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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 η^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 η^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.

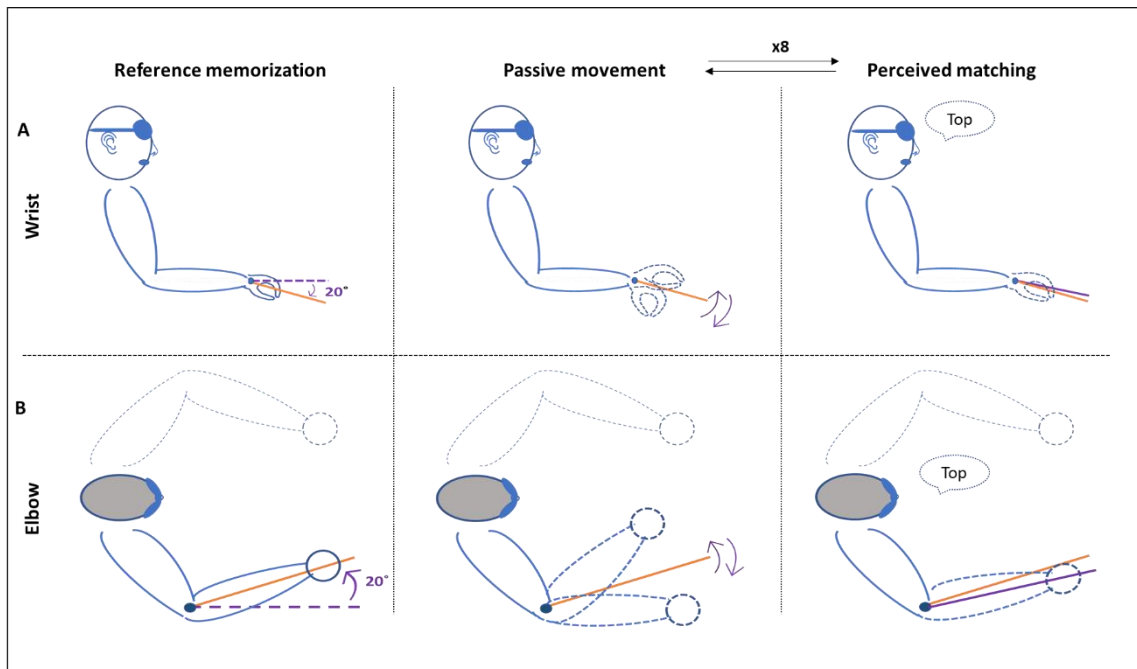
152 Joint rotations were recorded with precision potentiometers (linear, 10 k Ω ,
153 Vishay) mounted beneath the pivot point of the corresponding lever arms. Each
154 potentiometer was connected to an analog-to-digital converter, and signals were
155 sampled at 10 Hz. Data were recorded using a LabView 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.

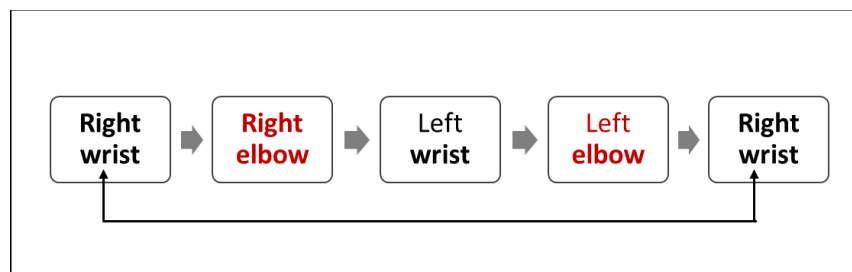
B. Top view of the participant.

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.*

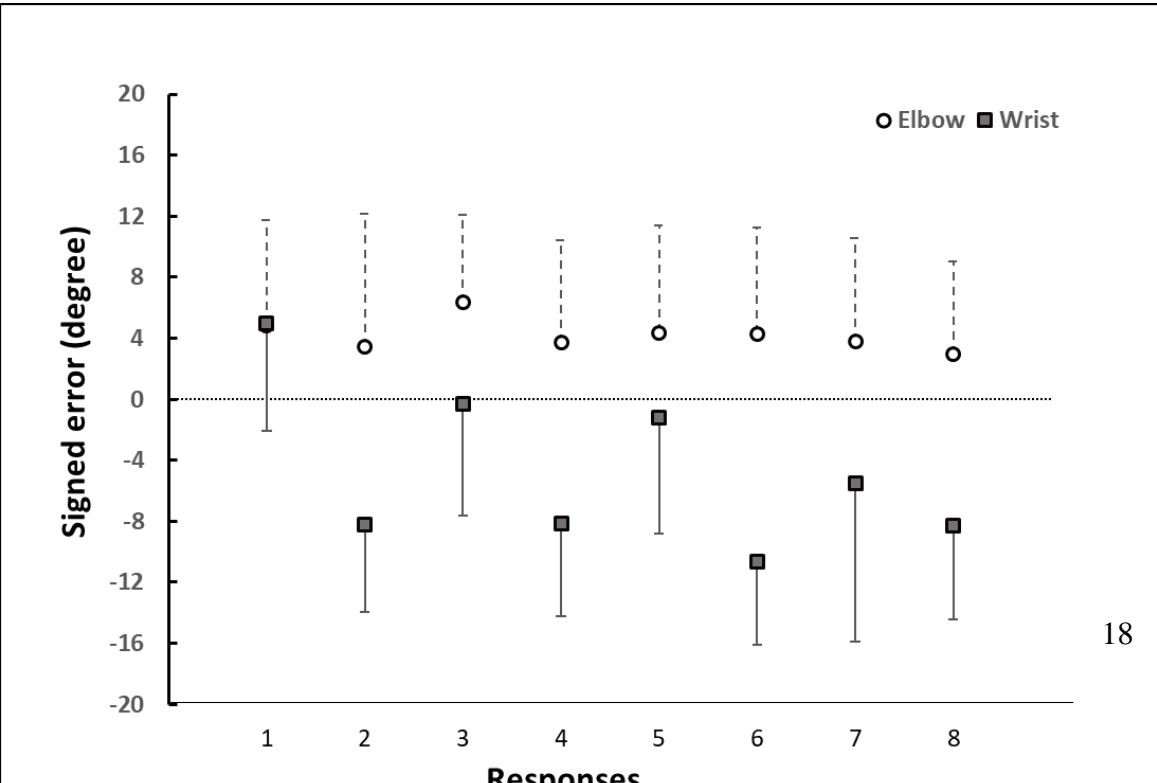
248 Calculating the signed error allowed us to assess the direction of the error, with positive
249 errors corresponding to perceiving the joint as more flexed than the reference angle.
250 Figure 3 shows that signed error varied as a function of the joint and the response
251 number. A 2x2x8 ANOVA [Joint (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

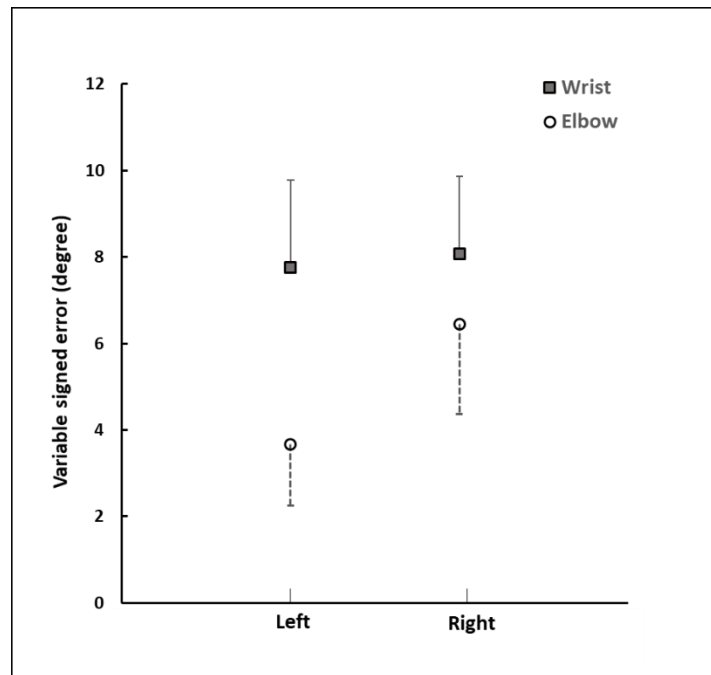


Figure 4: Variable Signed Error at the Wrist (filled squares), and Elbow (empty circles), for Each Response. Error bars represent standard deviation around the participants' mean.

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.

319

320

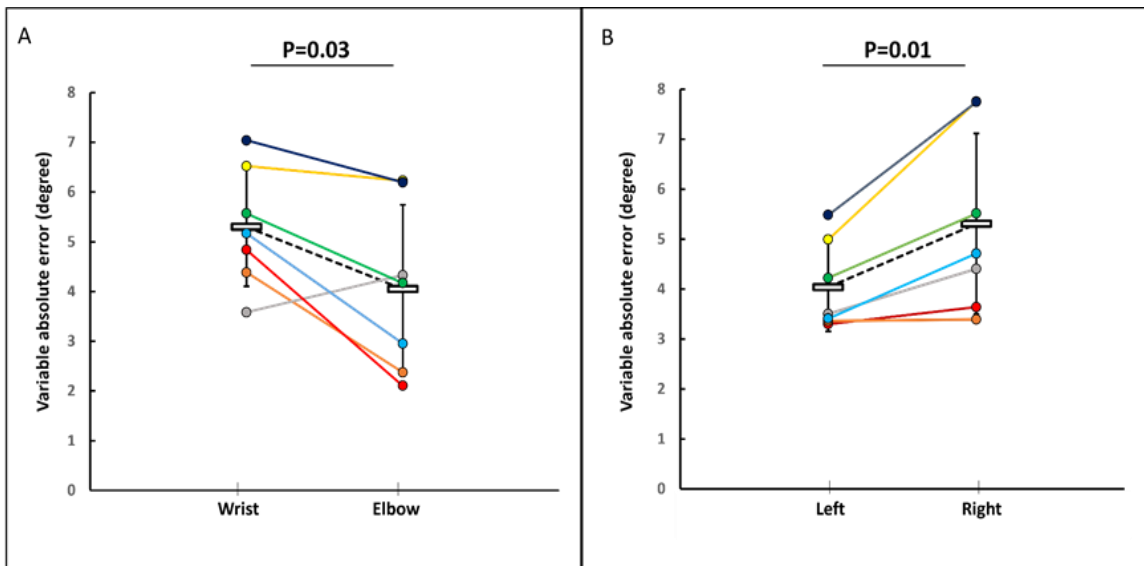


Figure 5: Variable Absolute Error for each Participant (colored dots) and Group Means (empty rectangles). Error bars represent the standard deviation around the participant's mean. (A) Joint effect. (B) Laterality effect.

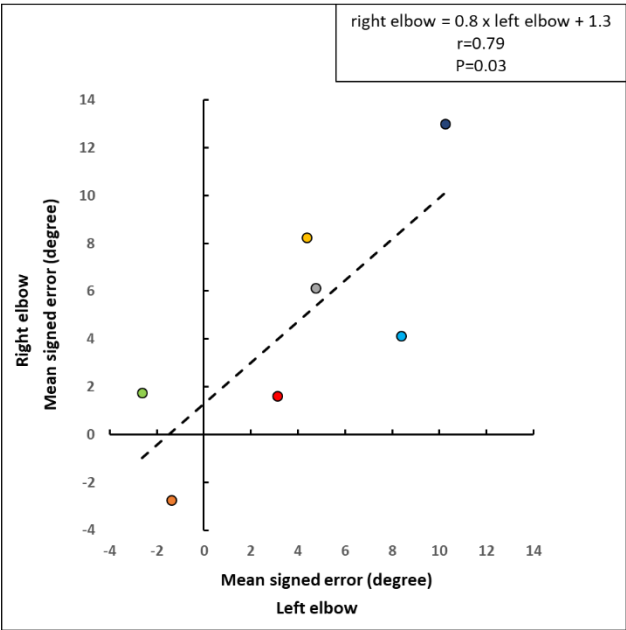
321

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 = $1.0 \times \text{right wrist} - 1.3$, $r=0.83$,
337 $p=0.01$) and at the right and left wrists (left wrist = $1.0 \times \text{right wrist} + 0.02$, $r=0.86$,
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 = $0.9 \times \text{left wrist} + 0.4$, $r=0.83$, $p=0.01$). 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

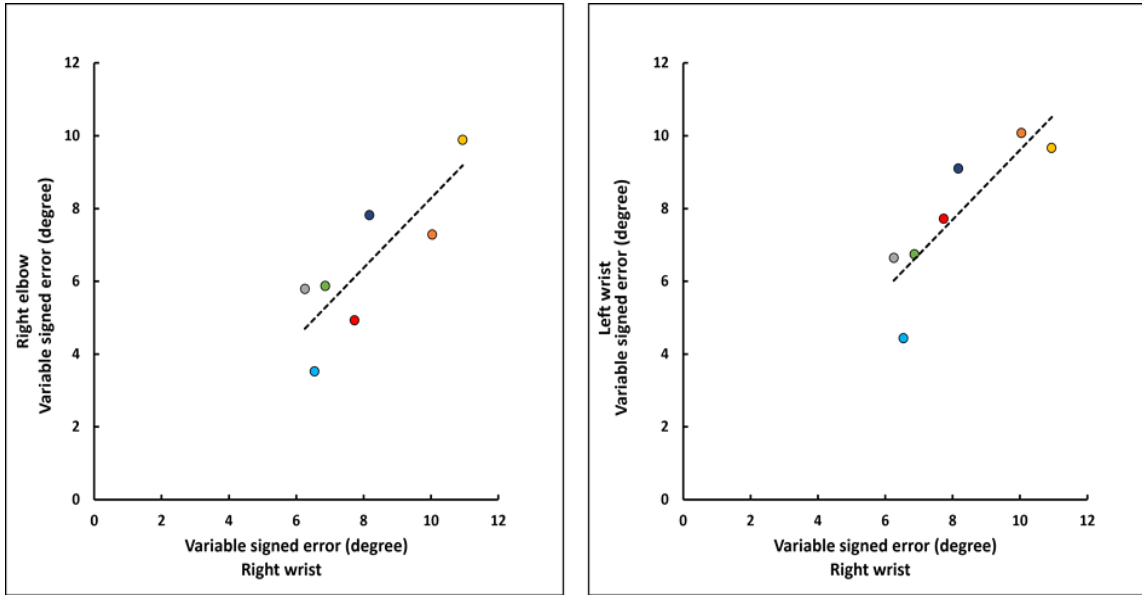


Figure 7: Relationship between Variable Signed Errors of Each Participant (according to the same color code as in Figures 5 and 6). Each linear regression (dashed line) is displayed to aid visualization. (A) Right wrist and right elbow. (B) Right and left wrists.

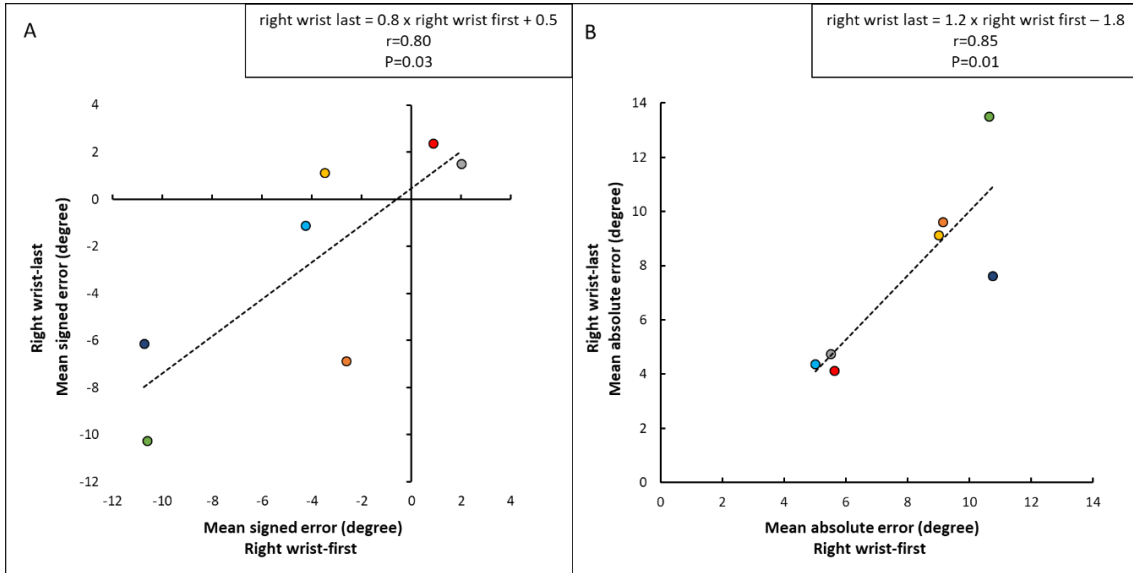
349

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.

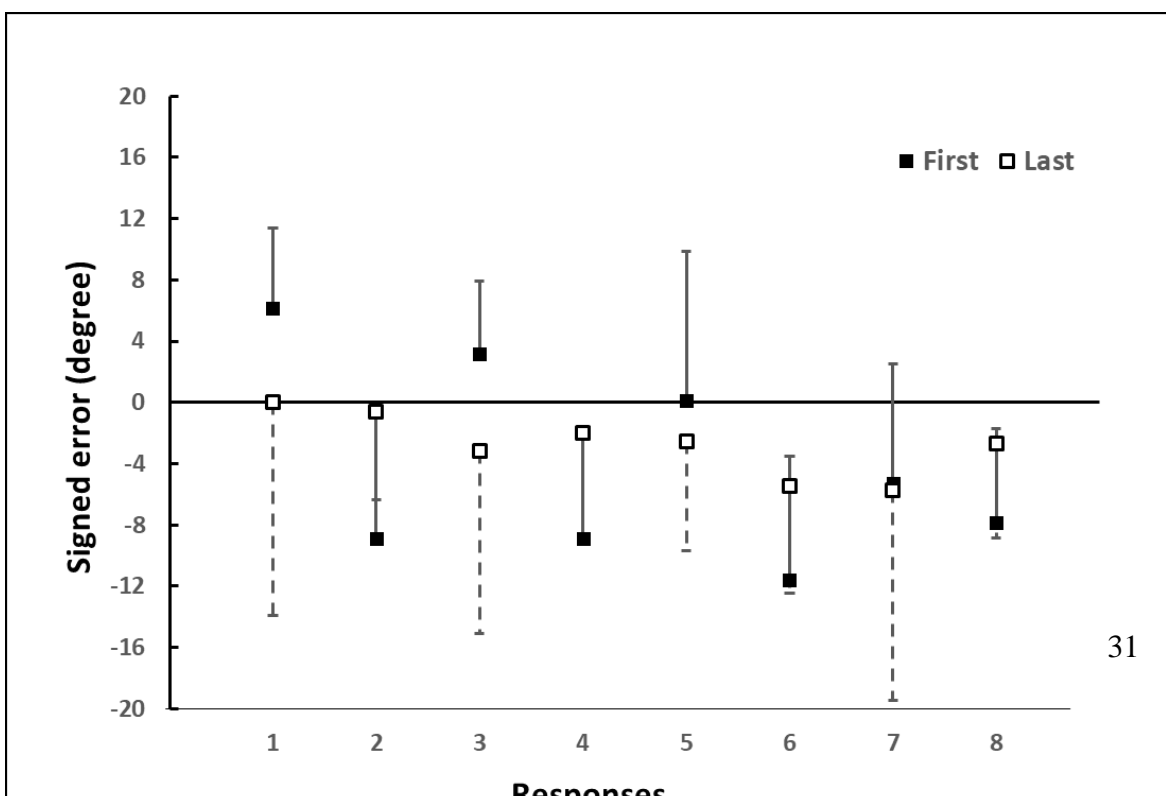
367

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.

526 **References**

- 527 Adamo, D. E., & Martin, B. J. (2009). Position sense asymmetry. *Experimental Brain*
528 *Research*, 192(1), 87–95. <https://doi.org/10.1007/s00221-008-1560-0>
- 529 Allen, T. J., Ansems, G. E., & Proske, U. (2007). Effects of muscle conditioning on
530 position sense at the human forearm during loading or fatigue of elbow flexors and
531 the role of the sense of effort. *Journal of Physiology*, 580(2), 423–434.
532 <https://doi.org/10.1113/jphysiol.2006.125161>
- 533 Banks, R., & Stacey, M. (1988). Quantitative Studies on Mammalian Muscle Spindles
534 and their Sensory Innervation. In P. Hník, T. Soukup, R. Vejsada, & J. Zelená
535 (Eds.), *Mechanoreceptors*. Springer, Boston, MA.
536 https://doi.org/https://doi.org/10.1007/978-1-4899-0812-4_49
- 537 Carey, L. M., Oke, L. E., & Matyas, T. A. (1996). Impaired limb position sense after
538 stroke: A quantitative test for clinical use. *Archives of Physical Medicine and*
539 *Rehabilitation*, 77(12), 1271–1278. [https://doi.org/10.1016/S0003-9993\(96\)90192-](https://doi.org/10.1016/S0003-9993(96)90192-6)
540 [6](https://doi.org/10.1016/S0003-9993(96)90192-6)
- 541 Cole, J. (2016). *Losing touch: A man without his body*. Oxford University Press.
- 542 Colley, A. (1984). Spatial Location Judgements by Right and Left-Handers. *Cortex*,
543 20(1), 47–53. [https://doi.org/10.1016/S0010-9452\(84\)80022-2](https://doi.org/10.1016/S0010-9452(84)80022-2)
- 544 Darling, W. G., & Hondzinski, J. M. (1999). Kinesthetic perceptions of earth- and body-

545 fixed axes. *Experimental Brain Research*, 126, 417–430.
546 <https://doi.org/10.1007/s002210050748>

547 Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for
548 fast reaching movements. *Trends in Cognitive Sciences*, 4(11), 423–431.
549 [https://doi.org/10.1016/S1364-6613\(00\)01537-0](https://doi.org/10.1016/S1364-6613(00)01537-0)

550 Elangovan, N., Herrmann, A., & Konczak, J. (2014). Assessing Proprioceptive
551 Function: Evaluating Joint Position Matching Methods Against Psychophysical
552 Thresholds. *Physical Therapy*, 94(4), 553–561.
553 <https://doi.org/https://doi.org/10.2522/ptj.20130103>Forestier, N., Teasdale, N., &
554 Nougier, V. (2002). Alteration of the position sense at the ankle induced by
555 muscular fatigue in humans. *Medicine and Science in Sports and Exercise*, 34(1),
556 117–122. <https://doi.org/10.1097/00005768-200201000-00018>

557 Fuentes, C. T., & Bastian, A. J. (2010). Where is your arm? Variations in
558 proprioception across space and tasks. *Journal of Neurophysiology*, 103(1), 164–
559 171. <https://doi.org/10.1152/jn.00494.2009>

560 Gandevia, S. C. (2014). Proprioception, tensegrity, and motor control. *Journal of Motor*
561 *Behavior*, 46(3), 199–201. <https://doi.org/10.1080/00222895.2014.883807>

562 Gandevia, S. C., & Burke, D. (1992). Does the nervous system depend on kinesthetic
563 information to control natural limb movements? *Behavioral and Brain Sciences*,

564 15(4), 614–632. <https://doi.org/10.1017/s0140525x0007254x>

565 Gandevia, S. C., Smith, J. L., Crawford, M., Proske, U., & Taylor, J. L. (2006). Motor
566 commands contribute to human position sense. *Journal of Physiology*, 571(3),
567 703–710. <https://doi.org/10.1113/jphysiol.2005.103093>

568 Gardner, E. P., & Johnson, K. O. (2013). The somatosensory system: receptors and
569 central pathways. In E. R. Kandel, J. H. Schwartz, T. M. Jessel, S. A. Siegelbaum,
570 & A. J. Hudspeth (Eds.), *Principles of neural science* (Fifth, pp. 475–496).
571 McGraw-Hill Companies.

572 Goble, D. J., & Brown, S. H. (2007). Task-dependent asymmetries in the utilization of
573 proprioceptive feedback for goal-directed movement. *Experimental Brain*
574 *Research*, 180(4), 693–704. <https://doi.org/10.1007/s00221-007-0890-7>

575 Goble, D. J., & Brown, S. H. (2008a). The biological and behavioral basis of upper limb
576 asymmetries in sensorimotor performance. *Neuroscience and Biobehavioral*
577 *Reviews*, 32(3), 598–610. <https://doi.org/10.1016/j.neubiorev.2007.10.006>

578 Goble, D. J., & Brown, S. H. (2008b). Upper limb asymmetries in the matching of
579 proprioceptive versus visual targets. *Journal of Neurophysiology*, 99(6), 3063–
580 3074. <https://doi.org/10.1152/jn.90259.2008>

581 Goble, D. J., & Brown, S. H. (2010). Upper limb asymmetries in the perception of
582 proprioceptively determined dynamic position sense. *Journal of Experimental*

- 583 *Psychology: Human Perception and Performance*, 36(3), 768–775.
584 <https://doi.org/10.1037/a0018392>
- 585 Goble, D. J., Hurvitz, E. A., & Brown, S. H. (2009). Deficits in the ability to use
586 proprioceptive feedback in children with hemiplegic cerebral palsy. *International*
587 *Journal of Rehabilitation Research*, 32(3), 267–269.
588 <https://doi.org/10.1097/MRR.0b013e32832a62d5>
- 589 Goble, D. J., Lewis, C. A., & Brown, S. H. (2006). Upper limb asymmetries in the
590 utilization of proprioceptive feedback. *Experimental Brain Research*, 168(1–2),
591 307–311. <https://doi.org/10.1007/s00221-005-0280-y>
- 592 Goble, D. J., Mousigian, M. A., & Brown, S. H. (2012). Compromised encoding of
593 proprioceptively determined joint angles in older adults: The role of working
594 memory and attentional load. *Experimental Brain Research*, 216(1), 35–40.
595 <https://doi.org/10.1007/s00221-011-2904-8>
- 596 Hall, L. A., & McCloskey, D. I. (1983). Detections of movements imposed on finger,
597 elbow and shoulder joints. *Journal of Physiology*, 335, 519–533.
598 <https://doi.org/https://doi.org/10.1113/jphysiol.1983.sp014548>
- 599 Han, J., Adams, R., Waddington, G., & Anson, J. (2013a). Ability to discriminate
600 movements at multiple joints around the body: global or site-specific. *Perceptual*
601 *and Motor Skills*, 116, 59–68. <https://doi.org/10.2466/24.10.23.PMS.116.1.59-68>

602 Han, J., Anson, J., & Waddington, G. (2013b). Proprioceptive performance of bilateral
603 upper and lower limb joints : side-general and site-specific effects. *Experimental*
604 *Brain Research*, 226, 313–323. <https://doi.org/10.1007/s00221-013-3437-0>

605 Izumizaki, M., Tsuge, M., Akai, L., Proske, U., & Homma, I. (2010). The illusion of
606 changed position and movement from vibrating one arm is altered by vision or
607 movement of the other arm. *Journal of Physiology*, 588(15), 2789–2800.
608 <https://doi.org/10.1113/jphysiol.2010.192336>

609 Jayasinghe, S. AL, Sarlegna, F. R., Scheidt, R. A., & Sainburg, R. L. (2021).
610 Somatosensory deafferentation reveals lateralized roles of proprioception in
611 feedback and adaptive feedforward control of movement and posture. *Current*
612 *Opinion in Physiology*, 19, 141–147. <https://doi.org/10.1016/j.cophys.2020.10.005>

613 Khabie, V., Schwartz, M. C., Rokito, A. S., Gallagher, M. A., Cuomo, F., &
614 Zuckerman, J. D. (1998). The effect of intraarticular anesthesia and elastic bandage
615 on elbow proprioception. *Journal of Shoulder and Elbow Surgery*, 7(5), 501–504.
616 [https://doi.org/10.1016/s1058-2746\(98\)90202-6](https://doi.org/10.1016/s1058-2746(98)90202-6)

617 King, J., Harding, E., & Karduna, A. (2013). The shoulder and elbow joints and right
618 and left sides demonstrate similar joint position sense. *Journal of Motor Behavior*,
619 45(6), 479–486. <https://doi.org/10.1080/00222895.2013.832136>

620 Kurian, G., Sharma, N. K., & Santhakumari, K. (1989). Left-arm dominance in active

- 621 positioning. *Perceptual and Motor Skills*, 68(3 Pt 2), 1312–1314.
622 <https://doi.org/10.2466/pms.1989.68.3c.1312>
- 623 Lakie, M., & Campbell, K. S. (2019). Muscle thixotropy — where are we now? *Journal*
624 *of Applied Physiology*, 126(6), 1790–1799.
625 <https://doi.org/10.1152/jappphysiol.00788.2018>
- 626 Laprevotte, J., Papaxanthis, C., Saltarelli, S., Quercia, P., & Gaveau, J. (2021).
627 Movement detection thresholds reveal proprioceptive impairments in
628 developmental dyslexia. *Scientific Reports*, 11(1), 1–7.
629 <https://doi.org/10.1038/s41598-020-79612-4>
- 630 Lephart, S. M., & Fu, F. H. (2000). *Proprioception and neuromuscular control in joint*
631 *stability*. Human kinetics.
- 632 Li, K. Y., & Wu, Y. H. (2014). Clinical evaluation of motion and position sense in the
633 upper extremities of the elderly using motion analysis system. *Clinical*
634 *Interventions in Aging*, 9, 1123–1131. <https://doi.org/10.2147/CIA.S62037>
- 635 Marini, F., Hughes, C. M. L., Morasso, P., & Masia, L. (2017). The effects of age and
636 amplitude on wrist proprioceptive acuity. *IEEE International Conference on*
637 *Rehabilitation Robotics*, 609–614. <https://doi.org/10.1109/ICORR.2017.8009315>
- 638 Matthews, P. B. C. (1972). *Mammalian Muscle Receptors and Central Actions*. Edward
639 Arnold.

- 640 Matthews, P. B. C. (1988). Proprioceptors and their contribution to somatosensory
641 mapping: Complex messages require complex processing. *Canadian Journal of*
642 *Physiology and Pharmacology*, 66(4), 430–438. <https://doi.org/10.1139/y88-073>
- 643 Naito, E., Nakashima, T., Kito, T., Aramaki, Y., Okada, T., & Sadato, N. (2007).
644 Human limb-specific and non-limb-specific brain representations during
645 kinesthetic illusory movements of the upper and lower extremities. *European*
646 *Journal of Neuroscience*, 25(11), 3476–3487. [https://doi.org/10.1111/j.1460-](https://doi.org/10.1111/j.1460-9568.2007.05587.x)
647 [9568.2007.05587.x](https://doi.org/10.1111/j.1460-9568.2007.05587.x)
- 648 Naito, E., Roland, P. E., Grefkes, C., Choi, H. J., Eickhoff, S., Geyer, S., Zilles, K., &
649 Ehrsson, H. H. (2004). Dominance of the right hemisphere and role of area 2 in
650 human kinesthesia. *Journal of Neurophysiology*, 93(2), 1020–1034.
651 <https://doi.org/10.1152/jn.00637.2004>
- 652 Pearson, K. (2001). Proprioceptive Sensory Feedback. *In Encyclopedia of Life Sciences*.
653 Nature Publishing Group. <https://doi.org/10.1038/npg.els.0000071>
- 654 Proske, U., & Gandevia, S. C. (2012). The proprioceptive senses: Their roles in
655 signaling body shape, body position and movement, and muscle force.
656 *Physiological Reviews*, 92(4), 1651–1697.
657 <https://doi.org/10.1152/physrev.00048.2011>
- 658 Proske, U., Tsay, A., & Allen, T. (2014). Muscle thixotropy as a tool in the study of

659 proprioception. *Experimental Brain Research*, 232, 3397–3412.
660 <https://doi.org/10.1007/s00221-014-4088-5>

661 Ramsay, J. R., & Riddoch, M. J. (2001). Position-matching in the upper limb:
662 Professional ballet dancers perform with outstanding accuracy. *Clinical*
663 *Rehabilitation*, 15(3), 324–330. <https://doi.org/10.1191/026921501666288152>

664 Ribeiro, F., & Oliveira, J. (2007). Aging effects on joint proprioception: The role of
665 physical activity in proprioception preservation. *European Review of Aging and*
666 *Physical Activity*, 4(2), 71–76. <https://doi.org/10.1007/s11556-007-0026-x>

667 Rothwell, J. C., Traub, M. M., Day, B. L., Obeso, J. A., Thomas, P. K., & Marsden, C.
668 D. (1982). Manual motor performance in a deafferented man. *Brain*, 105(3), 515–
669 542. <https://doi.org/10.1093/brain/105.3.515>

670 Roy, E. A., & MacKenzie, C. (1978). Handedness Effects in Kinesthetic Spatial
671 Location Judgements. *Cortex*, 14(2), 250–258. [https://doi.org/10.1016/S0010-](https://doi.org/10.1016/S0010-9452(78)80051-3)
672 [9452\(78\)80051-3](https://doi.org/10.1016/S0010-9452(78)80051-3)

673 Sainburg, R. L. (2014). Convergent models of handedness and brain lateralization.
674 *Frontiers in Psychology*, 5, 1–14. <https://doi.org/10.3389/fpsyg.2014.01092>

675 Sarlegna, F. R., Gauthier, G. M., Bourdin, C., Vercher, J. L., & Blouin, J. (2006).
676 Internally driven control of reaching movements: A study on a proprioceptively
677 deafferented subject. *Brain Research Bulletin*, 69(4), 404–415.

678 <https://doi.org/10.1016/j.brainresbull.2006.02.005>

679 Sarlegna, F. R., Malfait, N., Bringoux, L., Bourdin, C., & Vercher, J. L. (2010). Force-
680 field adaptation without proprioception: Can vision be used to model limb
681 dynamics? *Neuropsychologia*, *48*(1), 60–67.
682 <https://doi.org/10.1016/j.neuropsychologia.2009.08.011>

683 Schober, P., & Schwarte, L. A. (2018). Correlation coefficients: Appropriate use and
684 interpretation. *Anesthesia and Analgesia*, *126*(5), 1763–1768.
685 <https://doi.org/10.1213/ANE.0000000000002864>

686 Scott, S. H., & Loeb, G. E. (1994). The computation of position sense from spindles in
687 mono- and multiarticular muscles. *Journal of Neuroscience*, *14*(12), 7529–7540.
688 <https://doi.org/10.1523/jneurosci.14-12-07529.1994>

689 Scott, Stephen H. (2016). A Functional Taxonomy of Bottom-Up Sensory Feedback
690 Processing for Motor Actions. *Trends in Neurosciences*, *39*(8), 512–526.
691 <https://doi.org/10.1016/j.tins.2016.06.001>

692 Sevrez, V., & Bourdin, C. (2015). On the Role of Proprioception in Making Free
693 Throws in Basketball. *Research Quarterly for Exercise and Sport*, *86*(3), 274–280.
694 <https://doi.org/10.1080/02701367.2015.1012578>

695 Smith, J. L., Crawford, M., Proske, U., Taylor, J. L., & Gandevia, S. C. (2009). Signals
696 of motor command bias joint position sense in the presence of feedback from

697 proprioceptors. *Journal of Applied Physiology*, 106(3), 950–958.
698 <https://doi.org/10.1152/jappphysiol.91365.2008>

699 Sturnieks, D. L., Wright, J. R., & Fitzpatrick, R. C. (2007). Detection of simultaneous
700 movement at two human arm joints. *Journal of Physiology*, 585(3), 833–842.
701 <https://doi.org/10.1113/jphysiol.2007.139089>

702 Tripp, B. L., Uhl, T. L., Mattacola, C. G., Srinivasan, C., & Shapiro, R. (2006). A
703 comparison of individual joint contributions to multijoint position reproduction
704 acuity in overhead-throwing athletes. *Clinical Biomechanics*, 21(5), 466–473.
705 <https://doi.org/10.1016/j.clinbiomech.2005.12.015>

706 Tuthill, J. C., & Azim, E. (2018). Proprioception. *Current Biology*, 28(5), R194–R203.
707 <https://doi.org/10.1016/j.cub.2018.01.064>

708 Waddington, G., & Adams, R. (1999). Ability to discriminate movements at the ankle
709 and knee is joint specific. *Perceptual and Motor Skills*, 89, 1037–1041.
710 <https://doi.org/10.2466/pms.1999.89.3.1037>

711 Walsh, L. D., Proske, U., Allen, T. J., & Gandevia, S. C. (2013). The contribution of
712 motor commands to position sense differs between elbow and wrist. *Journal of*
713 *Physiology*, 591(23), 6103–6114. <https://doi.org/10.1113/jphysiol.2013.259127>

714 White, O., & Proske, U. (2009). Illusions of forearm displacement during vibration of
715 elbow muscles in humans. *Experimental Brain Research*, 192(1), 113–120.

