

1 Proprioception is subject-specific and improved
2 without performance feedback

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21 **Abstract**

22 Accumulating evidence indicates that the human's proprioception map appears
23 subject-specific. However, whether the idiosyncratic pattern persists across time with
24 good within-subject consistency has not been quantitatively examined. Here we
25 measured the proprioception by a hand visual-matching task in multiple sessions over
26 two days. We found that people improved their proprioception when tested
27 repetitively without performance feedback. Importantly, despite the reduction of
28 average error, the spatial pattern of proprioception errors remained idiosyncratic.
29 Based on individuals' proprioceptive performance, a standard convolutional neural
30 network classifier could identify people with good accuracy. We also found that
31 subjects' baseline proprioceptive performance could not predict their motor
32 performance in a visual trajectory-matching task even though both tasks require
33 accurate mapping of hand position to visual targets in the same workspace. Using a
34 separate experiment, we not only replicated these findings but also ruled out the
35 possibility that performance feedback during a few familiarization trials caused the
36 observed improvement in proprioception. We conclude that the conventional
37 proprioception test itself, even without feedback, can improve proprioception but
38 leave the idiosyncrasy of proprioception unchanged.

39

40

41 **Keywords**

42 Proprioception, kinaesthesia, visuomotor mapping, motor performance, motor
43 learning

44

45

46 **Introduction**

47 Knowing the spatial position of one's hand is important for humans to maintain
48 postures and perform actions. Both visual and proprioceptive cues are used for
49 locating hands in space (Welch 1986; Van Beers et al. 1999). Though visual
50 information plays a dominant role when both types of cues are available (Jeannerod
51 1988, 1991; Helms Tillery et al. 1994), proprioception continuously updates the
52 nervous system about the hand location. It has been found that the hand location, if
53 informed by proprioception alone, gradually drifts without visual calibration (Wann
54 and Ibrahim 1992; Brown et al. 2003b, a). However, how proprioception changes over
55 time has not been systematically investigated.

56

57 Previous studies have revealed that the accuracy of proprioception varies in the hand
58 space, leading to spatial patterns of proprioceptive errors that are heterogeneous
59 among individuals (van Beers et al. 1998; Haggard et al. 2000; Fuentes and Bastian
60 2009). On the group level, the accuracy of proprioception was affected by the distance
61 from the body, with small proprioceptive errors in the areas close to the body and
62 large errors in the areas away from the body (Wilson et al. 2010). The proprioceptive
63 estimation of the left hand was biased to the left while that of the right hand to the
64 right (Jones et al. 2010; Rincon-Gonzalez et al. 2011). Besides these general patterns
65 on the group level, proprioception showed large inter-individual differences in the
66 spatial pattern of accuracy (Brown et al. 2003b; Smeets et al. 2006). Measured by
67 visual-matching tasks, the proprioception maps remained similar across conditions
68 within a participant but differed widely across participants (Helms Tillery et al. 1994;
69 Rincon-Gonzalez et al. 2011). As another indirect evidence of within-subject
70 consistency, people also found that the proprioception map measured by a visual-
71 matching task and by a pointing task were strongly correlated within a participant
72 (Vindras et al. 1998).

73

74 However, to our knowledge, the subject-specificity of the proprioception map has
75 never been systematically examined. Many previous studies reached their conclusions
76 by eyeballing of data (Brown et al. 2003b; van den Dobbelaer et al. 2004; Smeets et
77 al. 2006). Other studies calculated the within-subject correlation coefficients between
78 measurements from different conditions and found they were significantly larger than
79 zero (Wann and Ibrahim 1992; Desmurget et al. 2000). However, this kind of
80 correlation results only shows the similarity between conditions as opposed to the
81 idiosyncrasy of proprioception maps between subjects. A couple of studies computed
82 the within-subject correlation of proprioception maps and the between-subject
83 correlation, but they did not compare these correlations, possibly due to a limited
84 number of participants (Helms Tillery et al. 1994; Vindras et al. 1998; Rincon-
85 Gonzalez et al. 2011). In sum, no previous study has quantitatively examined the
86 idiosyncrasy of the proprioception map, leaving the question open about to what
87 extent one's proprioception map can be distinguished from others'.

88

89 Proprioception underlies motor performance in various tasks (Rosenbaum 2009).
90 Recent studies also found that motor learning and proprioceptive training could
91 benefit each other if these two tasks were similar. Proprioceptive training by passively
92 moving one's hand around a target circle could improve the subsequent motor
93 learning of drawing the target (Wong et al. 2012). Moreover, after a brief period of
94 motor learning, i.e., tracing a series of visual targets, participants improved their
95 accuracy of proprioception for more than 24 hours (Wong et al. 2011). Furthermore,
96 the proprioceptive improvement was limited in the region where participants
97 performed motor learning. With these findings, it is tempting to conjecture that
98 proprioceptive capacity might be able to predict the motor performance of the tasks
99 that require proprioceptive control of movements. A straightforward way to test this

100 hypothesis is to examine the relationship between the baseline accuracy of
101 proprioception and the baseline motor performance in the same workspace.

102

103 Here we used a hand visual-matching task with 100 target positions to obtain the
104 proprioceptive error map in the reachable space. To quantitatively study the subject-
105 specificity of proprioception map across time, we measured proprioception multiple
106 times over two days. To examine whether the baseline proprioceptive performance
107 can predict motor performance, we then tested a trajectory production task that
108 required accurate hand matching of visual templates. We found that the within-subject
109 variance of proprioception errors was much smaller than the between-subject
110 variance. Furthermore, based on people's proprioception tested on the first day, a
111 simple convolutional neural network classifier was able to identify the participant
112 based on the proprioception map measured on the second day with an accuracy
113 around 70% (base rate 1/47). We also found that proprioception measured by the
114 visual-matching task could not predict the motor performance in the trajectory
115 production task. Surprisingly, the accuracy of proprioception improved across days,
116 even though our measurements did not provide performance feedback. In a separate
117 experiment, we replicated our major findings and ruled out the possibility that limited
118 performance feedback during the familiarization trials caused the improvement in
119 proprioception across sessions.

120

121 **Methods**

122 **Participants**

123 A total of forty-seven graduate students and undergraduate students (30 males, age:
124 21.0 ± 2.2 yr, mean \pm SD) of Peking University were recruited for two experiments,

125 twenty-six for Experiment 1 and twenty-one for the Experiment 2. All participants
126 were confirmed to be right-handed by the Edinburgh handedness inventory (Oldfield,
127 1971). All participants were new to the experimental task, naive to the purpose of the
128 study, provided written informed consent before participating, and they received
129 either course credit or monetary compensation for their time. All experimental
130 protocols were approved by the Institutional Review Board of Peking University.

131

132 Experimental setup

133 The experimental setup had been used in our previous researches (Yin and Wei 2014;
134 Wei et al. 2014; Yin et al. 2016; Jiang et al. 2018). In all experiments, participants sat
135 in front of a digitizing tablet and held the digital stylus with their left hand (Fig. 1A).
136 They were instructed to match the tip of the stylus with either a point target or a
137 trajectory target that was displayed on a horizontal display. The display was first
138 projected on a back-projection screen horizontally placed above the tablet (LCD
139 projector; Acer P1270, refreshing rate of 75Hz). The display was then reflected by a
140 semi-silvered mirror placed horizontally at the chest level; the reflection matched in
141 height with the tablet where the participant's hand was. The participants viewed the
142 stimulus and feedback in the mirror while their view of the hand and arm was
143 occluded. The stylus movement on the tablet was one-to-one mapped onto the visual
144 display after calibration. Participants were required to perform the location matching
145 as accurate as possible with their preferred pace. They also centered their body with
146 the tablet during the whole experiment. The task was controlled by a customized
147 program written in MATLAB (Mathworks, Natick, MA; Psychophysics Toolbox).

148

149 Tasks

150 *Visual matching task*

151 In each trial, a white light dot (50 mm diameter) was presented on the semi-silvered
152 mirror to indicate the target position. The participants matched the target with the
153 digital stylus held by the left hand. To obtain an accurate proprioception map, we
154 included 100 target positions, which formed a 5 (row) \times 20 (column) matrix in the
155 workspace in front of the seated subject (Fig. 1B). The workspace was 48.76 cm wide
156 and 26.96 cm long, located 20 cm in front of the seated participant. The distance
157 between the adjacent columns was 24.38 mm, and that between the adjacent rows was
158 53.92 mm. Each target was measured once, and the order of targets was randomized.
159 After the participants pressed the space bar of a keyboard with their right hand, the
160 computer speaker played a beep sound to confirm the measurement. No performance
161 feedback was given. The target disappeared directly while the next target appeared in
162 a new position to start the next trial. The participants were allowed to move freely
163 from one target position to the next at their own pace. Before formal data collection,
164 we gave participants 16 familiarization trials for the visual matching task. Each trial
165 was associated with a different target, and the 16 targets were evenly spaced to form a
166 4 \times 4 matrix to cover the whole workspace. None of them overlapped with the targets
167 in the formal test. For these familiarization trials, the actual position of the stylus was
168 indicated by a green dot (50 mm diameter) for one second after the participant pressed
169 the confirmation key. The 16 target positions were shown one by one from the bottom
170 to the top and from left to right.

171

172 *Trajectory matching task*

173 The trajectory matching task was modified from a similar task in one of our previous
174 studies (Dam et al. 2013). In the workspace of the visual matching task described
175 above, we asked participants to produce a curved trajectory to “copy” a target
176 trajectory that was visually presented on the projection screen (Fig. 1B). Each trial

177 began with participants holding their left hand at a starting position indicated by a
178 dashed circle (40 mm diameter) at the bottom center of the workspace. After 100 ms,
179 the starting position changed from blue to green, and a beep sound was played to
180 signal the incoming movement. Then, a target trajectory (a 20 mm-wide red line)
181 appeared, stretching from the start position to the upper edge of the workspace. The
182 target trajectory was prescribed by the formula: $x = \alpha \times y + \beta \times \sin(\pi y)$, where y
183 indicated the displacement in the depth direction and x indicated the displacement in
184 the mediolateral direction. Numerically, y ranged between 0 and 1, where 1 represents
185 211 mm on the screen. Thus, the main direction and curvature of the curved trajectory
186 were determined by α and β , respectively. Participants were instructed to make a fast
187 movement to match the target trajectory without corrections accurately. During the
188 movement, no cursor feedback was given to show their actual hand position. After
189 reaching the upper edge of the workspace, another sound was played to indicate the
190 end of the trial. The participant returned the stylus to the starting position without
191 continuous cursor guidance. The hand location was only displayed as a white cursor
192 (30 mm diameter) when it was within 5 cm around the starting position. No
193 performance feedback was given, and a new trajectory appeared after one second.

194

195 To assess people's performance for trajectory matching, we used fifteen target
196 trajectories that were evenly distributed over the whole workspace (Fig. 1B). These
197 trajectories were set by varying α from -1 to 1 and β from -0.9 to 0.8. All target
198 trajectories started from the starting position at ($x = 0$, $y = 0$) and ended when $y = 1$.
199 The target trajectories were presented in a random order, and each appeared twice in a
200 row. Before the formal test, we gave each participant four trials to familiarize the task
201 with a single target trajectory ($\alpha = 0$, $\beta = 0.1$), which was not used in the formal
202 experiment. In the first two practice trials, people received terminal feedback by
203 viewing the actual movement trajectory made along with the target trajectory

204 immediately after the movement end. The next two practice trials were the same as
205 the formal trial without terminal feedback.

206

207 The participant was not allowed to start a movement before the start position turned
208 green. Also, no backward movement towards the body was allowed. Warning
209 messages, i.e., "Do not move before the start position turns green" or "Do not move
210 backward," were shown on the screen if these trials were detected. To avoid slow
211 movement, we computed their average movement speed on each trial and compared it
212 to the lowest speed allowed (165 mm/s). Movements slower than this threshold were
213 regarded as invalid, and a warning message ("Too slow") was displayed at the trial
214 end to urge participants to move faster. All invalid trials were repeated immediately.

215

216 Experimental protocols

217 *Experiment 1*

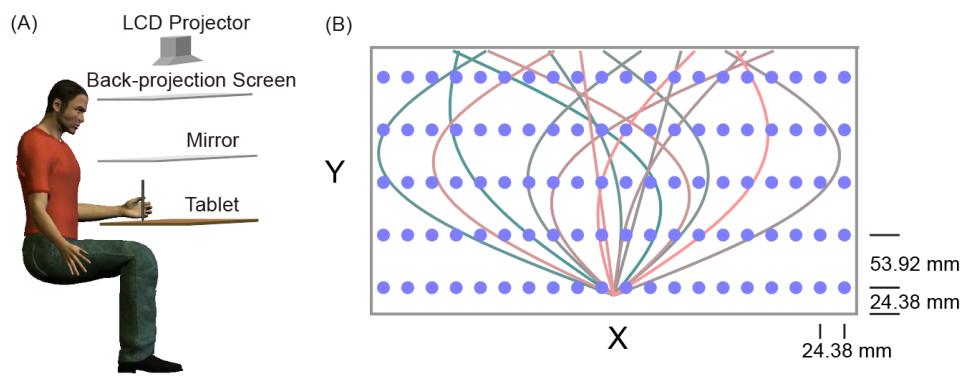
218 Experiment 1 was designed to test whether the proprioceptive performance was
219 subject-specific and stable across days and whether it correlates to motor
220 performance. It included three sessions with the first two sessions on day 1 and the
221 third one on day 2 (Fig. 1C). There was a forty-minute rest between the first two
222 sessions and a twenty-four hours interval between the last two sessions. The trajectory
223 matching task was performed at the end of the first proprioception measurement, and
224 it took about five minutes. Session 1 and session 3 started with a sixteen-trial
225 familiarization, which provided participants with feedback at the end of each trial.

226

227 *Experiment 2*

228 We found that proprioception improved across sessions without any performance
229 feedback in Experiment 1. One confound was that the 16 familiarization trials before
230 session 3 provided performance feedback, which might improve people's
231 proprioceptive performance, as shown in the subsequent measurement sessions. In
232 Experiments 2, we removed the familiarization trials before session 3 and added a 4th
233 session with its own familiarization trials. Other procedures remained the same as in
234 Experiment 1. Therefore, Experiment 2 included four sessions, two on the first day
235 and two on the second day. We were particularly interested in the proprioceptive test
236 of session 3: the previously observed improvement in this session should be absent if
237 it was a result of familiarization trials with feedback. Similarly, we should observe an
238 improvement in session 4 if the familiarization trials mattered.

239



240

241 Fig.1. Experimental setup and material. A) Experimental setup. B) A schematic illustration of
242 screen display during the experiment. Blue dots indicate the 100 target positions in the visual-
243 matching task. Colored lines indicate the 15 target trajectories in the trajectory matching task.

244

245 Data Analysis

246 The overall proprioception accuracy was quantified by the average visual-matching
247 error at the 100 target positions in one session. The error was defined as the Euclid

248 distance between the location of the target position (x_t, y_t) and the actual position of
249 the stylus tip. To compare the proprioception error in different areas, we divided the
250 workspace evenly into left and right regions by the vertical midline, and into inside
251 and outside regions by the horizontal midline. Thus, the left region covered the ten
252 columns of targets on the left, and the right region covered the other ten columns of
253 targets on the right. The inside region covered the three rows close to the participant's
254 body, and the outside region covered the other two rows away from the body. To
255 quantify within-subjects and between-subjects variance of proprioception maps, we
256 compute the Pearson correlation coefficients of the error vectors across sessions and
257 between individuals, respectively. The same correlation analysis was also applied to
258 the Euclid distance.

259

260 As proprioception errors improved across sessions, we calculated the error reduction
261 as the percentage difference between the first session and the other sessions by
262 $100\% \times (\text{error}_1 - \text{error}_i)/\text{error}_1$, where error_1 refers to the proprioception error of
263 the first session and error_i refers to that of compared sessions ($i = 2, 3, 4$).

264

265 For the trajectory production task, the motor error was defined by the root mean
266 square error (RMSE) between the target trajectory and the participant's movement
267 trajectory. Each movement trajectory was evenly divided into 30 segments along the
268 y-axis between the start position and the upper edge. The horizontal deviation in the x
269 direction at the cut points of adjacent segments was used to compute the RMSE for
270 each trial:

$$271 \quad \text{RMSE} = \sqrt{\sum_{y=1}^{30} (x_y - x_{y,t})^2},$$

272 where x_y and $x_{y,t}$ is the horizontal ordinate (x value) of the movement trajectory and
273 the target trajectory at the cut points, respectively. For each participant, we computed
274 their average motor error and average proprioceptive error in session 1, and then
275 computed the Pearson correlation between these two baseline performance measures
276 across participants. If the data did not meet the Gaussian assumption, the Spearman's
277 correlation was computed instead.

278

279 Average proprioception errors were compared between sessions or between regions
280 by repeated-measures ANOVAs. Post hoc comparisons between groups were
281 conducted with Bonferroni corrections. The homoscedasticity and normality
282 assumptions were examined before ANOVAs were performed. All dependent
283 variables met these assumptions unless otherwise mentioned. For the data violating
284 homoscedasticity assumptions, Greenhouse-Geisser correction was applied for
285 ANOVAs. For the data violating normal distribution, the natural logarithm function
286 was applied to transform the data into a normal distribution before ANOVAs. One-
287 sample t-tests were used to compare the error reduction percentage of each session
288 with zero. Paired t-tests were used for within-subject comparisons if normality
289 assumptions were satisfied. Otherwise, Wilcoxon t-tests were used. Correlation
290 coefficients were submitted to Fisher's Z transformation before comparisons. All
291 analyses were performed with MATLAB (The MathWorks, Natick, MA) and SPSS
292 version 19 (IBM, Somers, NY). The significance level was set at $p < 0.05$.

293

294 Convolutional neural network classifier

295 We used the convolutional neural network (CNN) algorithm to investigate to what
296 extent one's proprioception map was distinguishable from others'. We hypothesize
297 that if the proprioception map is idiosyncratic and stable, a classifier trained by one or

298 two sessions of proprioceptive performance will be able to identify the individual
299 from other individuals based on her/his later performance. Since the data structure of
300 the proprioception map is a matrix similar to a digital image, our CNN classifier was
301 constructed as a typical image classifier (Machine Learning Toolbox, MATLAB
302 2018b, Natick, MA). The input of the CNN classifier was a $2 \times 5 \times 20$ proprioception
303 error matrix, where the first dimension was the error direction (x and y, two
304 dimensions) at each target position and the other two dimensions representing the
305 coordinate dimensions of the 100 targets. The CNN classifier contained an input
306 layer, a convolution layer, and a normalization layer. A rectified linear unit was
307 applied as an activation function, followed by a drop out layer and a fully connected
308 layer. Finally, a SoftMax function was applied to change the output into the
309 probability of each class. The kernel size of the convolution layer was 3, and the
310 number of output filters was 13. The cross-entropy was used as the loss function, and
311 the Stochastic Gradient Descent with momentum (SGDM) was used to optimize the
312 CNN classifier. The initial learning rate was set at 0.01. The CNN classifier was
313 trained for 250 to 500 epochs according to the size of the training set, and the input
314 sequence was shuffled every epoch.

315

316 In Experiment 1, proprioception maps in the first two sessions from each participant
317 served as the training set, and the maps in the third session made up the test set. In
318 Experiment 2, we used session 1, 2, and 3 as the training set and used session 4 as the
319 test set. We also collapsed participants from both experiments to test the classification
320 results: all sessions in Experiment 1 and the first three sessions in Experiment 2 were
321 used. Besides using the first two sessions (session 1 and session 2) to predict the last
322 session (session 3), we also tried to use session 1 to predict session 3, use session 2 to
323 predict session 3, and use session 1 to predict session 2. After training, the CNN
324 classifier was tested by identifying a participant from all participants based on his/her
325 proprioception map in the test set. The performance of the classifier was indexed by

326 the classification accuracy, i.e., the percentage of correctly identified error maps in the
327 test set.

328

329 **Results**

330 In Experiment 1, we found that repetitive measurements of proprioception improved
331 subjects' accuracy of visual matching task. This result is surprising, given that no
332 performance feedback was provided during the measurement. Despite the
333 improvement in the accuracy of proprioception, the spatial characteristics of the
334 proprioception map remained idiosyncratic, as shown by relatively large between-
335 subject variance and relatively small within-subject variance. Further support was that
336 the CNN classifier could identify people with decent accuracy based on her/his
337 proprioception map. Experiment 2 replicated the major findings of Experiment 1 and
338 ruled out the brief performance feedback during the familiarization trials as the cause
339 of improvement in proprioception across sessions.

340

341 **Experiment 1**

342 Experiment 1 aimed to examine whether the proprioceptive performance is
343 idiosyncratic and stable across a day. Interestingly, the average proprioception error
344 significantly reduced over the three sessions ($F(2,50) = 12.368, p < 0.001$, one-way
345 ANOVA; Fig 2A). The average proprioception errors of three sessions were $3.098 \pm$
346 0.776 cm, 2.944 ± 0.767 cm, and 2.420 ± 0.581 cm, respectively (means \pm SD, same
347 below). Post hoc pairwise comparisons indicated the proprioception error of the third
348 session was significantly smaller than that of the first session ($p < 0.001$) and the
349 second session ($p = 0.003$). However, there was no significant difference between the
350 first and the second session ($p = 0.787$), which means the proprioceptive accuracy

351 only improved significantly on the second day. The error reductions for the second
352 and third sessions were $3.15 \pm 20.95\%$ and $19.05 \pm 20.72\%$, respectively. Only the
353 third session had error reduction that was significantly larger than zero ($t(25) = 4.657$,
354 $p < 0.001$, one-sample t-test). For the trajectory matching task, the average movement
355 error was 2.172 ± 0.595 cm. The movement error did not correlate to the average
356 proprioception error in session 1 (Fig 2B, $r = 0.267$, $p = 0.187$) or session 2 ($r =$
357 0.295 , $p = 0.143$). Thus, the accuracy of proprioception measured by the visual-
358 matching task appears not predictive of the performance of the trajectory production
359 task, though both tasks require accurate localization of the hand in the reachable space
360 with visual targets.

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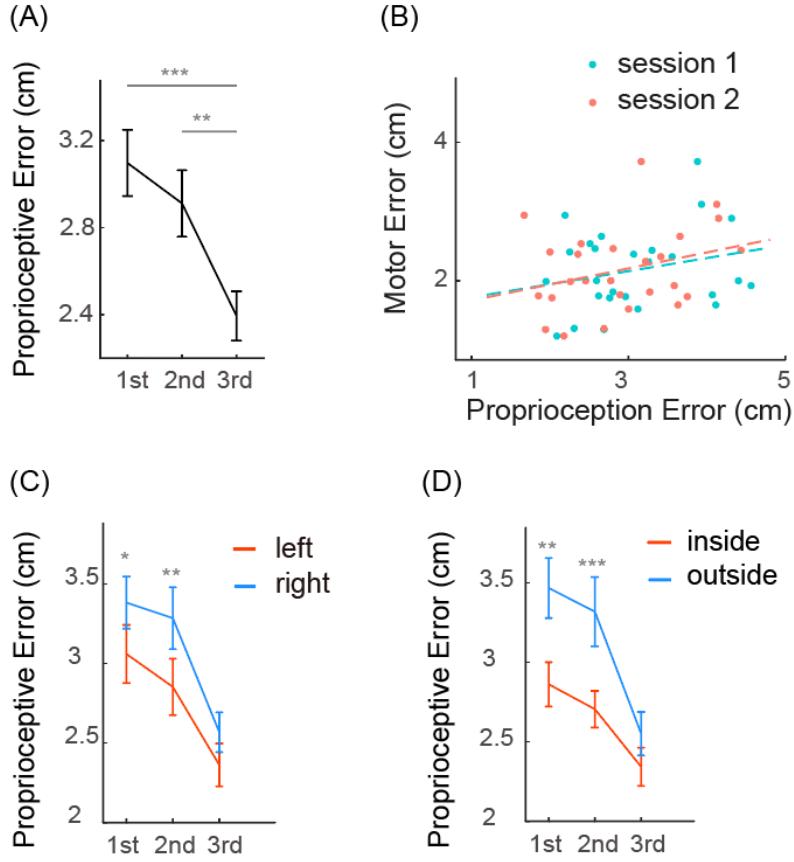
362 On the group level, the proprioception map showed similar spatial heterogeneity as in
363 previous studies (van Beers et al. 1998; Haggard et al. 2000; Fuentes and Bastian
364 2009). In the reachable workspace, the proprioceptive error was larger on the right
365 side than on the left side. The proprioception error of the left region were $3.061 \pm$
366 0.934 cm, 2.855 ± 0.905 cm, and 2.363 ± 0.690 cm for session 1, 2 and 3,
367 respectively. The proprioception error of the right region were 3.386 ± 0.838 cm,
368 3.287 ± 0.994 cm, and 2.569 ± 0.637 cm, respectively (Fig 2C. left). The
369 proprioception error of the left region was significantly smaller than that of the right
370 region in session 1 ($t(25) = -2.587$, $p = 0.016$, paired t-test) and 2 ($t(25) = -2.983$, $p =$
371 0.006 , paired t-test), but not in session 3 ($t(25) = -1.850$, $p = 0.076$, paired t-test). On
372 the other hand, the proprioceptive error was larger on the far side of the workspace
373 than on the near side. The proprioception errors of the near region were 2.861 ± 0.771
374 cm, 2.704 ± 0.588 cm, and 2.341 ± 0.613 cm for the three sessions, respectively. The
375 proprioception errors of the far region were 3.465 ± 0.961 cm, 3.316 ± 1.113 cm, and
376 2.549 ± 0.696 cm, respectively (Fig 2C., right). Again, the difference between these
377 two regions was significant in session 1 ($t(25) = -2.992$, $p = 0.006$, paired t-test) and 2
378 ($t(25) = -5.665$, $p < 0.001$, paired t-test), but not in session 3 ($t(25) = -1.835$, $p = 0.078$,

379 paired t-test). The improvement from session 1 to session 3 was also larger in the far
380 region (0.916 ± 0.915 cm) than in the close region (0.520 ± 0.767 cm, $t(25) = -3.506$,
381 $p = 0.002$, paired t-test). However, the improvement of the right region (0.745 ± 0.733
382 cm) and the left region (0.612 ± 0.945 cm) was not significantly different ($t(25) = -$
383 1.040 , $p = 0.308$, paired t-test). In summary, participants performed better in the left
384 region and in the near region when proprioception was measured in the reachable
385 workspace. These regional differences tended to decrease with improvement in
386 proprioceptive errors over successive sessions. It is worth noting that the
387 measurement session did not provide any feedback about their performance. The only
388 occasion that performance feedback was provided was the 16 familiarization trials
389 before session 3.

390

391 The error vectors of all participants at 100 target positions were averaged to construct
392 a group-level proprioception error map (Fig 3A). The error map of sessions 1, 2, and 3
393 shared a certain level of similarity. For example, the error vectors of session 1
394 generally pointed to the same directions as those of session 2 and 3. For all sessions,
395 most of the error vectors pointed rightwards with larger error magnitudes when more
396 away from the left shoulder.

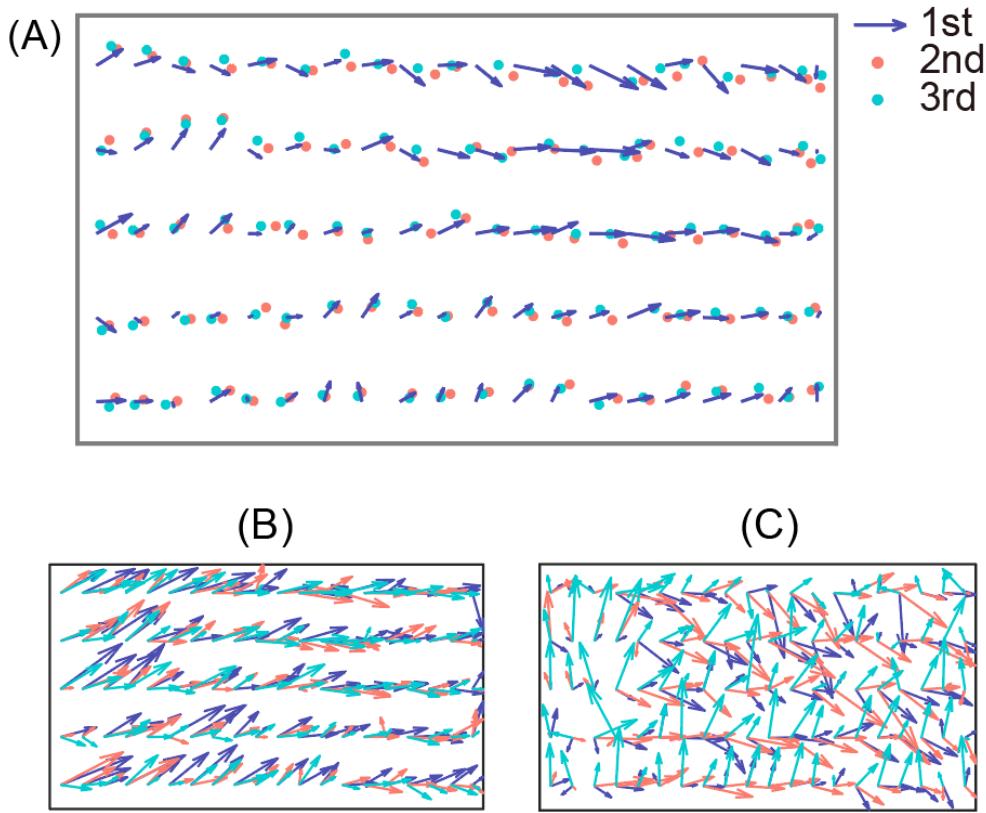
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398

399 Figure 2: Proprioception error and motor error in Experiment 1. A) Average proprioception
400 error in different measurement sessions. B) Scatter plot of motor errors and proprioception
401 errors from individual participants. The proprioception errors are plotted separately for
402 session 1 and session 2. The dots lines indicate their corresponding linear fits. C) Average
403 proprioception error of the left region and the right region. D) Average proprioception error of
404 the inside region and the outside regions. Error bar denotes SE. * $p < 0.05$; ** $p < 0.01$; *** $p <$
405 0.001.

406



407

408 Figure 3: Proprioception maps on the group level and from two selected participants. A) Error
409 map averaged over all participants. The purple arrow denotes the error vector of session 1
410 with its tail at the target location and its head at the actual hand location. The red and green
411 dots denote the actual hand location in session 2 and 3, respectively. B) Proprioception maps
412 from a typical participant whose error patterns remained similar across measurement sessions.
413 The inter-session correlation coefficient was 0.68, 0.73 and 0.73 for session 1 vs. 2, 2 vs. 3,
414 and 1 vs. 3, respectively. C) Proprioception maps from a typical participant whose error
415 patterns changed dramatically across sessions. The inter-session correlation coefficient was
416 0.58, -0.04, -0.08, respectively.

417

418 To quantitatively examine the similarity between proprioception maps, we calculated
419 the correlation of proprioception maps between session 1 and 2, between session 2
420 and 3, and between session 1 and 3 for each participant. The average correlation

421 coefficients were 0.462 ± 0.216 , 0.499 ± 0.196 and 0.412 ± 0.245 , respectively.

422 Examining individual participants, we found that 25 (sessions 1 and 2), 24 (sessions 2

423 and 3), and 23 (sessions 1 and 3) out of the 26 participants showed significant

424 correlations. These results indicate that the proprioception map remained stable across

425 sessions for most participants (see a typical participant in Fig 3B), and only a couple

426 of participants showed large changes across sessions (see a typical participant in Fig

427 3C). We found that correlation coefficients were significantly larger than zero on the

428 population level (all $t(25)s > 7$, $ps < 10^{-7}$). To establish a baseline correlation between

429 error maps, we computed all possible pairwise correlations between every two

430 participants ($n = 26*25$ for each of the three session pairs). For example, for the

431 correlation between session 1 and session 2, we calculated the correlation coefficients

432 between the 1st participant's proprioception map in session 1 with proprioception

433 maps of participants 2 to 26 in session 2, and thus obtained 25 correlation coefficients.

434 The same procedure was applied for each participant, resulting in $25*26$ correlation

435 coefficients that characterized the between-subject similarity of proprioception maps.

436 The between-subject correlation coefficients were 0.153 ± 0.251 , 0.147 ± 0.224 , and

437 0.139 ± 0.223 for session 1 and 2, session 2 and 3, and session 1 and 3, respectively.

438 These correlation coefficients were also significantly larger than zero due to the large

439 sample size (all $t(649)s > 15$, $ps < 10^{-7}$). Importantly, for all three types of pairwise

440 correlations, the within-subject correlation coefficients were significantly larger than

441 the between-subject correlation coefficients (all $t(649)s > 5$, $ps < 10^{-6}$, t-test; Fig 4A).

442 Thus, proprioception maps indeed demonstrated cross-session consistency within

443 individuals.

444

445 The within-subject and between-subject Euclidean distances between proprioception

446 maps were also compared to evaluate the participant specificity in the same way as

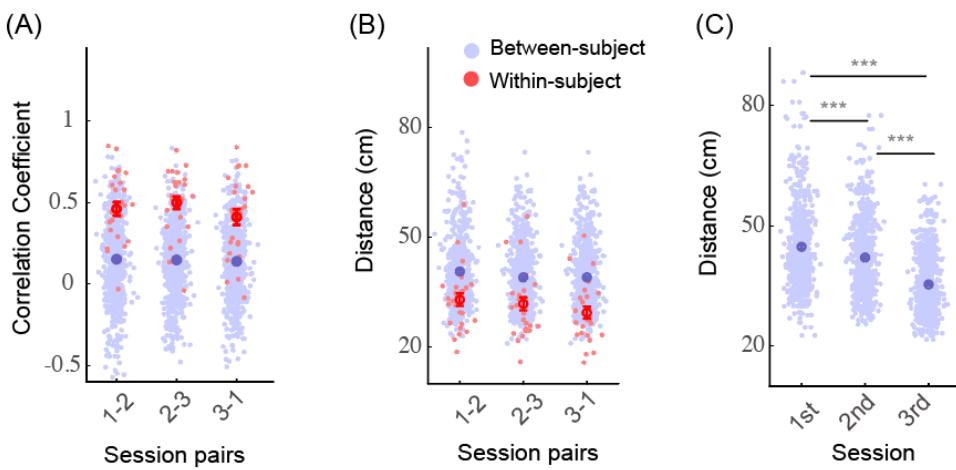
447 the correlation coefficient (Fig 4B). The within-subject distances (mean: 29.4-33.0

448 cm, SD: 8.2-9.1cm) were significantly smaller than the between-participant distances

449 (mean: 39.0-40.6cm, SD: 8.9-9.1cm) for all three groups (all Z s < -4, all p s < 0.001,
450 Wilcoxon t-test). In sum, proprioception errors remain idiosyncratic across sessions
451 and days despite the improvement in average proprioception error.

452

453 We observed that the between-subject variance declined across time. The distance
454 between the proprioception map of every two participants decreased across three
455 successive sessions ($n = 650$, Kendall's $W = 0.236$, $p < 0.001$, Fig 4C). Post hoc
456 pairwise comparison showed a significant decrease between every two successive
457 sessions (first-second: $Z = 3.913$, $p < 0.001$; second-third: $Z = 9.391$, $p < 0.001$,
458 Wilcoxon t-test), which indicates the idiosyncratic pattern of proprioception might
459 decrease with repetitive measurements.



460
461 Figure 4: subject-specificity of proprioception error map in Experiment 1. A) Correlation
462 coefficients between session pairs. Blue dots denote between-subject coefficients. Red dots
463 denote within-subject coefficients. Error bars denote mean and SE, the same below. B)
464 Comparisons of Euclidean distance between pairs of proprioception maps. C) The Euclidean
465 distance of proprioception maps from each pair of participants within a session. Each blue dot
466 stands for a distance measure between a pair of participants, and the error bar denotes mean
467 and SE. *** $p < 0.001$.

468

469 A convolutional neural network (CNN) classifier was trained and tested with the
470 proprioception maps to perform people identification. The CNN classifier was trained
471 for 350 echoes with the data from the first two sessions and tested with the data from
472 session 3. The training accuracy reached 100%, and the testing accuracy reached up to
473 73.08% (19/26), which was substantially higher than the chance level (1/26). This
474 means that the classifier was able to correctly identify most individuals by their
475 performance in session 3 on day 2 if their performance on day 1 was provided. From
476 this perspective, the spatial pattern of proprioception error was a person-specific
477 feature even when it changed over time with learning.

478

479 Experiment 2

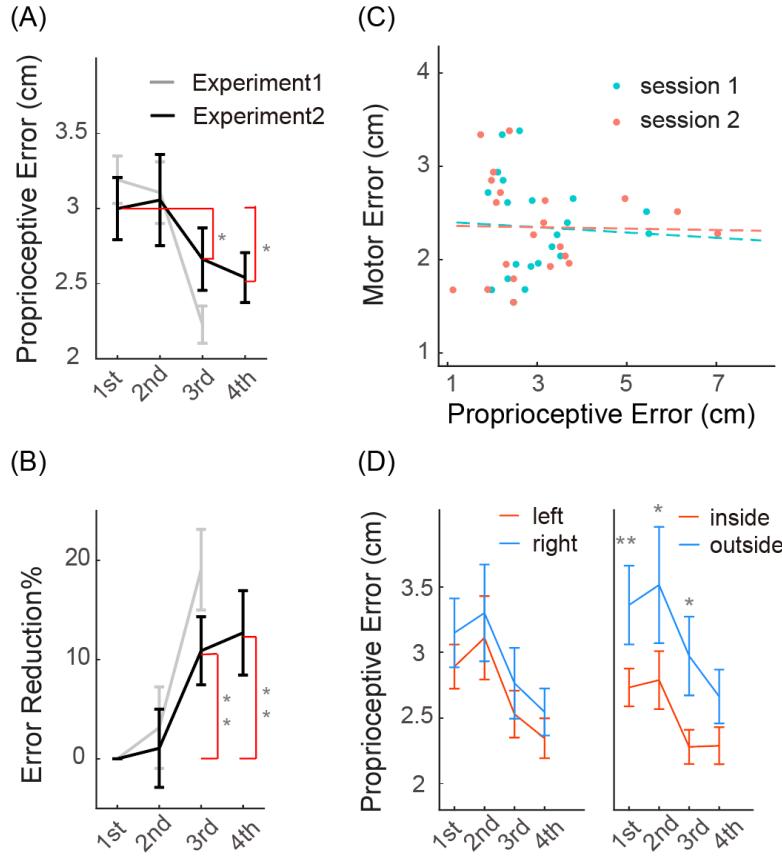
480 In Experiment 1, we observed significant improvement of proprioception accuracy
481 across sessions despite that no performance feedback was provided during the
482 measurement. One trivial explanation is that the 16-trial familiarization with feedback
483 before session 3 might serve as a learning session for the visual-matching task. In
484 Experiment 2, we thus canceled the 16-trial familiarization before session 3 to
485 examine this possibility. On day 2, we also added another 16-trial familiarization after
486 session 3 and before session 4 to further examine whether familiarization trials with
487 feedback would lead to the improvement in the proprioception test. Consistent with
488 Experiment 1, the proprioceptive accuracy improved with repetitive measurements
489 ($F(2.10,42.04) = 4.528, p = 0.015$, one-way ANOVA; Fig 5A). Post-hoc pairwise
490 comparisons indicated that the proprioception error of both session 3 ($p = 0.025$) and
491 session 4 ($p = 0.048$) was significantly smaller than the first two sessions on day 1.
492 The error reductions of session 2, 3, and 4 were $1.03 \pm 18.89\%$, $10.88 \pm 16.43\%$ and
493 $12.69 \pm 20.39\%$ respectively (means \pm SD; Fig 5B), with the latter two significantly
494 larger than zero (session 2: $t(20) = 0.258, p = 0.799$; session 3: $t(20) = 3.035, p =$

495 0.007; session 4: $t(20) = 2.853, p = 0.010$, one-sample t-test). The improvement in
496 session 3 confirmed that the improvement observed in Experiment 1 was caused by
497 repetitive measurements as opposed to feedback-based learning in the 16
498 familiarization trials. Providing familiarization trials with feedback before session 4
499 did not further improve the performance ($p = 1.000$), further against the possibility of
500 feedback-based learning.

501

502 Experiment 2 also replicated other findings in Experiment 1 (Figure 5). There was no
503 significant correlation between the trajectory-matching error (2.346 ± 0.527 cm, mean
504 \pm SD) and the proprioception error in session 1 ($r = -0.105, p = 0.649$, Spearman
505 correlation, Fig 5C) or session 2 ($r = -0.087, p = 0.707$, Spearman correlation).
506 Comparing average proprioceptive errors in different workspaces, we found that the
507 means of error in the right region was larger than that in the left region in all four
508 sessions, although none of comparisons reached significance ($p: 0.110 - 0.859$, Fig
509 5D. left, Wilcoxon t-test). The error of the near region was significantly smaller than
510 the error of the far region in the first three sessions (session 1: $Z = -2.868, p = 0.004$;
511 session 2: $Z = -2.103, p = 0.035$; session 3: $Z = -2.520, p = 0.012$, Fig 5D. right,
512 Wilcoxon t-test), but not in session 4 ($Z = -0.921, p = 0.357$, Wilcoxon t-test). Similar
513 to Experiment 1, the improvement from session 1 to session 4 was larger in the far
514 region than in the close region ($t(20) = -2.228, p = 0.038$), but the improvement was
515 similar between the left region and the right region ($t(20) = -0.399, p = 0.694$).

516



517

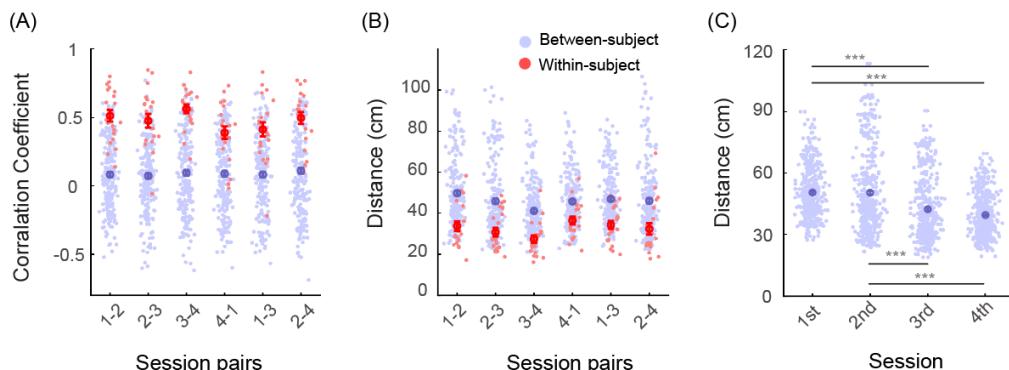
518 Figure 5: Proprioception error and motor error in Experiment 2. A) Average proprioception
 519 error. The black line denotes the average proprioception error for each session. The grey line
 520 denotes the corresponding values measured in Experiment 1. B) Reduction of proprioception
 521 error reduction as a percentage of error in session 1. The black line and the grey line denote
 522 the results from Experiment 1 and 2, respectively. C) Scatter plot of motor errors and
 523 proprioception errors from individual participants. The proprioception errors are plotted
 524 separately for session 1 and session 2. The dots lines indicate their corresponding linear fits.
 525 D) Comparisons of proprioception error between the left and right regions (left), and between
 526 the inside and outside regions (right). Error bar denotes SE. * $p < 0.05$, ** $p < 0.01$.

527

528 In Experiment 2, we continued to observe that the idiosyncratic pattern of
 529 proprioception maps persisted across sessions. For the six session-pairs (session 1 vs
 530 2, session 2 vs 3, session 3 vs 4, session 1 vs 4, session 1 vs 3, session 2 vs 4), the

531 within-subject correlation coefficients had a mean of 0.35-0.548 and a standard
532 deviation of 0.161-0.260. The between-subject correlation coefficients had a mean of
533 0.070-0.099 and a standard deviation of 0.239-0.291. All the within-subject
534 correlation coefficients were significantly larger than the corresponding between-
535 subject correlation coefficients (all $ts > 6$, $ps < 10^{-5}$, t-test, Fig 6A). Furthermore, the
536 within-participant distances (mean: 27.2-36.9 cm, SD: 7.9-12.6 cm) were smaller than
537 the between-participant distances for all six comparison pairs (mean: 40.7-49.9 cm,
538 SD: 13.1-17.3 cm, all $Zs > 3.3$, $ps \leq 0.001$, Wilcoxon t-test, Fig 6B). Similar to
539 Experiment 1, the between-subject distances within each session decreased over time
540 ($n = 210$, Kendall's $W = 0.256$, $p < 0.001$, Fig 6C). Post-hoc pairwise comparisons
541 found significant differences between sessions (1st-3rd, 2nd-3rd, 1st-4th, 2nd-4th, all
542 $ps < 0.001$). Thus, the between-subject difference between proprioception maps
543 decreased across days but not within days.

544



545

546 Figure 6: subject-specificity of proprioception error map in Experiment 2. A) Correlation
547 coefficients between session pairs. Blue dots denote between-subject coefficients. Red dots
548 denote within-subject coefficients. Error bars denote mean and SE, the same below. B)
549 Comparisons of Euclidean distance between pairs of proprioception maps. C) The Euclidean
550 distance of proprioception maps from each pair of participants within a session. Each blue dot
551 stands for a distance measure between a pair of participants, and the error bar denotes mean
552 and SE. *** $p < 0.001$.

553

554 The same CNN classifier, as in Experiment 1, was used to perform people
555 identification based on proprioception maps. To start with, the participants'
556 proprioception maps from session 1 and 2 made up the training set, and that of session
557 3 as the test set. After training for 350 echoes, the classifier was able to classify the
558 proprioception from the test set with 76.19% accuracy (16/21). Then, session 1 to 3
559 were used to train the CNN classifier, and session 4 was used to test it. We obtained a
560 61.9% testing accuracy (13/21). We also collapsed the data from both experiments to
561 perform people identification with 47 subjects. Using proprioception maps of session
562 1 and 2 as the training set and third session as the test set, we obtained a testing
563 accuracy of 72.34% (34/47). With this large dataset, we also used data from the first
564 measurement session only as the training set to predict the others. The accuracy could
565 reach 53.19% (25/47) when using session 1 to predict session 2, 55.32% (26/47) when
566 using session 1 to predict session 3, and 61.70% (29/47) when using session 2 to
567 predict session 3. Hence, the CNN classifier could identify individuals with a
568 reasonable accuracy based on a single session of proprioception data. The accuracy
569 can be further improved if an additional session of data was provided as the training
570 data. The overall performance of people identification thus supports that
571 proprioception maps are relatively stable and idiosyncratic among people.

572

573 **Discussion**

574 Whether the idiosyncratic pattern of proprioception map persists over time with good
575 within-subject consistency has not been quantitatively investigated in previous
576 research. We used the visual-matching task, a conventional method for measuring
577 proprioception for locating the hand, to repetitively measure proprioception across
578 sessions and across days. We found that 1) humans can improve their proprioception
579 accuracy through repetitive measurements though no performance feedback was

580 given during the measurement, 2) the spatial pattern of proprioception error is subject-
581 specific and remains idiosyncratic across day despite the improvement of accuracy, 3)
582 participants' proprioception measured in the visual-matching task fails to predict their
583 performance in the trajectory-matching task though both tasks demand accurate
584 location of the hand.

585

586 It has been known for long that the error pattern of proprioception varies widely
587 among people (Helms Tillery et al. 1994; Brown et al. 2003a; Smeets et al. 2006;
588 Rincon-Gonzalez et al. 2011), but whether the idiosyncrasy of proprioception maps
589 persists over time has never been tested. We found that the within-subject correlation
590 of proprioception maps between measurement sessions and days was substantially
591 larger than the between-subject correlation. Furthermore, the within-subject
592 dissimilarity between sessions was much smaller than the between-subject one. These
593 findings suggest that the spatial pattern of proprioception map indeed remain
594 consistent over time. Leveraging on the within-subject consistency, a simple CNN
595 classifier could perform people identification based on proprioception maps with fair
596 accuracy. We postulate that subject-specific error pattern might be shaped by
597 individuals' unique sensorimotor experience in their lifetime since, after all,
598 movement history (Voight et al. 1996; Lee et al. 2003; Forestier and Bonnetblanc
599 2006) and motor learning experience (Wong et al. 2011, 2012) have considerable
600 influence on one's proprioception.

601

602 The improvement of proprioception without feedback was surprising at first sight.
603 However, although feedback is considered essential for various learning, perceptual
604 learning studies have reported that people can improve without performance feedback
605 in visual perceptual tasks, such as motion-direction discrimination task (Ball and
606 Sekuler 1987) and texture discrimination task (Karni and Sagi 1991). Researchers

607 even have found that the learning rate is similar with and without feedback in a
608 direction discrimination task (Fahle and Edelman 1993). These perceptual
609 improvements are generally attributed to the neural plasticity at the cellular level in
610 the visual system (Petrov et al. 2006). We have similarly found that people can
611 improve their accuracy in the visual-matching tasks with no performance feedback.
612 This finding was observed in two different groups of participants who were tested in
613 two separate experiments. Importantly, our Experiment 2 dropped the 16-trial
614 familiarization trials, thus completely eliminated performance feedback, but continued
615 to observe the improvement of proprioception across days. It is unlikely that this
616 improvement was a result of learning of the task itself since the visual-matching task
617 was easy, and people did not show any improvement between sessions within a day.
618 Hence, we conclude that proprioceptive performance can be improved by repetitive
619 measurements, even when no performance feedback is provided, at least for the
620 widely-used visual-matching paradigm.

621

622 For both experiments, the proprioceptive improvement only appeared on the second
623 day, and no improvement was found in session 2 on day 1. Moreover, there was no
624 significant improvement between sessions 3 and 4 on day 2 for Experiment 2. It
625 appears that a night of rest is necessary for the improvement of proprioceptive
626 accuracy. In fact, these findings echo similar findings in other types of perceptual
627 learning where a rest during the night has been shown necessary. For example, in
628 visual studies, one night of sleep is necessary for bringing a performance
629 improvement in a texture discrimination task on the second day (Karni et al. 1994).
630 This improvement is absent if participants are deprived of REM sleep during the night
631 (Walker, Stickgold, Jolesz, & Yoo, 2005). An alternative possibility for our finding is
632 that the manifest of improvement in session 2 might be masked by the trajectory
633 matching task after session 1. Repetitive, active movements could increase the
634 proprioception error in the following measurement session (Kwon et al. 2013). This

635 effect is possibly related to thixotropic behavior of muscles, i.e., intrafusal fibers of
636 muscle spindles become less sensitive to stretch after intensive muscle contraction
637 (Proske et al. 2014). Since muscle spindles play a critical role in proprioception,
638 muscle thixotropy after the motor task could potentially negatively impact the
639 proprioceptive performance measured in session 2. Admittedly, we cannot determine
640 which explanation can account for the lack of improvement within a day, and this
641 issue warrants further investigations.

642

643 The visual-matching task used in the present study is a conventional method to
644 measure proprioceptive accuracy (van Beers et al. 1998, 2002; Haggard et al. 2000;
645 Goble et al. 2010; Wilson et al. 2010). If the measurement task itself can reduce the
646 proprioception error, we need to consider its validity as a measurement instrument.
647 For example, a few studies have investigated how visuomotor adaptation of reaching
648 tasks affects proprioception of the hand (Cressman and Henriques 2010; Goble et al.
649 2010; Ostry et al. 2010; Wong et al. 2011, 2012). These studies typically involve
650 measurements of the proprioception before and after visuomotor adaptation. Our
651 findings suggest that at least part of the changes observed in this kind of study is
652 related to improvement across successive measurements of proprioception. Thus,
653 extra caution is required for the repetitive use of proprioception measurements, such
654 as the visual-matching task.

655

656 We found that locating the left hand was more accurate in the left workspace than in
657 the right workspace, and in the area close to the body than away from the body.
658 Furthermore, on the group level, participants perceived their left hand to be more left
659 than its actual position. These spatial patterns of proprioceptive errors were consistent
660 with previous studies (Wilson et al. 2010; Jones et al. 2010). Interestingly, the
661 regional difference of proprioception accuracy tends to diminish over the sessions in

662 both experiments: we observed larger improvement in the far region than in the near
663 region to the body, closing the gap of accuracy between regions. As the overall
664 accuracy improved, the between-subject variance of proprioception maps also
665 decreased. Taken together, we observe a trend that improvement in proprioceptive
666 accuracy reduces the heterogeneity and idiosyncrasy of proprioception maps at the
667 same time. Whether this trend will continue with more learning sessions is worth
668 further investigations.

669

670 Our findings indicate that better accuracy in proprioception does not translate to better
671 performance in the trajectory-matching task. The visual-matching task employed here
672 to measure proprioception requires participants to keep their limb stationary with
673 respect to a reference position (Wann and Ibrahim 1992; van Beers et al. 2002; Brown
674 et al. 2003a; Goble et al. 2010). Arguably, this method can only measure participants'
675 ability to localize their body parts in a static state. The motor performance of our
676 trajectory-matching task, instead, rely on proprioception in a dynamic sense to
677 produce an accurate movement trajectory. The ability to sense the motion of a moving
678 effector is referred to as kinaesthesia (Jones et al. 2010). Indeed, the accuracy of static
679 proprioception and that of kinaesthesia do not correlate well (Grob et al. 2002). Our
680 findings further suggest that an individual's performance in static proprioception does
681 not predict her/his motor performance that critically depends on accuracy in locating a
682 moving effector.

683

684 However, this conclusion appears contradictory to previous findings of the beneficial
685 effect of motor learning on proprioception (Wong et al. 2011) and the beneficial effect
686 of proprioceptive training on motor learning (Wong et al. 2012). We postulate that
687 Wong and colleagues' findings can be better explained by learning generalization
688 between similar tasks. For example, in their first study, the motor learning task

689 required participants to grasp a handle to steer a cursor towards a visual target (Wong
690 et al. 2011). This task was thus similar to our proprioception measurement task in
691 which participants needed to move to and stay at a visual target with their hand. Their
692 subsequent proprioception measurement was conducted by judging the relative
693 position of a passively located hand, which grasped the same handle, with respect to a
694 visual target in the same workspace. Thus, their motor learning task and
695 proprioception measurement task were similar since both involved locating the hand
696 at the end of a movement relative to a visual target. Similarly, in their latter study, the
697 proprioceptive training was performed by passively moving the hand by the handle to
698 “copy” a target circle (Wong et al. 2012). The subsequent motor learning task was
699 performed by actively copying the same target circle. These two tasks thus involved
700 similar target trajectories and kinesthetic inputs during the movements. It is thus not
701 surprising that both studies found improved performance in one task after learning the
702 other as a result of a possible near transfer of learning between similar tasks. As
703 discussed above, our visual-matching task was different from our trajectory matching
704 task since they relied on different aspects of proprioception and involved different
705 visual targets. We postulate that these differences thus lead to a lack of correlation in
706 performance between the two tasks. The difference between our study and Wong and
707 colleagues' study also highlights the independence of static proprioception and
708 kinaesthesia.

709
710 Our experiments have some methodological limitations that need considerations in
711 future studies. For instance, our visual matching task includes a large number of target
712 positions as a means to cover a large workspace, resulting in a relatively long
713 measurement session (around 20 minutes) and a lack of repetition at each target.
714 Whether these factors affect the precision and accuracy of proprioceptive
715 measurements is unknown. Some of the previous studies chose to two alternative
716 force choices (2AFC) to judge the relative position of their hand to a visual reference

717 position after movement. Arguably, 2AFC gives a better measurement of
718 proprioception though it is more time-consuming for obtaining a proprioception map.
719 We suggest that future study should tradeoff between accuracy and duration of
720 proprioceptive measurements while keeping in mind that proprioceptive measurement
721 itself is a form of perceptual learning.

722

723 Conclusion

724 Our quantitative approach demonstrates that the spatial pattern of proprioception error
725 is indeed subject-specific and relatively stable across time. The idiosyncrasy of
726 proprioception map can be utilized to identify people with fair accuracy based on
727 individual's performance in the proprioception measurement task. Notably, we have
728 also found that a conventional proprioception measurement, the visual-matching task,
729 is able to improve people's proprioception accuracy even when no performance
730 feedback is given. This result suggests that extra caution should be taken in future
731 experiments where repetitive measurements of proprioception are needed. Finally, we
732 have found that proprioceptive accuracy measured with static postures fails to predict
733 the performance of a motor task that requires accurate positioning of a moving hand,
734 suggesting a functional independence between static proprioception and kinaesthesia.

735

736 Author Contribution

737 T.W. analyzed data; T.W. prepared figures; T.W. drafted manuscript; T.W. and K.W.
738 edited and revised manuscript; T.W. and K.W. conceived and designed research;
739 T.W. and K.W. interpreted results of experiments; T.W., Z.Z., Y.Y., H.H. and I.K.
740 performed experiments; T.W., Z.Z., Y.Y., H.H., I.K. and K.W. approved final version
741 of manuscript.

742

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