their involvement. The experiment was  
144 approved by the national ethics committee CERSTAPS (IRB00012476-2020-03-06-60).

#### 145 *Experimental setup*

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

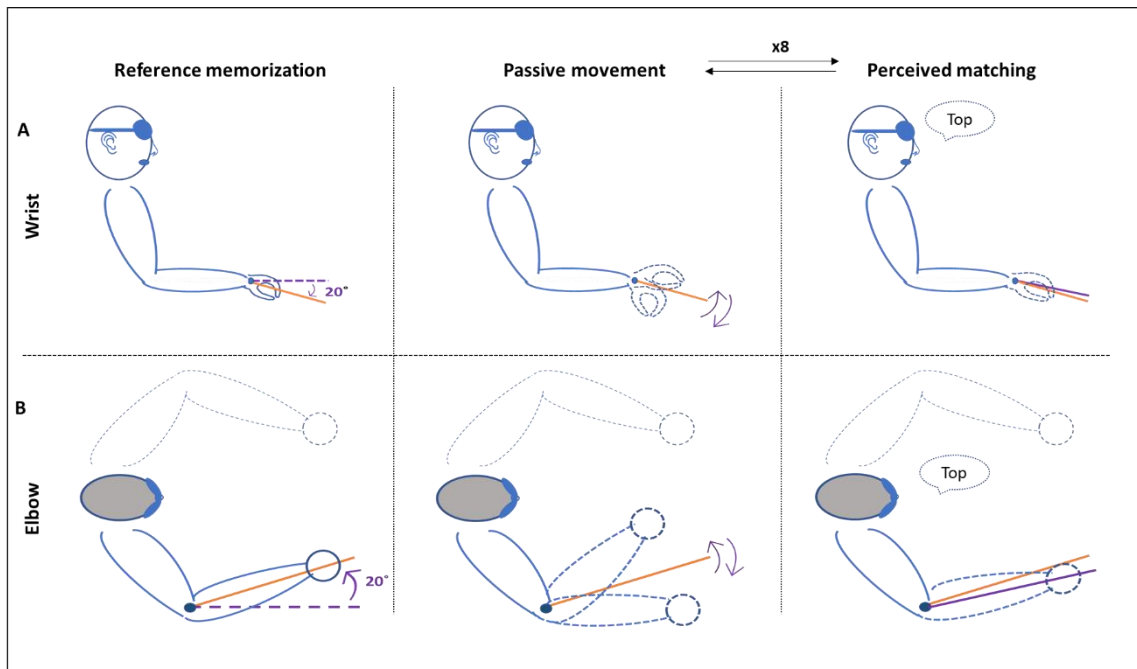
152 Joint rotations were recorded with precision potentiometers (linear, 10 k $\Omega$ ,  
153 Vishay) mounted beneath the pivot point of the corresponding lever arms. Each  
154 potentiometer was connected to an analog-to-digital converter, and signals were  
155 sampled at 10 Hz. Data were recorded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

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

#### 162 *Experimental procedure and conditions*

163 Two experimenters presented the apparatus to the participants. While one joint was  
164 being tested, the others were locked. Figure 1 illustrates the ipsilateral passive matching  
165 task. For each of the seven participants, a session corresponded to eight responses  
166 collected for each of the four experimental conditions. Each session was composed as  
167 following: as in Sevrez and Bourdin (2015), one experimenter moved the body segment  
168 corresponding to the tested joint (forearm for elbow and hand for wrist) from a  
169 randomly varied starting position toward the reference angle. The reference angles were  
170 20° of flexion for the elbow with respect to the full extension of the participant's arm in  
171 the device, and 20° of flexion for the wrist with respect to its neutral position. Once the  
172 reference angle was reached, the experimenter stabilized the joint at that angle as the  
173 participant was instructed to memorize the reference joint angle and to verbally indicate  
174 when they were ready to proceed. Participants were given the time deemed necessary to  
175 memorize the reference angle (typical time: 2 - 8 seconds), and the experimenter then

176 moved the participant's body segment cyclically around the reference angle over the  
177 same range (by approximately  $\pm 20^\circ$  for the elbow and  $\pm 25^\circ$  for the wrist) and over  
178 approximately the same speed (below  $5^\circ/\text{second}$ ) for each participant. During the cyclic  
179 movement, participants were instructed to say 'top' each time they estimated that the  
180 joint angle corresponded to the memorized reference angle. On each 'top' signal, the  
181 second experimenter recorded the signalled angle value by clicking on a mouse while  
182 the experimenter continued the passive cyclic movement without interruption until eight  
183 responses were recorded, which marked the end of the session. In no case were  
184 participants given knowledge regarding their performance, as in Goble & Brown  
185 (2010).



186

Figure 1: Illustration of the Ipsilateral Passive Matching Task.

A. Side view of the participant.

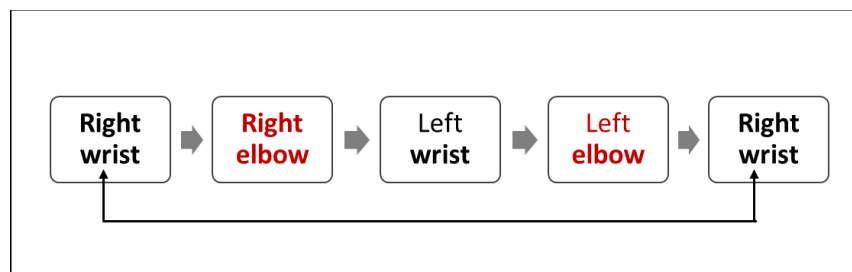
B. Top view of the participant.

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.

187

188           The first session corresponded to the right wrist, the second to the right elbow,  
189   the third to the left wrist, and the fourth to the left elbow. In order to be able to compare  
190   individual differences, we fixed the order of the sessions, as illustrated in Figure 2.  
191   However, to assess whether performance varied along the whole experiment and to  
192   assess test-retest reliability, we used a fifth session consisting of repeating the first  
193   session (performed with the right wrist) at the end of the experiment. Participants were  
194   given a short break between sessions, but they were not given any feedback about their  
195   performance during the experiment.  
196

Figure 2: Order of the Experimental Sessions.



197

198 *Data analysis*

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

- 202 ● The signed error was calculated as the angular difference between the reported  
203 joint angle and the true reference angle (as in Goble & Brown, 2007) and was  
204 used to determine the existence of any directional bias in matching accuracy.  
205 Positive signed errors were assigned to more flexed joint angles compared to the  
206 reference, and negative signed errors were assigned to more extended joint  
207 angles.
- 208 ● The variable signed error was calculated as the standard deviation around the  
209 mean of each participant's eight signed errors. It was used to assess the  
210 consistency of the directional bias.
- 211 ● The absolute error was calculated as the absolute difference between the  
212 reported joint angles and the reference angles (as in Goble & Brown, 2007) and  
213 was used to determine the extent of matching accuracy. The absolute error  
214 allowed us to focus on the magnitude of errors, irrespective of their positive or  
215 negative direction.

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

219           Eight responses were recorded for each of the five sessions, resulting in a total  
220           of 40 responses for each participant and 280 responses for all participants. We used a  
221           2x2x8 analysis of variance (ANOVA) with repeated measures to determine the main  
222           effects of joint (wrist, elbow), laterality (right, left), and response (1 to 8) as well as  
223           their interactions for both signed and absolute errors. We used 2x2 ANOVAs with  
224           repeated measures to determine the main effects of the Joint (wrist, elbow) and  
225           Laterality (right, left) as well as their interaction for both variable signed errors and  
226           variable absolute errors.

227           We used linear correlation analyses to determine the relationship of the  
228           participants' errors between the two wrists, the two elbows, and the wrist and elbow of  
229           each limb; and to determine the relationship of the participants' errors with their age.  
230           Pearson correlation coefficients ( $r$ ) were calculated and interpreted according to their  
231           sizes [strong ( $r=0.7-0.89$ ), moderate ( $r=0.5-0.69$ ), or weak ( $r=0.1-0.39$ ), as in Schober  
232           and Schwarte (2018)].

233           We assessed within-day test-retest reliability, or in other words, the potential  
234           effect of test variability (due to repetition, fatigue, change of mood, etc.) when  
235           comparing data from the first and last session. We analysed the correlation of these data

236 and calculated the Pearson correlation coefficient ( $r$ ). In addition, we used a 2x8  
237 ANOVA with repeated measures to determine the main effects of Test (first test, last  
238 test) and Response (1 to 8) as well as their interaction on mean errors. We used a paired  
239  $t$ -test to determine the effect of Test on variable errors.

240 All data presented a normal distribution as verified with the Kolmogorov-  
241 Smirnov method. Statistical significance was set at  $p < 0.05$ . Post hoc comparisons were  
242 performed based on Tukey's honestly significant difference method (Adamo & Martin,  
243 2009; Goble & Brown, 2007). All ANOVA analyses and all post hoc comparisons were  
244 pre-planned. Data are available upon reasonable request.

## 245 **Results**

246

### 247 *Signed error: differences between joints and responses.*

248 Calculating the signed error allowed us to assess the direction of the error, with positive  
249 errors corresponding to perceiving the joint as more flexed than the reference angle.  
250 Figure 3 shows that signed error varied as a function of the joint and the response  
251 number. A 2x2x8 ANOVA [Joint (elbow, wrist) x Laterality (left, right) x Response (1  
252 to 8)] revealed a significant joint effect ( $F(1,6)=14.9$ ,  $p=0.008$ , partial  $\eta^2=0.713$ ) on the  
253 signed error, which differed at the wrist ( $M = -4.7$ ,  $SD = 2.5^\circ$ ) compared to the elbow

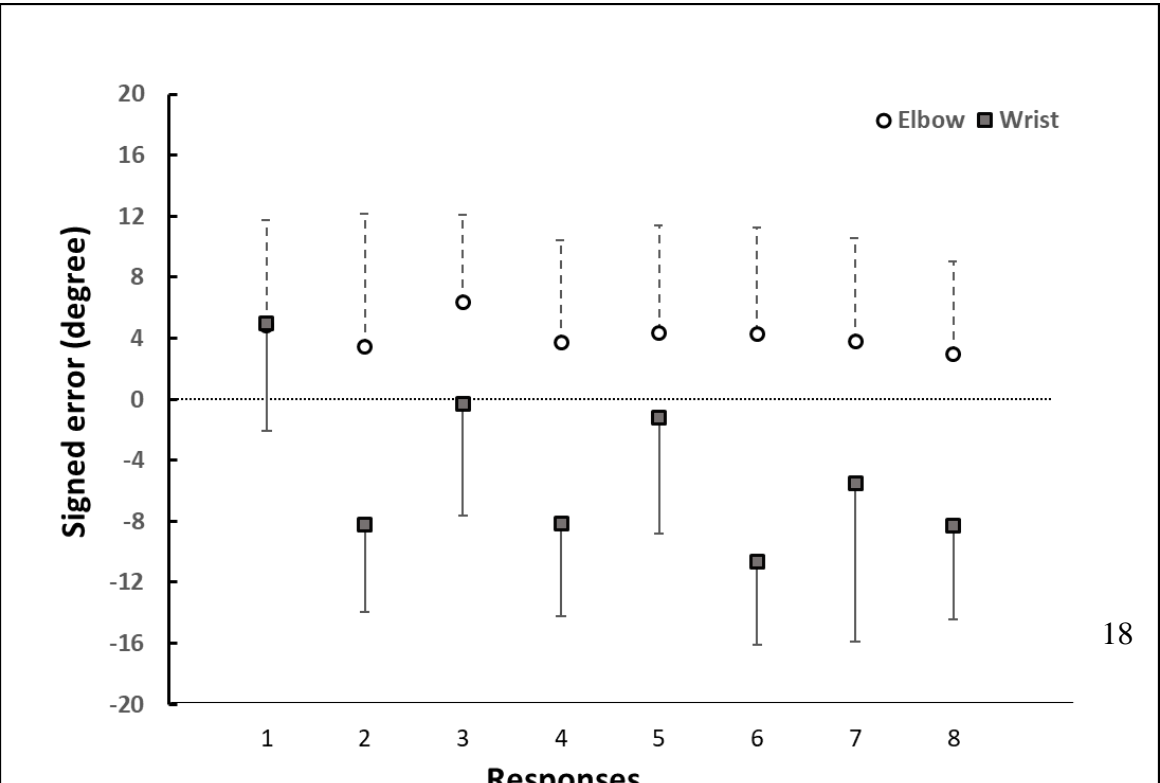


254 ( $M = 4.2$ ,  $SD = 4.6^\circ$ ). However, one cannot conclude from this analysis whether  
255 proprioceptive perception is more accurate for one joint or the other, as error magnitude  
256 was  $\sim 4.5^\circ$  in both conditions. This ANOVA also revealed a significant response effect  
257 ( $F(7,42)=5.3$ ,  $p<0.001$ , partial  $\eta^2=0.473$ ). Tukey's post-hoc analysis showed that the  
258 signed error in the first response significantly differed from the second, fourth, sixth,  
259 and eighth responses, and the signed error in the sixth response also differed from that  
260 in the third response.

261         There was a significant joint and response interaction effect ( $F(7,42)=6.3$ ,  
262  $p<0.001$ , partial  $\eta^2=0.511$ ) as shown in Figure 3, with a response effect on signed error  
263 only at the wrist and not at the elbow. An oscillatory pattern and a shift from positive to  
264 negative errors can be seen on wrist data, but the main statistical finding from post-hoc  
265 tests was that the first response differed from most other responses. Indeed, Tukey's  
266 post-hoc analysis showed that at the wrist, the signed error of the first response  
267 significantly differed from almost all the subsequent responses (i.e., responses 2, 4, 6, 7,  
268 and 8). From the second response to the last one, participants responded when their  
269 wrist was slightly less flexed than the reference angle. The second response differed  
270 from the third and the fifth. The third differed from the fourth, sixth and eighth. The  
271 fourth differed from the fifth and the fifth differed from the sixth and eighth. In contrast,  
272 at the elbow, there was no significant difference between responses which were  
273 consistently biased toward a slight flexion compared to the reference angle. There was

274 no significant laterality effect ( $F(1,6)=1.1, p=0.34, \text{partial } \eta^2=0.152$ ), and there were no  
275 other significant interactions [Laterality x Joint ( $F(1,6)=0.01, p=0.91, \text{partial } \eta^2=0.002$ ),  
276 Laterality x Response ( $F(7,42)=0.3, p=0.96, \text{partial } \eta^2=0.041$ ), double interaction  
277 ( $F(7,42)=0.7, p=0.70, \text{partial } \eta^2= 0.101$ )].

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





280 *Variable signed error: differences between upper-limbs and joints*

281 A 2x2 ANOVA on the variable signed error revealed a significant joint effect  
282 ( $F(1,6)=34.6, p=0.001, \text{partial } \eta^2 =0.853$ ), as the variable signed error at the elbow ( $M$   
283  $=5.1, SD = 1.7^\circ$ ) was significantly smaller than at the wrist ( $M = 7.9, SD = 1.9^\circ$ ). A  
284 significant laterality effect ( $F(1,6)=17.4, p=0.006, \text{partial } \eta^2=0.743$ ) was associated with  
285 a smaller variable signed error at the left arm ( $M = 5.7, SD = 1.5^\circ$ ) compared to the right  
286 ( $M = 7.3, SD = 1.9^\circ$ ). There was also a significant interaction effect of laterality and  
287 joint ( $F(1,6)=10.3, p=0.018, \text{partial } \eta^2=0.633$ ), illustrated in Figure 4, showing that the  
288 variable signed error was smaller at the left elbow ( $M = 3.7, SD = 1.4^\circ$ ) compared to  
289 the right elbow ( $M =6.4, SD = 2.1^\circ, p=0.008$ ), the left wrist ( $M =7.8, SD= 2.0^\circ, p$   
290  $=0.001$ ) and the right wrist ( $M = 8.1, SD= 1.8^\circ, p<0.001$ ). There were no significant  
291 differences between the variable signed error at the left and right wrists ( $p=0.94$ ), the  
292 right elbow and the right wrist ( $p=0.08$ ), and the right elbow and the left wrist ( $p=0.17$ ).  
293 In summary for this analysis, the smallest variable signed error was found at the left  
294 elbow compared to the right elbow and both wrists.

295

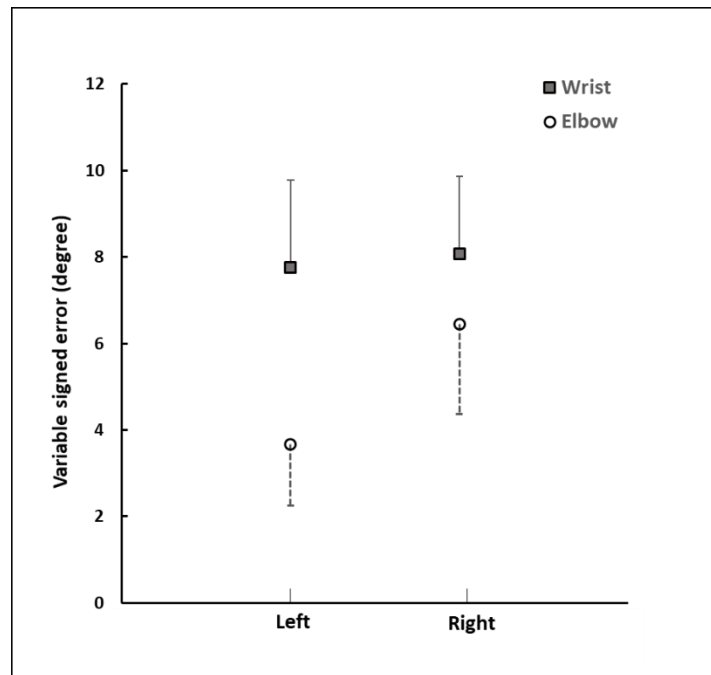


Figure 4: Variable Signed Error at the Wrist (filled squares), and Elbow (empty circles), for Each Response. Error bars represent standard deviation around the participants' mean.

296

297 *Absolute error: no significant differences between limbs, joints, or responses*

298 A 2x2x8 ANOVA on mean absolute error revealed only a significant interaction effect  
299 of joint and response ( $F(7,42)=4.2$ ,  $p=0.001$ , partial  $\eta^2=0.409$ ), but post-hoc analysis  
300 showed no significant pairwise differences. Overall, there were no significant main  
301 effects for laterality ( $F(1,6)=1.2$ ,  $p=0.32$ , partial  $\eta^2=0.163$ ), joint ( $F(1,6)=3.1$ ,  $p=0.12$ ,

302 partial  $\eta^2=0.342$ ), and response ( $F(7,42)=0.5$ ,  $p=0.81$ , partial  $\eta^2=0.081$ ) and no other  
303 significant interactions for laterality and joint ( $F(1,6)=0.5$ ,  $p=0.50$ , partial  $\eta^2=0.080$ ),  
304 laterality and response ( $F(7,42)=0.5$ ,  $p=0.86$ , partial  $\eta^2=0.071$ ), or double interaction  
305 ( $F(7,42)=0.4$ ,  $p=0.88$ , partial  $\eta^2=0.067$ ). Overall, participants' absolute error averaged  
306  $5.6$  ( $SD = 2.7^\circ$ ) at the left elbow,  $6.8$  ( $SD = 3.3^\circ$ ) at the right elbow,  $7.7$  ( $SD = 1.6^\circ$ ) at  
307 the left wrist and  $7.9$  ( $SD = 2.5^\circ$ ) at the right wrist.

#### 308 *Variable absolute error: differences between limbs and joints*

309 Consistent with the statistical analysis of the variable signed error, a 2x2 ANOVA on  
310 the variable absolute error revealed significant main effects of joint ( $F(1,6)=7.4$ ,  $p=0.03$ ,  
311 partial  $\eta^2=0.554$ ) and laterality ( $F(1,6)=11.8$ ,  $p=0.01$ , partial  $\eta^2=0.663$ ). Figure 5 shows  
312 that the variable absolute error at the elbow ( $M = 4.1$ ,  $SD = 1.7^\circ$ ) was smaller than at the  
313 wrist ( $M = 5.3$ ,  $SD = 1.2^\circ$ ). Also, the variable absolute error at the left limb ( $M = 4.0$ ,  
314  $SD = 0.9^\circ$ ) was smaller than at the right limb ( $M = 5.3$ ,  $SD = 1.8^\circ$ ). Group means and  
315 individual data are reported in Figure 5 to highlight the systematic nature of the results.  
316 There was no significant interaction effect for laterality and joint ( $F(1,6)=1.7$ ,  $p=0.24$ ,  
317 partial  $\eta^2=0.220$ ). In summary, the variable absolute error was smaller at the elbow  
318 compared to the wrist, and at the left limb compared to the right limb.

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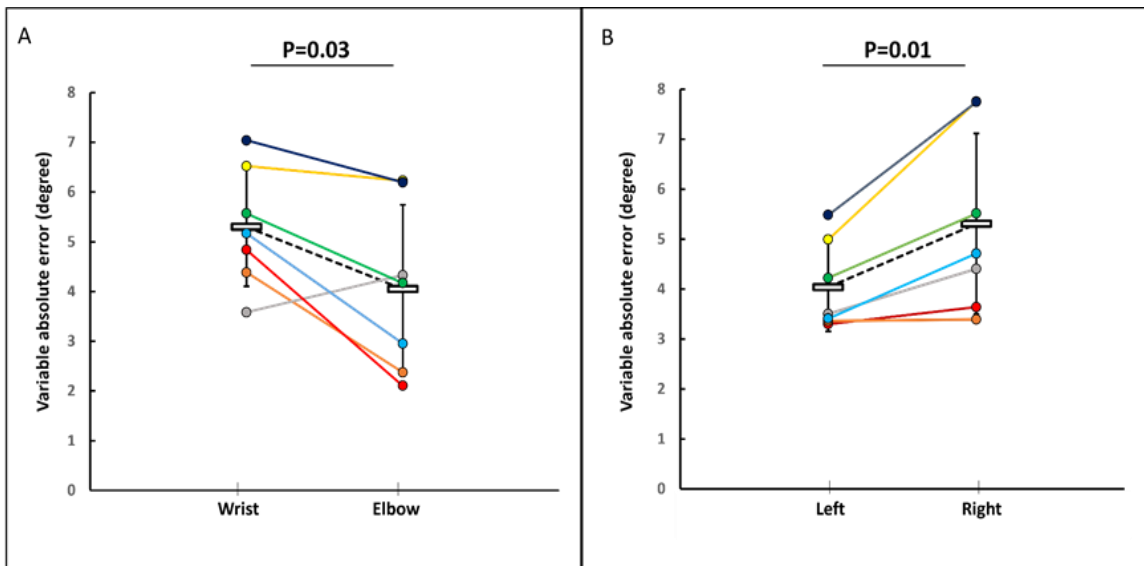


Figure 5: Variable Absolute Error for each Participant (colored dots) and Group Means (empty rectangles). Error bars represent the standard deviation around the participant's mean. (A) Joint effect. (B) Laterality effect.

321

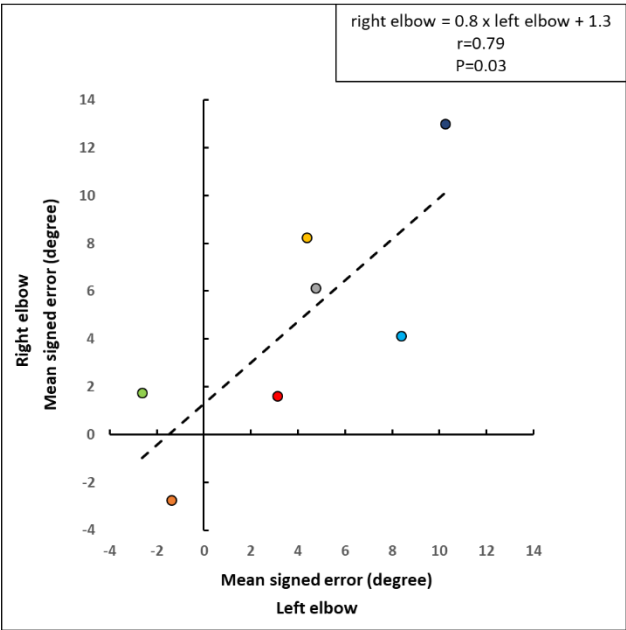


322 *Correlations between errors across participants*

323 Correlations were used to determine whether participants with smaller or greater errors  
324 for a specific condition tended to have smaller or greater errors for another condition.  
325 For the signed error, we found a strong linear, positive correlation between errors at the  
326 left and right elbows across participants (right elbow =  $0.8 \times \text{left elbow} + 1.3$ ,  $r=0.79$ ,  
327  $p=0.03$ ). This is shown in Figure 6 in which, for instance, one participant (blue dot) had  
328 the largest signed error at the right elbow and at the left elbow. No other significant  
329 correlations were found between errors at the left and right wrists ( $r=-0.03$ ,  $p=0.94$ ), left  
330 wrist and left elbow ( $r=-0.72$ ,  $p=0.07$ ), nor right wrist and right elbow ( $r=-0.33$ ,  
331  $p=0.47$ ).

332

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.



334

335           For the variable signed error, we found strong positive correlations between  
336 errors at the right wrist and the right elbow (right elbow = 1.0 x right wrist - 1.3,  $r=0.83$ ,  
337  $p=0.01$ ) and at the right and left wrists (left wrist = 1.0 x right wrist + 0.02,  $r=0.86$ ,  
338  $p=0.006$ ). As shown in Figure 7, one participant (yellow dot) presented the highest  
339 variable signed error at both the right elbow and wrist (left panel), and the second  
340 higher variable signed error at the left wrist (right panel). Another participant (light blue  
341 dot) had the least variable signed error at the right elbow (left panel) and the left wrist  
342 (right panel) while having the second least variable signed error at the right wrist. There  
343 was also a strong correlation between errors at the right elbow and left wrist (right  
344 elbow = 0.9 x left wrist +0.4,  $r=0.83$ ,  $p=0.01$ ). No significant correlations were found  
345 between errors at the left wrist and left elbow ( $r=0.35$ ,  $p=0.39$ ), nor at the left and right  
346 elbows ( $r=0.58$ ,  $p=0.13$ ).

347

348

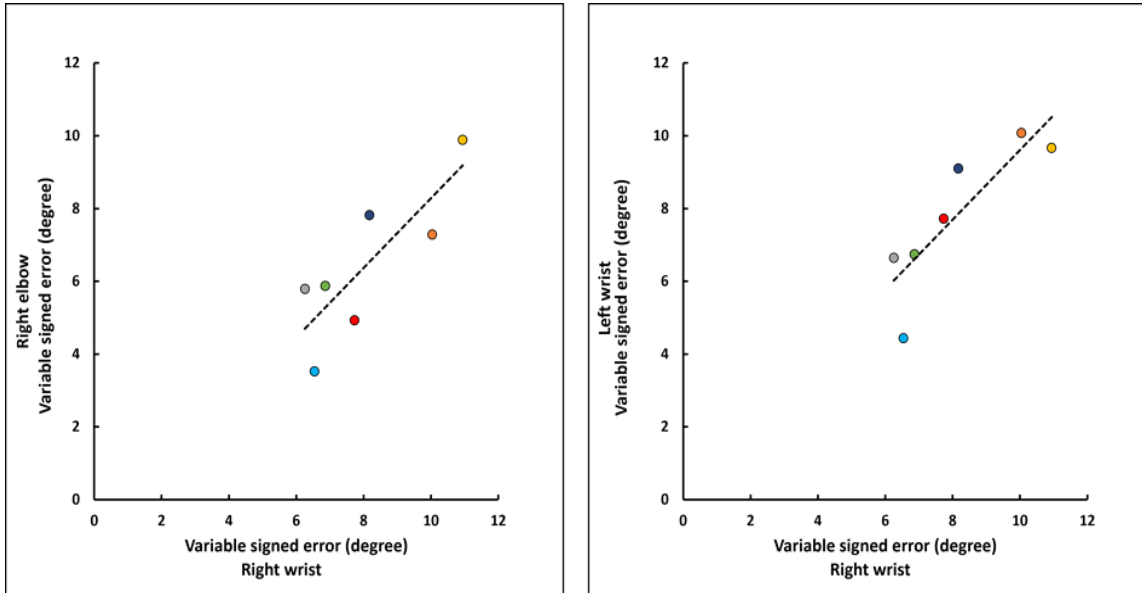


Figure 7: Relationship between Variable Signed Errors of Each Participant (according to the same color code as in Figures 5 and 6). Each linear regression (dashed line) is displayed to aid visualization. (A) Right wrist and right elbow. (B) Right and left wrists.

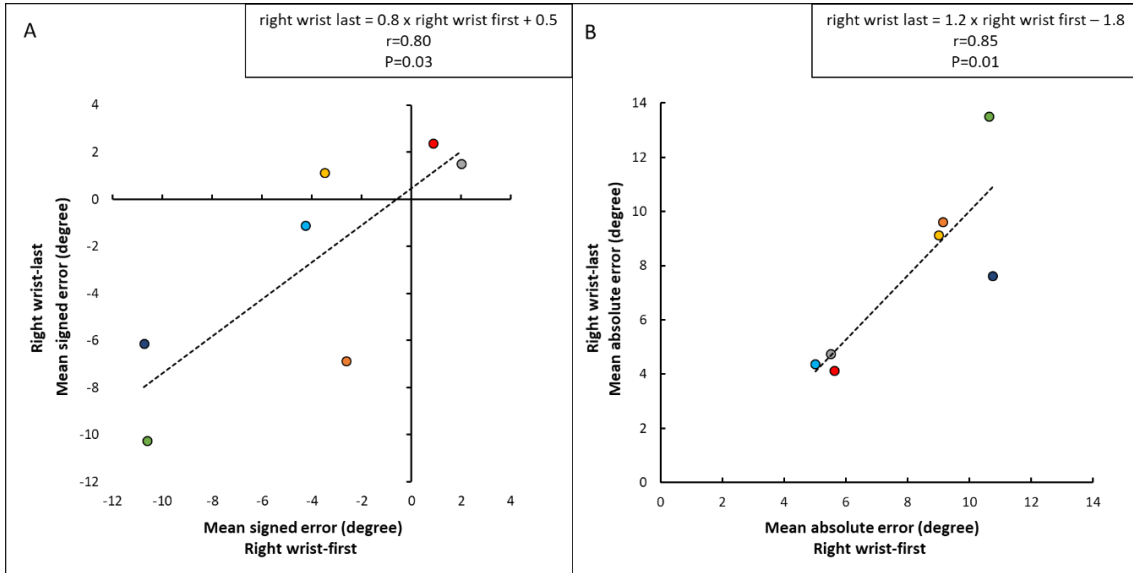
349

350 For the absolute error, no significant linear correlations were found [left wrist  
351 and left elbow ( $r=-0.08$ ,  $p=0.86$ ), right wrist and right elbow ( $r=0.57$ ,  $p=0.18$ ), left and  
352 right wrists ( $r=0.41$ ,  $p=0.36$ ), left and right elbows ( $r=0.58$ ,  $p=0.17$ )]. For the variable  
353 absolute error, no significant linear correlations were found [left wrist and left elbow  
354 ( $r=0.33$ ,  $p=0.47$ ), right wrist and right elbow ( $r=0.42$ ,  $p=0.35$ ), left and right wrists  
355 ( $r=0.48$ ,  $p=0.28$ ), left and right elbows ( $r=0.63$ ,  $p=0.13$ )]. For the absolute errors as well  
356 as all other errors, there were no significant correlations with participants' ages (all  $P >$   
357  $0.35$ ).

#### 358 *Test-retest reliability*

359 The right wrist was tested at the beginning and at the end of the experiment. Strong  
360 significant correlations were found between the first and the last tests for the signed  
361 error (right wrist last =  $0.8 \times$  right wrist first +  $0.5$ ,  $r=0.80$ ,  $p=0.03$ ) and the absolute  
362 error (right wrist last =  $1.2 \times$  right wrist first -  $1.8$ ,  $r=0.85$ ,  $p=0.01$ ), as shown in Figure  
363 8. No other significant correlations were found for the variable signed error ( $r=0.37$ ,  
364  $p=0.4$ ) nor the variable absolute error ( $r=0.01$ ,  $p=0.8$ ).

365



366

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.

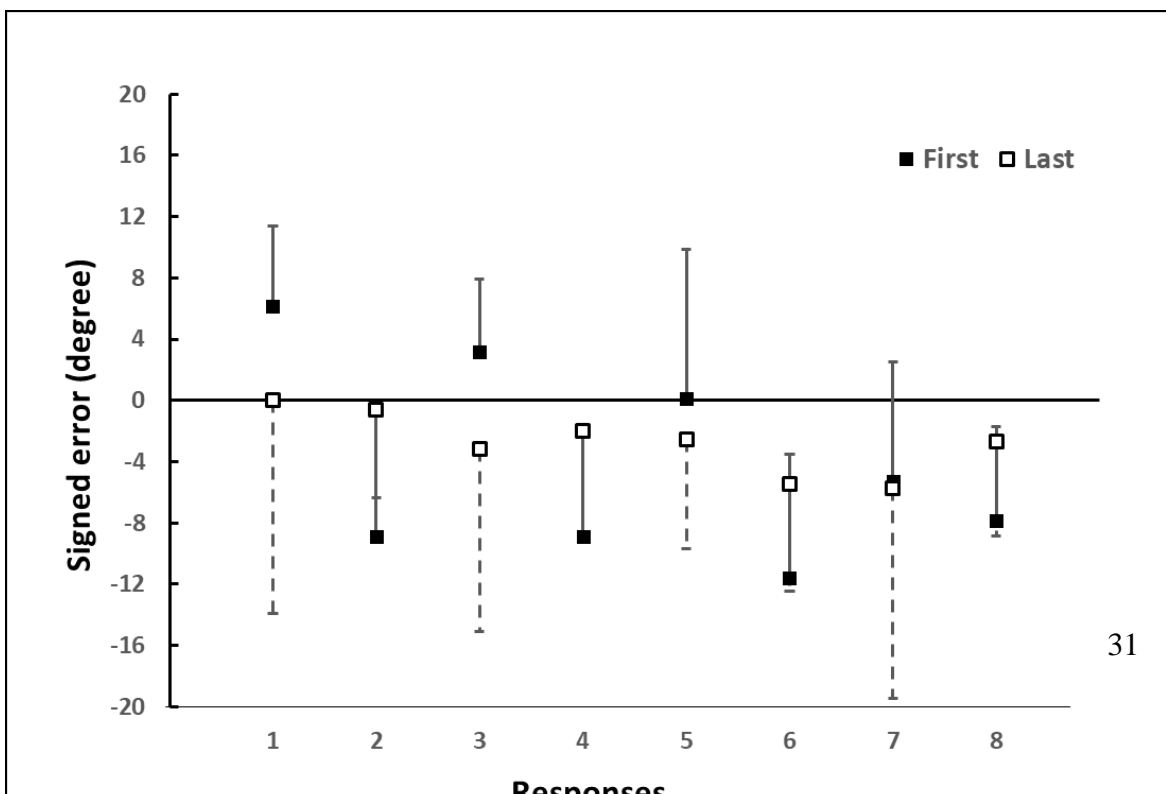
367

368 A 2x8 ANOVA [Test (First, Last) x Response (1 to 8)] on the signed error  
369 revealed no significant main test effect ( $F(1,6)=3.7$ ,  $p=0.10$ , partial  $\eta^2=0.383$ ).  
370 However, there was a significant response effect ( $F(7,42)=3.5$ ,  $p=0.005$ , partial  
371  $\eta^2=0.365$ ) and a significant interaction effect of test and response ( $F(7,42)=2.4$ ,  $p=0.04$ ,  
372 partial  $\eta^2=0.287$ ), as shown in Figure 9. While for the first test, some responses  
373 significantly differed from others (response 1 differed from response 2, 4 6, and 8; and  
374 response 3 significantly differed from response 6), no significant differences were found  
375 between responses for the last test.

376 For the absolute error, there was no significant main effect of test ( $F(1,6)=0.3$ ,  
377  $p=0.63$ , partial  $\eta^2=0.042$ ), nor response ( $F(7,42)=0.8$ ,  $p=0.63$ , partial  $\eta^2=0.117$ ), nor was  
378 there a significant interaction ( $F(7,42)=1.9$ ,  $p=0.08$ , partial  $\eta^2=0.247$ ). Also, paired  $t$ -  
379 tests revealed no significant test effect for the variable signed error ( $t(6)=0.2$ ,  $p=0.86$ ;  
380 Cohen's  $d=0.07$ ) and the variable absolute error ( $t(6)=1.0$ ,  $p=0.38$ ; Cohen's  $d=0.36$ ).

381

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.







384

## Discussion

385 This study sought to test the hypotheses that upper limb proprioception assessed  
386 through a passive matching task would be better at the elbow than at the wrist and at the  
387 non-preferred versus preferred arm. In general, our findings are consistent with both  
388 hypotheses (at least in this small sample of right-handers). We found that proprioception  
389 was more precise at the elbow than at the wrist as revealed by the small variable errors  
390 at the elbow. This was associated with better stability of the responses at the elbow. We  
391 also found that proprioception at the left limb was less variable than at the right limb.  
392 We now further discuss these findings in greater detail.

### *Proprioceptive perception is more precise at the elbow compared to the wrist*

394 Proprioception at the elbow was less variable than at the wrist, and this was especially  
395 clear for the non-preferred arm, for both signed and absolute errors. This finding  
396 concurs with findings from Li and Wu, (2014), and Sevrez and Bourdin (2015) whose  
397 studies showed that perceiving unseen passive positions and motions at the elbow joint  
398 was more accurate than at the wrist. Similarly, Hall and McCloskey (1983) found that  
399 proprioceptive acuity was higher at upper limb joints more proximal to the brain  
400 (shoulder and elbow) than a more peripheral joint (middle finger's most distal joint).  
401 The better proprioceptive perception at proximal joints may reflect the important role  
402 these joints play in determining the location of the endpoint (Scott & Loeb, 1994).

403 Proprioceptive differences between the elbow and wrist joints may also be associated  
404 with the larger spindle counts found at the muscles crossing the elbow compared to  
405 those crossing the wrist (Scott & Loeb, 1994). Muscle spindles are known to provide  
406 most of the afferent information for proprioception (Gandevia & Burke, 1992; Tuthill &  
407 Azim, 2018) by detecting the change in fascicle length per degree of joint rotation with  
408 great sensitivity (Hall & McCloskey, 1983). The distribution of spindles among and  
409 within individual muscles is highly specific and constant among individuals (Banks &  
410 Stacey, 1988; Matthews, 1972, 1988). The heterogeneous distribution of spindles would  
411 appear to benefit the elbow over the wrist.

412         It is possible that the reference angle and movement plane differentially  
413 influenced proprioceptive perception at the elbow, compared to the wrist. Goble &  
414 Brown (2010) previously showed that larger reference angles induced larger  
415 proprioceptive errors at the elbow, although Marini et al. (2017) failed to find an angle  
416 effect on the wrist in flexion-extension degree of freedom. The reference angle for the  
417 elbow was approximately in the middle of the elbow's range of motion, while the  
418 reference angle for the wrist corresponded approximately to the third of the wrist's  
419 range of motion (from a fully flexed position). Moreover, the elbow was moved in the  
420 horizontal plane while the wrist was moved in the vertical plane. While Sturnieks et al.  
421 (2007) found no significant difference in detection thresholds for wrist movements in  
422 the two planes, Darling and Hondzinski (1999) suggested that the gravitational vertical

423 axis could be one of the preferred axes for proprioceptive perception. Therefore,  
424 movement plane, and/or gravity, may have influenced matching errors in the present  
425 study. Further research is needed to compare proprioceptive perception between joints  
426 in the same movement plane and using the same reference angle with respect to the  
427 range of motion.

428 *Proprioceptive perception is more precise at the non-preferred upper limb*

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

442 preferred limb advantage in proprioception.

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

456 This lateralization of proprioception may, to a certain extent, be associated with the  
457 functional roles of each upper limb. The postural and motor control of the nonpreferred  
458 arm may rely more on proprioceptive information than the preferred arm (Sainburg,  
459 2014). Goble and Brown (2008a) found a proprioceptive advantage at the nonpreferred  
460 arm in the proprioceptive condition during an active elbow matching task. They

461 reported that both mean absolute errors and variable absolute errors were smaller for the  
462 non-preferred elbow. One working hypothesis is that the nonpreferred arm relies more  
463 on proprioceptive information compared to the preferred arm which can be controlled  
464 based on efficient feedforward and visual feedback mechanisms for several tasks.

465 Another possible explanation for the asymmetric proprioceptive perception  
466 found here and elsewhere in the literature is a hemispheric lateralization of  
467 proprioceptive processing. The better proprioceptive perception for the non-preferred  
468 arm of right-handers would be associated with a right hemisphere specialization for  
469 processing proprioceptive signals, a hypothesis that has been further supported by  
470 neuroimaging studies. For instance, Naito et al. (2004, 2007) investigated brain regions  
471 responsible for processing signals from muscle spindle proprioceptors using tendon  
472 vibration and these researchers provided evidence for right hemisphere dominance for  
473 processing proprioceptive signals. This hemispheric specialization would suggest that  
474 individuals with right-hemisphere damage would be more prone to proprioceptive  
475 deficits. This was reported by Goble et al. (2009) who tested children with hemiplegic  
476 cerebral palsy in an ipsilateral elbow active matching task (see also Leonard & Milner,  
477 1995).

478 Our results of interlimb differences in proprioceptive perception contrast with  
479 those of other studies that found no significant laterality effect when using ipsilateral  
480 active matching tasks at the elbow (Goble et al., 2006; Goble & Brown, 2007) and wrist

481 (Adamo & Martin, 2009) of right-handed participants, or when using an ipsilateral  
482 passive matching task at the wrist (Carey et al., 1996) and elbow (Khabie et al., 1998).  
483 However, these studies did not assess variable errors that are considered important to  
484 characterize proprioceptive performance. Also, some of these studies reported a better  
485 accuracy of the non-preferred limb during contralateral active matching tasks (Adamo  
486 & Martin, 2009; Goble et al., 2006; Goble & Brown, 2007). Moreover, Goble & Brown  
487 (2010) reported better proprioceptive perception at the non-preferred elbow in a passive  
488 detection task. While elbow proprioception does appear to be better at the non-preferred  
489 limb, further research with active and passive and with contralateral and ipsilateral  
490 matching is necessary to clarify the issue of lateralization of proprioceptive perception.

#### 491 *Limitations and Directions for Further Study*

492 This study has some limitations requiring our findings to be interpreted carefully. Our  
493 participant sample size was limited to seven. Although this number is sufficient for  
494 detecting statistically significant differences, increasing the sample size and further  
495 varying participant ages would allow more generalizability of these findings. Also, we  
496 did not control potentially confounding factors such as participants' working memory,  
497 their sport and physical activity (see for instance Goble et al., 2012 and Ribeiro &  
498 Oliveira, 2007, and muscle thixotropy. Muscle thixotropy describes the fact that  
499 resistance of muscles is temporarily reduced during movement, whether due to

500 externally applied or internally generated forces. Even though our data were collected  
501 during a continuous movement, it is possible that muscle thixotropy, during the static  
502 state of reference memorization, influenced the ensuing responses, as muscle thixotropy  
503 is maximum in stationary conditions and is known to influence proprioception (Proske  
504 et al. 2014; Lakie & Campbell 2019). Future work should thus take into account muscle  
505 thixotropy to design protocols to evaluate proprioception. Finally, we used a continuous  
506 movement task that may have influenced the reported errors by introducing a response  
507 delay between the ‘top’ of the participant and the mouse click of the experimenter. Even  
508 though we did our best to minimize the potential influence of the delay on our measures  
509 by using a low movement speed and the same experimenter in all conditions, further  
510 work should rely on direct, automated measures.

### 511 *Conclusion*

512 Overall, proprioceptive perception appears to be more consistent at the non-preferred  
513 arm compared to the preferred arm, and more consistent at the elbow compared to the  
514 wrist. Our findings thus suggest that the precision of proprioception, as reflected by the  
515 variability of our measures, differs across joints and limbs. The joint specificity and  
516 lateralization of proprioceptive measures suggest that assessing proprioception at a  
517 single joint is not representative of a general assessment of an individual’s  
518 proprioception. Multiple joint testing may be necessary to screen for possible



519 proprioceptive deficits. Our findings may also be considered when designing  
520 rehabilitation protocols, as it remains unclear whether proprioceptive training at one  
521 joint will generalize to another joint, on the same or opposite limb. To conclude, the  
522 present study suggests that signed errors and variable signed errors may be the most  
523 discriminative measures when assessing the influence of laterality and joint differences  
524 on upper limb proprioception. Our findings thus highlight the importance of analysing  
525 variable errors when assessing proprioceptive perception.

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