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The half of the story we did not know about prism adaptation

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1 **Abstract:**

2 Since 1910 (Helmholtz, treatise on physiological optics), it is known that pointing under deviating
3 prisms induces an initial error in the direction of the deviation, immediately followed by a gradual
4 correction of the error, and an after effect (AE) in the opposite direction after prisms removal, the
5 hallmark of prisms adaptation (PA). Several sensorimotor effects are also produced by PA on
6 proprioceptive, visual and visuo-proprioceptive frames of reference, the latter being called total
7 aftereffect shift (TS) of prism adaptation. Yet, after more than one century, we face a puzzling
8 result: while pointing under prisms exposure, people rapidly achieve an optimal performance and
9 reduce their error by 100%. Invariably, though, when AE is measured (TS) people only show at best
10 50% of the induced optical deviation, as if the other half was lost somewhere. Here we show that
11 the other half of prism adaptation AE is not lost, and actually emerges clearly and consistently
12 across several experiments when assessing for a so far largely neglected component: the shift
13 induced at the level of the adapted hand. Here we report that this effect is robust and highly specific
14 and we suggest calling it hand-centred aftereffect. These findings reveal that, in PA processes,
15 beside visual and proprioceptive frame of reference, also hand centred ones are involved.
16 Consistently with this view, taking into account the hand aftereffect, the total amount of the
17 aftereffect reaches 76-to-94%, depending on the measure and experiment, thus explaining the
18 largest part of optical shift, previously unnoticed. We suggest this novel aspect of PA would be
19 considered in future clinical studies in relation with responder/non-responder patients' profile to
20 inform integrated models of PA that might allow for optimising patient-tailored PA procedures.

21 **Keywords:**

22 Prism adaptation, aftereffect, hand proprioception, frame of reference

23

24 **Highlights:**

25 - Prism adaptation has specific effect on proprioception of the hand

26 - The previously 'lost' aftereffect emerges clearly at the level of the hand

27 - The hand aftereffect is specifically centred on the adapted hand

28 - In prism adaptation there are other frame of reference previously unsuspected

29

30 **1 Introduction**

31 When pointing to a visible target while looking through prismatic lenses, we initially tend to
32 misreach the target, erring in the direction of the optical shift. This error is corrected after few
33 repetitions if we are allowed vision of the target and (even just the terminal) movement error. When
34 pointing to the same target after prismatic lenses are removed, we typically display a pointing error
35 in the opposite direction: this phenomenon is called aftereffect (AE), the result and the hallmark of
36 prism adaptation (PA; Redding, Rossetti, & Wallace, 2005).

37 Despite its appealing apparent simplicity, the AE is a fairly complex phenomenon. The total
38 aftereffect is thought to result from the absolute sum of the visual shift (VS), which is in the same
39 direction of the optical shift, and the proprioceptive shift (PS), which is in the opposite direction
40 (Redding & Wallace, 1988; Wilkinson, 1971). While the PS refers to the hand-head reference
41 frame, based upon proprioceptive inputs, the VS refers to the eye-head reference frame,
42 based upon visual inputs. The total shift (TS) thus refers to the total amount of shift induced by PA
43 in the eye-hand reference frame (Prablanc et al., 2019; Redding et al., 2005; Redding & Wallace,
44 1997a, 2002). Typically, the difference between localisation performance of targets in different
45 modalities before and after adaptation is measured to quantify the amplitude of the AE (Redding et
46 al., 2005). The amplitude of the VS can be obtained by asking participants to determine when a
47 laterally moving visual cue lies right in front of them (straight ahead), while the PS is measured
48 asking participants to point straight ahead while blindfolded (Redding et al., 2005). Instead, an
49 Open Loop Pointing (OLP) procedure is typically used to measure the TS, participants pointing to a
50 visual target position without feedback of their hand movement nor of the landing position
51 (Bultitude et al., 2017; Schintu et al., 2014, 2017).

52 When considering the TS, which is the most often reported AE measure (see Table 1), one
53 would expect that its quantity should reflect the amount of lateral deviation induced by prisms.
54 During the prisms exposure phase, both healthy and most previously reported cases of brain-
55 damaged patients (Michel, Bonnetain, & White, 2017) are indeed able to reduce the initial error to,

56 virtually, zero with a slower rate of error correction (Facchin, Bultitude, Mornati, Peverelli, &
57 Daini, 2019). Such an efficient error correction ability, which has sometimes been shown to predict
58 neglect patients' improvement (Làdavas, Bonifazi, Catena, & Serino, 2011; Serino, Angeli,
59 Frassinetti, & Làdavas, 2006), would imply that adaptation processes are in place to fully take into
60 account the initial optical deviation. This, in turn, should predict that after prisms removal the fully
61 corrected error would translate into a fully compensated behaviour, thus bringing to AE opposite in
62 direction, but equivalent in amount, to the optical deviation induced by the prisms. In sharp contrast
63 to such a straightforward prediction, the TS does not represent the total amount of prism deviation.
64 Actually, it only explains about 38% of it (see Table 1). Depending on the used prisms, the optical
65 deviation, the type of arm movements, the procedure used during adaptation and the specific setup,
66 the AE ranges from 13% to 73% of the prisms deviation. Most of the reported studies found an
67 aftereffect average of 38% of total prism deviation, while the sum of VS and PS is slightly higher
68 than TS, reaching 40% of prism deviation (see Table 1 for details).

69
70 ***** Table 1 about here *****

71
72
73 Why the AE does not express the entire prism deviation? In the present study, we address
74 this question and hypothesize that the 'lost' part of the aftereffect has remained concealed for
75 decades in a previously underestimated component: the change in the felt position of the hand after
76 prism adaptation or Hand AE. Historically, the role of hand proprioception in prism adaptation has
77 been taken into account mostly at the theoretical level. Harris (1963) used the change in the felt
78 position of the hand as an explanatory concept for adaptation to laterally displacing prism. The
79 same point of view was also considered in a review by Kornheiser (1976). Despite the fact that
80 simple exposure (not adaptation) to prisms was already known to displace the judgment of the hand
81 position based on proprioception (Folegatti, De Vignemont, Pavani, Rossetti, & Farnè, 2009; van

82 Beers, Sittig, & Gon, 1999), there was sparse and scarce evidence that prism adaptation would also
83 cause such a displacement (Craske, 1966; Craske & Gregg, 1966; Scarpina, Stigchel, Nijboer, &
84 Dijkerman, 2015; Wallach & Huntington, 1973).

85 The results of a recent study, aimed at assessing the proprioceptive component of PA,
86 provided some initial evidence that PA may induce a drift in the felt position of the hands, though
87 apparently limited to certain combinations of pointing hand and prisms direction (Scarpina et al.,
88 2015). Interestingly, the authors found that leftward PA seemed to affect hand proprioception in the
89 direction of the optical deviation (leftward), thus opposite to the TS typically observed after PA.
90 The role of hand proprioception is thus the focus of our interest here, for its potential to explain the
91 puzzling result we are facing since the discovery of the effects of pointing through prisms (von
92 Helmholtz, 1910): if the felt hand position is displaced on the opposite direction of the TS, this
93 could explain (at least some of) the lost part of AE compared to the full prism strength. In
94 particular, if during (e.g., leftward) PA, hand proprioception is shifted in the same direction of the
95 optical deviation (i.e., leftward) and opposite to the TS direction (i.e., rightward), the AE as
96 measured by TS would consequently be smaller than the total deviation and the additional change in
97 hand felt position could concur to account for the lost part of the AE. Moreover, the change in
98 proprioception of the hand could represent an additional frame of reference to be included into
99 models of PA. On this basis, we designed a series of four experiments aimed at assessing,
100 measuring, comparing and defining the effects of PA on hand proprioception.

101

102 **2 Experiment 1**

103 The first experiment aimed at testing for the presence and direction of a change in the perceived
104 position of the hand after PA. In this experiment, we compared performances between a PA
105 (experimental) group and SHAM (control) group, which performed the same PA procedure while
106 wearing neutral prism goggles.

107

108 *2.1 Methods*

109 *2.1.1 Subjects*

110 Forty right-handed (assessed by Edinburgh questionnaire; Oldfield, 1971) healthy subjects
111 participated in the first experiment. They were randomly assigned to the experimental or to the
112 control group. Twenty participants took part as experimental group (15 females, mean age 21.5
113 years, SD = 2.14) and twenty participants as a control group (14 females, mean age 21 years, SD =
114 1.97). In all experiments, participants gave informed consent and were paid for their participation.
115 The study was approved by the ethics committee (CPP SUD EST IV) and was conducted in
116 accordance with the ethical standards of the 1964 Declaration of Helsinki. Since the prism glasses
117 used in this experiment (as well as in the following ones) do not permit to wear other glasses, all
118 participants had normal vision or corrected to normal vision with contact lenses.

119

120 ***** Table 2 about here *****

121

122 *2.1.2 Experimental setup*

123 Participants sat at a table in a dark and sound-attenuated room, facing the experimental apparatus
124 composed by a table covered by a semi-silvered mirror on a wooden frame. The wooden frame was
125 open to the subject and to the examiner side and the participants' hand rested on the table under the
126 mirror. Above the mirror, a ruler was positioned on two lateral supports, so that participants could
127 see the numbers on it reflected at the same depth as their (unseen) hand on the table (about 40cm).
128 A light below the mirror allowed participants to have a vision of the hand and target during closed
129 and open loop pointing movements. Conversely, when the light was off, the hand was unseen by
130 participants and the reflected ruler become visible. The participants' proximal border of the mirror
131 was black covered (by 5 centimetres) to prevent them from seeing the hand starting position when
132 performing pointing movements. This setup was adapted from studies using the rubber hand
133 illusion (Folegatti et al., 2009; Tsakiris & Haggard, 2005). In order to perform prism adaptation, a

134 white panel was positioned on the table under the mirror. A tactile mark placed on the participant's
135 side set the starting point for the participants' right index finger. Three coloured dots were marked
136 on the distal edge of the panel (examiner side) corresponding to the subject body-midline at 0°, 10°
137 leftwards and 10° rightwards. They represented the targets for the pointing movements: the midline
138 one was used to perform the OLP task measuring the TS and the lateral dots were used for the
139 adaptation procedure (both detailed below). Another ruler, visible only to the examiner on the
140 vertical edge of the white panel, allowed him to measure the pointing error, to the nearest 0.5 cm.
141 The distance between the participants' eyes and the targets was about 57 cm.

142

143 *2.1.3 Procedure*

144 The first experiment consisted of three blocks of experimental tasks repeated before and after
145 adaptation and de-adaptation procedure. In the first block, participants performed the baseline open
146 loop pointing and the proprioceptive judgment task, in this order. Subsequently, they wore
147 prismatic or neutral glasses and performed the adaptation procedure consisting of 150 pointing
148 movements to the two lateral points in, random order. The glasses were then removed and subjects
149 performed the proprioceptive judgment and open loop pointing tasks. Then, they performed the de-
150 adaptation procedure consisting of 150 pointing movements in random order without wearing
151 glasses. Finally, participants performed again the proprioceptive judgment and open loop pointing
152 tasks. The whole procedure (similar in the following experiments) is schematized in Figure 1.

153

154 ***** Figure 1 about here *****

155

156 *2.1.4 Visual Proprioceptive Hand Judgment task*

157 In this task, participants were required to estimate the position of their hidden right index finger by
158 means of a ruler reflected on the semi-silvered mirror covering their hand. Participants' right hand
159 was positioned by the examiner on the table, 7.5 cm to the right of the body midline, at 40 cm of

160 distance under the mirror, in a comfortable position. They had to report the number on the ruler
161 corresponding to the position where they felt their index finger was, by mentally projecting a
162 vertical line from the finger to the ruler. During the proprioceptive judgment task, the lights under
163 the mirror were switched off, making the hand invisible and the ruler visible. Participants were
164 required to repeat the proprioceptive judgment 6 times, with the ruler always presented with a
165 random offset in order to avoid response strategies. The mismatch between the true position of the
166 finger and the number indicated by the participant was calculated and resulted in a positive number
167 if the displacement was rightward and a negative number if it was leftward. This measure was
168 derived from rubber hand illusion studies, whereby one finger position is typically taken as a proxy
169 for the hand felt position (Folegatti et al., 2009; Tsakiris & Haggard, 2005).

170

171 *2.1.5 Prism Adaptation*

172 Subjects were required to make 150 pointing movements directed toward either of the two lateral
173 dots, in a random sequence. The experimenter made sure that pointing movements were performed
174 as fast as possible, without trajectory corrections. The examiner recorded the pointing errors: a
175 positive value represented a rightward error and a negative value a leftward error. During
176 adaptation, participants in the PA group wore 15° base right prisms (leftward optical deviation,
177 Optique Peter, Lyon, France; <https://optiquepeter.com>), while participants in the SHAM control
178 group wore neutral glasses of comparable weight. The posterior and anterior surface of prism lens
179 were curved with a spherical radius of 4.75D for 15° glasses and 4.00D for neutral Sham glasses
180 (using $n=1.523$) and the diameter of lens was 50mm. Throughout the procedure, participants were
181 masked from the prism used (Prism / Sham) and they did not see the prisms glasses before were
182 worn. During the de-adaptation procedure, neither group wore glasses.

183

184 *2.1.6 Aftereffect - Open Loop Pointing*

185 To assess the TS aftereffect, an open loop pointing task (OLP) was performed toward a dot aligned
186 with the body midline, at 57cm of distance. Participants had to look at the target, close their eyes,
187 and point as fast and accurately as possible. To prevent vision through the procedure, a black panel
188 was positioned by the examiner between the participants' eyes and the target, before pointing. This
189 OLP task was executed six times.

190

191 *2.1.7 Statistical analyses*

192 For the purpose of comparing results across experiments, all the responses were converted in
193 degrees of visual angle. Positive values represent rightward bias and negative values stand for
194 leftward bias. If not specified, tasks were analysed separately through mixed ANOVA using the
195 repeated factor Condition with three levels (Pre PA, Post PA and Post DEA) and the between factor
196 Group with two levels (Prism, Sham) on the error made by the participants (in degrees). Post-hoc
197 comparisons were performed using Bonferroni correction. In this and the following experiments,
198 normality assumption was checked and whereby **sphericity** assumption would be violated, the
199 Greenhouse–Geisser correction was **applied**. When necessary, the amplitude of the aftereffects was
200 calculated as Post- minus Pre- condition. Effect size are reported using partial eta squared or
201 Cohen's d. Data were analysed and reported graphically using R statistical environment (R Core
202 Team, 2017) and JASP software (JASP Team, 2017).

203

204 **2.2 Results**

205 *2.2.1 Aftereffect - Open Loop Pointing*

206 To evaluate the total aftereffect (TS), a mixed ANOVA was performed with one between-subject
207 factor Group (PA, SHAM) and one within-subject factor Condition (Pre PA, Post PA, Post DEA).
208 The results showed a significant main effect of Group [$F_{(1,38)} = 76.75, p < 0.0001, \eta^2_p = 0.67$],
209 Condition [$F_{(2,76)} = 241.32, p < 0.0001, \eta^2_p = 0.86$] and a significant interaction Group x Condition
210 [$F_{(2,76)} = 206.19, p < 0.0001, \eta^2_p = 0.84$]. Post-hoc comparisons showed significant differences, only

211 in the experimental PA group, between Pre and Post PA ($p < 0.0001$), between Post PA and Post
212 DEA ($p < 0.0001$) and between Pre PA and Post DEA ($p < 0.005$). Results are depicted in Figure 2A.

213

214 2.2.2 *Visual Proprioceptive Hand Judgment task*

215 To assess differences in the proprioceptively felt position of the hand, a mixed ANOVA was
216 performed with the same factors as above. Results showed significant effects for the main factor

217 Condition [$F_{(2,76)} = 28.46$, $p < 0.0001$, $\eta^2_p = 0.42$] and the interaction Group x Condition

218 [$F_{(2,76)} = 30.70$, $p < 0.0001$, $\eta^2_p = 0.45$]. As shown in Figure 2B, Post-hoc comparisons showed

219 significant differences, only in the experimental PA group, between Pre and Post PA ($p < 0.0001$),

220 between Post PA and Post DEA ($p < 0.0001$) and between Pre PA and Post DEA ($p < 0.005$).

221

222 ***** Figure 2 about here *****

223

224 2.3 Discussion

225 As clearly depicted in Figure 2A, the results of this first experiment show a very accurate (near to
226 zero error) pointing performance before prism adaptation, then a (largely expected) rightward shift
227 for the experimental group after prismatic adaptation. As expected, the de-adaptation procedure was
228 almost fully effective, reducing the rightward shift towards the initial values (O'Shea et al., 2017).

229 Thus, while the experimental group showed typical processes of adaptation and de-adaptation, the
230 control group did not show any significant shift in any of the conditions. Most interestingly, we

231 observed that only in the experimental group the felt position of the hand was shifted –leftward–
232 after PA (Figure 2B). Similarly to the effects induced by de-adaptation on TS, the leftward hand

233 proprioceptive shift was also reduced after de-adaptation, though not returning **precisely** to baseline
234 values, **but with some degree of rightward shift**. Again, no significant differences were observed

235 between conditions in the control group (see Figure 2B). This effect was strong, significant and not
236 observable in the control group, which only showed a little, not significant, rightward drift (0.27°).

237 The aftereffect of PA on hand proprioception being in the same direction of the optical
238 deviation induced by the prisms, thus opposite to the TS direction, it could concur to explain the
239 part of the AE the TS size does not account for, when compared to the degrees of prism deviation.
240 In this first experiment, the TS aftereffect size was 6.05° to the right (40.3% of optical shift) and the
241 proprioceptive of hand aftereffect (HAE) was 3.09° (20.6% of optical shift) to the left. Since the
242 perceived position of the hand was leftward to the original position, the total amount of AE (TS +
243 HAE) was 9.14° , amounting to 60.9% of the total optical shift.

244

245 **3 Experiment 2**

246 The second experiment aimed at comparing the proprioceptive HAE with other aftereffect
247 measures, by using a standard setup in the domain sensorimotor analysis of PA. The other sensori-
248 motor measures added to the proprioceptive HAE were the visual subjective straight ahead (VSSA)
249 and the proprioceptive subjective straight ahead (PSSA), respectively estimating the VS and PS
250 following prism adaptation. To further assess the change in the hand felt position, the
251 proprioceptive judgment task (PJ) was performed similarly to experiment 1 and also through a
252 passive proprioceptive judgment task (see below).

253

254 *3.1 Methods*

255 *3.1.1 Subjects*

256 Based on the results obtained in experiment 1, we performed a power analysis in order to check the
257 smallest sample size to obtain a significant effect. Taking into account the planned experimental
258 design, considering the 80% power for detecting an effect size of 0.45 (Exp1) with an alpha of 0.05,
259 we estimated at least 10 participants were necessary. To obtain robust results across all the following
260 experiments, several of them including newly developed tasks, we chose to set the sample size at
261 16 participants per group. Sixteen right-handed healthy subjects (assessed by Edinburgh
262 questionnaire, 14 females, mean age 24.0 years SD = 4.5, Experimental group) and 16 right-handed

263 healthy subjects (13 females, mean age 25.4 years SD=3.2, Sham group; $W = 173$ $p = n.s.$), all
264 naive to the prism adaptation procedure, participated in this experiment.

265

266 *3.1.2 Experimental setup*

267 All tasks involved an experimental setup consisting in a white square board in which a chin rest was
268 attached on the participant's side; otherwise, the setup was the same as in experiment 1. Close to the
269 chin rest base, a home-pad aligned with the mid-sagittal axis served as a tactile starting position for
270 the pointing movements performed with the right index, which was unseen in the starting position.
271 Three targets dots were marked, as in experiment 1, at the distal edge of the board on the examiner
272 side at about 57 cm far from participant's eyes. A ruler, positioned on the vertical margin of the
273 board, visible only to the examiner, allowed him to measure the pointing error. This PA setup was
274 similar to those used in other studies of our lab (Schintu et al., 2014, 2017). In addition, a ruler was
275 positioned using two lateral supports. The ruler was positioned 20 cm away from eyes and a height
276 of 20cm from the board and it was directly visible to the subject.

277

278 *3.1.3 Procedure*

279 Experiment 2 consisted of four main tasks based on either vision or proprioception (detailed below):
280 two tasks required to report the midline position (VSSA and PSSA), while the other two required to
281 report the felt position of the hand (**VPHJ and PPHJ**). Together with the open loop pointing task
282 measuring the TS (procedures identical to Exp. 1), they were administered before and after the PA
283 procedure (also identical to Exp. 1). To balance task presentation, eight participants performed the
284 two visual tasks first and eight performed the proprioceptive tasks first. Within each group of eight,
285 four subjects performed the proprioceptive judgment first and four the straight-ahead judgment first.
286 The OLP task was always performed last, to confirm the presence of the aftereffect.

287

288 *3.1.4 Visual Subjective Straight Ahead (VSSA)*

289 To assess the visual subjective straight ahead, participants sit with their head on the chin-rest and
290 their arms on their legs. They were required to report the number lying exactly in front of their eyes.
291 Their estimate was recorded 6 times, with the ruler presented with a random offset to avoid
292 response strategies. The mismatch between the true straight ahead value and the number indicated
293 by the participant was calculated and resulted in a positive number if the displacement was
294 rightward and a negative number if it was leftward. Participants had to keep their eyes closed
295 between trials.

296

297 *3.1.5 Visual Proprioceptive **Hand** Judgment (VPHJ)*

298 The visual proprioceptive **hand** judgment (VPHJ) task consisted in placing participants' right hand
299 on the table and covering (without touching) it with a black fabric to prevent his view. The position
300 of the hand on the table was identical to that of experiment 1. Participants were required to report
301 the number on the ruler corresponding to the position where they felt to be their index finger. We
302 call this measure "visual" to distinguish it from the passive proprioceptive judgment task, described
303 below. Procedures and measurements were otherwise identical to those of experiment 1. The setup
304 is depicted in Figure 3A.

305

306 ***** Figure 3 about here *****

307

308 *3.1.6 Proprioceptive Subjective Straight Ahead (PSSA)*

309 In order to best match the different sensorimotor measures, the evaluation of proprioceptive
310 subjective straight ahead was performed in a slight different way than the classical pointing
311 technique. The passive proprioceptive mid-sagittal judgment (Hatada, Miall, & Rossetti, 2006;
312 Michel, Gaveau, Pozzo, & Papaxanthis, 2013) consisted in passively moving the participant's arm
313 from right to the left and vice versa, using the ruler as a guide. Participants were blindfolded and put
314 their right hand into a cloth wristband that was displaced by the experimenter from the right to the

315 left till about shoulders. The experimenter first displaced the participants' hand from right to left
316 with a continuous movement (approximately 2cm/s). Participants had to say "Now" when they felt
317 their index finger perfectly aligned in front of their mid-sagittal plane. The movement ended only
318 when the hand was in front of their left shoulder. Subsequently, the procedure was repeated from
319 left to right, acquiring another judgment. Measurements on the two opposite directions were
320 measured 3 times each, giving a total of 6 measures.

321

322 3.1.7 Passive Proprioceptive *Hand Judgment (PPHJ)*

323 This task was meant to obtain the proprioceptive judgment of the right hand position without using
324 vision. In this task, the right hand was positioned on the table as for the **VPHJ** task (and as in
325 experiment 1). The proprioceptive judgment was performed with the index finger of the left hand.
326 Participants were blindfolded and put their left hand into a cloth wristband that was displaced by the
327 experimenter from the right to the left (and vice versa) up to about the shoulders. Participants had to
328 say "Now" when their left index finger corresponded to the position where they felt to be their right
329 index finger. The task was performed on the two opposite directions for three times, for a total of 6
330 measurements. The setup is depicted in Figure 3B.

331

332 3.2 Results

333

334 3.2.1 Aftereffect - Open Loop Pointing

335 Results showed a significant effect of Condition [$F_{(2,60)} = 217.3, p < 0.0001, \eta^2_p = 0.88$], a significant
336 effect of Group [$F_{(1,30)} = 60.1, p < 0.0001, \eta^2_p = 0.67$] and a significant interaction Condition x Group
337 [$F_{(2,60)} = 217.6, p < 0.0001, \eta^2_p = 0.88$]. Post-hoc comparisons showed significant differences, in the
338 experimental PA group, between Pre and Post PA ($p < 0.0001$), between Post PA and Post DEA
339 ($p < 0.0001$) and between Pre PA and Post DEA ($p < 0.05$). In the control group, there was only a
340 significant difference between Pre PA and Post DEA ($p = 0.05$). Results are illustrated in Figure 4C.

341

342 3.2.2 Visual Subjective Straight Ahead (VSSA)

343 Results showed a significant main effect of Group [$F_{(1,30)} = 6.27, p < 0.05, \eta^2_p = 0.17$]. Condition was
344 not significant ($p = 0.17$) and the interaction Condition x Group was not significant ($p = 0.75$).

345 Results are visible in Figure 4A.

346

347 3.2.3 Proprioceptive Subjective Straight Ahead (PSSA)

348 The main effect of Condition had a significant effect [$F_{(2,60)} = 6.49, p < 0.005, \eta^2_p = 0.18$], also Group
349 had a significant effect [$F_{(1,30)} = 8.83, p = 0.01, \eta^2_p = 0.23$] and there was a significant interaction
350 Condition x Group [$F_{(2,60)} = 10.54, p < 0.0005, \eta^2_p = 0.26$]. Post-hoc comparisons showed significant
351 differences, only for the experimental PA group, between Pre and Post PA ($p < 0.005$), as well as
352 between Post PA and Post DEA ($p < 0.0001$). Results are displayed in Figure 4D.

353

354 3.2.4 Visual Proprioceptive Hand Judgment (VPHJ)

355 There was a significant effect of Condition [$F_{(2,60)} = 6.73, p < 0.005, \eta^2_p = 0.18$], Group had a
356 significant effect [$F_{(1,30)} = 4.12, p = 0.05, \eta^2_p = 0.18$] and there was a significant interaction Condition
357 x Group [$F_{(2,60)} = 15.1, p < 0.0001, \eta^2_p = 0.33$]. Post-hoc comparisons showed significant differences,
358 only in the experimental PA group, between Pre and Post PA ($p < 0.0005$) and between Post PA and
359 Post DEA ($p < 0.005$). Results are depicted in Figure 4B.

360

361 3.2.5 Passive Proprioceptive Hand Judgment (PPHJ)

362 Results showed a significant effect of Condition [$F_{(2,60)} = 11.35, p < 0.0005, \eta^2_p = 0.28$] and a
363 significant interaction of Condition x Group [$F_{(2,60)} = 9.53, p < 0.001, \eta^2_p = 0.24$]. Post-hoc
364 comparison revealed significant difference only in the PA group between Pre PA and Post PA
365 ($p < 0.0005$) and between Post PA and Post DEA ($p < 0.005$). Results are depicted in Figure 4E.

366

367 To compare the two modalities in which the HAE was assessed (**VPHJ-PPHJ**), a paired t-test was
368 performed on the aftereffect of PJ (Post- minus Pre-). Results did not show significant difference
369 between the two measures (**VPHJ** = -5.38 (3.93); **PPHJ** = -8.17 (6.55); $t_{(15)} = 1.8$, $p = 0.09$). To
370 **ascertain if HAE is a different measure from PSSA, the size of PSSA and proprioceptive judgments**
371 **of hand were compared.** Two separate paired sample t-test showed significant differences between
372 PSSA and **VPHJ** ($t_{(15)} = 7.09$, $p < 0.0001$, $d = 1.77$) and between PSSA and **PPHJ** ($t_{(15)} = 6.05$, $p <$
373 0.0001 , $d = 1.63$). Pearson correlation between the previous measures did not show any significant
374 relationship ($r < 0.16$, $p > 0.55$). In order to ascertain if the HAE is a different measure from TS, two
375 correlations were performed between the TS and the HAE as assessed by **VPHJ** and **PPHJ**. In either
376 case, the results were not significant ($r < 0.21$, $p > 0.4$).

377

378 ***** Figure 4 about here *****

379

380 **3.3 Discussion**

381 To ensure that our proprioceptive judgment tasks does indeed measure a different aftereffect,
382 specific for the hand, in experiment 2 we compared the HAE with most classical sensorimotor
383 measures of PA pertaining to other modalities and reference frames. First of all, we observed the
384 expected adaptation and de-adaptation effects using the OLP task to measure the TS aftereffect.
385 Second, although the VSSA was not affected by PA (as it was the case elsewhere using similar
386 procedures, see Schintu et al. 2017), visual inspection of Figure 4A indicates that the small and non-
387 significant shift was in the leftward direction, as should be expected following leftward PA. Also in
388 agreement with previous work, the proprioceptive subjective straight-ahead judgment, as measured
389 with our passive technique, showed a typical PS in the direction opposite to the prism deviation
390 (Michel et al., 2013; Redding et al., 2005). Most interestingly, the results of the **VPHJ** task
391 confirmed the effects found at the level of the hand aftereffect in experiment 1. In addition, using a
392 purely proprioceptive and passive task (**PPHJ**), the presence of a significant and leftward shift of the

393 hand position was also confirmed. Thus, despite using a different setup and different measures, the
394 presence of the HAE is replicated and extended. Experiment 2, besides providing this replication,
395 indeed makes sure that the HAE is not a different way of measuring the VS or TS, but it is specific
396 for the hand. Moreover, having collected complementary sensorimotor measures of PA, based on
397 different frames of reference, allows us to report two classes of directional aftereffects: the AE
398 **based** on the head, which was toward the right (PS and TS; respectively D and C in Figure 4) and
399 the AE centred on the hand, which was toward the left (**VPHJ** and **PPHJ**; respectively B and E in
400 Figure 4).

401 When considering the amount of total aftereffect with respect to the prisms deviation, the TS
402 alone accounts for only 40%, in line with what reported in previous studies (see Table 1). In
403 contrast, the sum of TS and **VPHJ** explains 76% of the prismatic shift or, if we take into account the
404 **PPHJ** (pure proprioceptive HAE), the sum of the AE's reaches 94% of the optical shift.

405

406 **4 Experiment 3**

407 It has long been known that the AE can be partially transferred to the non-adapted **arm**; this process
408 is called intermanual transfer (Hamilton, 1964; Lefumat et al., 2015; Redding & Wallace, 2008,
409 2009). The third experiment aimed at testing whether the change in hand proprioception following
410 PA reported here is specific for the adapted hand, or there is a certain amount of intermanual
411 transfer. In this experiment, we therefore assessed **VPHJ**, **PPHJ** and **OLP** also on the non-adapted
412 left hand.

413

414 *4.1 Methods*

415 *4.1.1 Subjects*

416 Sixteen right-handed healthy subjects (assessed by Edinburgh questionnaire, 10 females, mean age
417 22.6 years SD = 4.5, Experimental group) and 16 right-handed healthy subjects (11 females, mean

418 age 28.19 years SD=5.0, Sham group; $W = 220.5$ $p = 0.0005$), all naïve to the PA procedures, were
419 participated in this experiment.

420

421 *4.1.2 Experimental setup*

422 The setup was the same used for the experiment 2. Because we were interested in evaluating the
423 effect of PA on the left, non-adapted, hand, we added a symmetrical reference point for the left
424 hand index judgment. The reference for left hand index is 7.5cm left of the midline.

425

426 *4.1.3 Procedure*

427 Participants performed six tasks, before and after leftward PA (procedures identical to the previous
428 experiments, in particular, the right hand was used for PA). Three tasks involved the left (non-
429 adapted) hand (LH) and three the right (adapted) hand (RH). To counterbalance the order, eight
430 subjects performed the task with their right hand first and eight with their left hand first. In each of
431 these subgroups, four participants performed the **VPHJ** first and four the **PPHJ** first. The OPL task,
432 performed with both hands, was the last task, using the same left-right order for the previous tasks.
433 The procedures for the **VPHJ**, **PPHJ** and OPL tasks were identical (mirror version for the left hand)
434 to those in the previous experiment.

435

436 **4.2 Results**

437

438 *4.2.1 Aftereffect - Open Loop Pointing RH & LH*

439 Results for the right hand showed a significant effect of Condition [$F_{(2,60)} = 181.3$, $p < 0.0001$, $\eta^2_p =$
440 0.85], a significant effect of Group [$F_{(1,30)} = 27.8$, $p < 0.01$, $\eta^2_p = 0.48$] and a significant interaction
441 Condition x Group [$F_{(2,60)} = 140.7$, $p < 0.0001$, $\eta^2_p = 0.82$]. Post-hoc comparisons showed significant
442 differences, only in the Prism group, between Pre and Post PA ($p < 0.0001$), between Post PA and
443 Post DEA ($p < 0.0001$). Results are depicted in Figure 5C.

444

445 Results for the left hand showed a significant effect of Condition [$F_{(2,60)} = 4.33$, $p < 0.01$, $\eta^2_p = 0.13$]
446 and a significant interaction Condition x Group [$F_{(2,60)} = 8.14$, $p < 0.001$, $\eta^2_p = 0.21$]. In the prism
447 Group, post-hoc comparisons revealed significant differences between Pre PA and Post PA
448 ($p < 0.0005$) and between Post PA and Post DEA ($p < 0.01$). Results are displayed in Figure 5F.

449

450 Redding and Wallace (2009) previously noticed that the sequence of tasks execution (RH-LH
451 versus LH-RH) can affect the TS aftereffect size. To evaluate this variable in the Prism group of
452 this experiment, we ran a mixed ANOVA with the between-subject factor task Sequence (RH-LH,
453 LH-RH) and the within-subjects factors Hand (left, right) and Condition (Pre-PA, Post-Pa, Post-
454 DEA). Results showed significant main effects of Hand [$F_{(1,14)} = 7.54$, $p < 0.05$, $\eta^2_p = 0.35$] and
455 Condition [$F_{(2,28)} = 156.25$, $p < 0.0001$, $\eta^2_p = 0.91$]. The significant interaction Condition x Sequence
456 [$F_{(2,28)} = 3.68$, $p < 0.05$, $\eta^2_p = 0.21$] confirmed that the order of presentation could influence the
457 amplitude of the aftereffect: namely, the RH-LH order was followed by a slightly larger amount of
458 AE. The Interaction Hand x Condition [$F_{(2,28)} = 158.28$, $p < 0.0001$, $\eta^2_p = 0.92$] was also significant,
459 indicating a smaller TS for the left hand **Post-PA**, the sign of inter manual transfer.

460

461 ***** Figure 5 about here *****

462

463 4.2.2 Visual Proprioceptive Judgment RH & LH

464 For the right hand there was a significant effect of Condition [$F_{(2,60)} = 6.55$, $p < 0.005$, $\eta^2_p = 0.18$] and
465 a significant interaction Group x Condition [$F_{(2,60)} = 5.41$, $p < 0.01$, $\eta^2_p = 0.15$]. Post-hoc comparisons
466 showed significant differences between Pre PA and Post PA ($p < 0.0005$) again only in the prism
467 Group. For the left hand, the results did not show any significant difference (**all ps > 0.15**). Results
468 for each hand are displayed in Figure 5A and 5D.

469

470 4.2.3 Passive Proprioceptive Judgment RH & LH

471 For the right hand, the results revealed a significant effect of Condition [$F_{(2,60)} = 11.16$, $p < 0.0001$,
472 $\eta^2_p = 0.27$], a main effect of Group [$F_{(1,30)} = 8.89$, $p < 0.01$, $\eta^2_p = 0.23$] and a significant interaction
473 Group x Condition [$F_{(2,60)} = 6.17$, $p < 0.005$, $\eta^2_p = 0.17$]. Post-hoc comparisons showed significant
474 differences in the prism Group between Pre PA and Post PA ($p < 0.0005$) and between Post PA and
475 Post DEA ($p < 0.001$).

476 For the left hand, the results showed a significant effect of Condition [$F_{(2,60)} = 12.28$, $p < 0.0001$, η^2_p
477 $= 0.29$]. Post-hoc comparisons showed a significant difference between Pre PA and Post PA
478 ($p < 0.005$) and Pre PA and Post DEA ($p < 0.0005$). Results for each hand are displayed in Figure 5B
479 and 5E.

480

481 4.3 Discussion

482 Results showed a partial, though significant, intermanual transfer of prism adaptation (Figure 5C &
483 5F). We determined the amount of intermanual transfer by comparing the amplitude of the
484 aftereffects and found intermanual transfer of PA of 19.4%, which is in line with previous findings
485 (Redding & Wallace, 2008). When the HAE was assessed via the **VPHJ** task, only the right
486 (adapted) hand showed a significant leftward shift of the hand felt position, which wiped out after
487 de-adaptation. When the HAE was assessed via the purely proprioceptive **PPHJ** task, the right hand
488 showed a leftward shift in proprioception similar to that observed in Experiment 2, whereas the
489 small rightward shift observed in the left hand after de-adaptation (as compared to baseline), is most
490 likely due to a proprioceptive drift that does not depend on PA (Wann & Ibrahim, 1992). **On the**
491 **other hand, for left hand, there a specular and significant drift as viewed for the control group for**
492 **the right hand.**

493 Overall, the results from the third experiment showed a certain amount of intermanual
494 transfer of PA from the right (adapted) to the left (non-adapted) hand for the TS. However, the
495 leftward HAE was significant only for the right adapted hand, as revealed by both the visual (**VPHJ**):

496 6.44° $p < 0.0005$) and the proprioceptive tasks (PPHJ: 4.88° $p < 0.0001$), but was absent for the non-
497 adapted hand (Figure 3), thus showing the HAE is specific for the adapted hand.

498

499 **5 Experiment 4**

500 With the last experiment, we aimed at establishing whether, besides being specific for the adapted
501 hand, the HAE is hand-centred. This hypothesis would predict that the HAE should be independent
502 of the hand spatial position. Instead, if the HAE is referenced to the previously proposed reference
503 frames (e.g., hand-head or eye-head), then its amount should vary according to the hand position
504 with respect to the head/eye position. Here we asked participants to perform both the VPHJ and
505 PPHJ tasks with the right hand on two novel spatial positions: namely, leftward and rightward as
506 compared to the position tested in experiments 1 to 3. In addition, to test whether an AE referenced
507 to the shoulder could constitute another component involved in the AE following PA, both visual
508 and proprioceptive versions of the PJ task were also performed in reference to this body-part.

509

510 *5.1 Methods*

511 *5.1.1 Subjects*

512 Sixteen right-handed healthy subjects (assessed by Edinburgh questionnaire, 13 females, mean age
513 25.3 years SD = 6.0, Experimental group) and 16 right-handed healthy subjects (11 females, mean
514 age 24.4 years SD=5.0, Sham group; $W = 139$ $p = 0.69$), all naïve to the PA procedures,
515 participated in this experiment.

516

517 *5.1.2 Procedure*

518 Presentation order was balanced between subjects: Half of the subjects performed the PPHJ tasks
519 first (hand and shoulder references) and the other half the VPHJ tasks first. The OLP task was
520 always performed as last task.

521

522 5.1.3 Experimental setup

523 The experimental setup was the same the one used for experiment 2 and 3. In this experiment, the
524 right hand could lie in one of two new spatial positions: a left position (LP) 7.5 cm leftward to the
525 midline and a right position (RP) that was 22.5cm to the right of the midline. These novel positions
526 corresponded to 15cm leftward and rightward as compared to the previous tested position. Besides,
527 procedures for all the tasks were identical to those used in the previous experiments. Participants
528 performed a total of 7 different tasks: the **VPHJ** (LP & RP) and the **PPHJ** (LP & RP) tasks
529 concerned the right hand; in addition, the **VPSJ** and the **PPSJ** tasks concerned the same
530 measurements of position sense referred to the shoulder. In the **VPSJ** task we asked participants to
531 report the number they perceived to be in front of their right shoulder. In the **PPSJ** task, participants
532 performed the passive proprioceptive judgment of the felt position of the right shoulder by stopping
533 the passive movements of their left hand, moved by the examiner, as in the previous experiments. In
534 both tasks, participants made 6 judgments.

535

536 5.2 Results

537 5.2.1 Aftereffect - Open Loop Pointing

538 Results showed a significant effect of Condition [$F_{(2,60)} = 161.9, p < 0.0001, \eta^2_p = 0.84$], a significant
539 effect of Group [$F_{(1,30)} = 28.7, p < 0.0001, \eta^2_p = 0.49$] and a significant interaction Condition x Group
540 [$F_{(2,60)} = 135.6, p < 0.0001, \eta^2_p = 0.82$]. Post-hoc comparisons showed significant differences, in the
541 experimental PA group, between Pre and Post PA ($p < 0.0001$), between Post PA and Post DEA
542 ($p < 0.0001$) and between Pre PA and Post DEA ($p < 0.05$).

543

544 To additionally assess whether there was any difference across experiments between the
545 amount of adaptation, as measured through the OPL task across PA groups, we ran a repeated
546 measure ANOVA with the between-subject factor Experiment (Exp. 1, 2, 3, 4) and the within-
547 subject factor Condition (Pre PA, Post PA and Post DEA). There was a significant main effect of

548 Condition [$F_{(2,128)} = 1032.44, p < 0.0001, \eta^2_p = 0.94$], but neither the main effect of Experiment
549 [$F_{(3,64)} = 0.06, p = 0.97$] nor the interaction Condition x Experiment were significant [$F_{(6,128)} = 1.27$
550 $p = 0.28$]. Data are reported in Table 2.

551

552 5.2.2 Visual Proprioceptive *Hand Judgment*

553 To assess the difference between positions we ran a repeated measure ANOVA with the within-
554 subject factor Position (LP, RP), the within-subject factor Condition (Pre-PA, Post-Pa, Post-DEA)
555 and the between factor Group (Prism, Sham). Results showed a significant effect of Position
556 [$F_{(1,30)} = 75.16, p < 0.0001, \eta^2_p = 0.72$], a significant effect of Condition [$F_{(2,60)} = 10.94, p < 0.0001, \eta^2_p$
557 $= 0.27$], as well as a significant interaction of Condition x Group [$F_{(2,60)} = 5.24, p < 0.01, \eta^2_p = 0.015$],
558 but no significant interaction between Position and Condition. In the Prism Group, concerning the
559 RP, Post-hoc comparisons showed significant differences between Pre PA and Post PA ($p < 0.01$)
560 and for LP, post-hoc comparisons showed significant differences between Pre PA and Post PA
561 ($p < 0.01$) and between Post PA and Post DEA ($p < 0.005$; Figure 6A).

562

563 ***** Figure 6 about here *****

564

565 A one-way ANOVA was performed to compare the amplitude of the HAE, as measured by the
566 **VPHJ** task (Post- minus Pre-), in the three positions (Exp. 2 and 4). No significant difference
567 emerged ($p = 0.69$; Figure 6C).

568

569 5.2.3 Passive Proprioceptive *Hand Judgment*

570 The same repeated measure ANOVA structure viewed for **VPHJ** reveal a significant effect of
571 Position [$F_{(1,30)} = 137.47, p < 0.0001, \eta^2_p = 0.82$], a significant effect of Condition [$F_{(2,60)} = 6.20,$
572 $p < 0.005, \eta^2_p = 0.17$], a significant interaction of Condition x Group [$F_{(2,60)} = 3.18, p < 0.05, \eta^2_p =$

573 0.10], but no significant interaction between Position and Condition. Only for LP Post-hoc
574 comparisons showed significant differences between Pre PA and Pos
575 t PA ($p < 0.05$; Figure 6D).

576 Again, to compare this effect amplitude across the three different positions (Exp.2 and 4),
577 we ran a one-way ANOVA on the amplitude effect (Post- minus Pre-). Results did not show
578 significant differences between the amplitude of the HAE effect across positions ($p = 0.12$; Figure
579 6F).

580

581 5.2.4 Visual Proprioceptive *Shoulder Judgment*

582 Results did not show any significant effect (all $ps > 0.26$; see Figure 6B).

583

584 5.2.5 Passive Proprioceptive *Shoulder Judgment*

585 Results did not show significant effect (all $ps > 0.16$; see Figure 6E).

586

587 ***** Figure 7 about here *****

588

589 ***** Table 3 about here *****

590

591 5.3 Discussion

592 We performed the fourth experiment to assess whether the HAE, besides being specific for the
593 adapted hand, is also centred on it. This hypothesis is confirmed by the presence of the HAE
594 irrespective of whether the adapted hand was either in the right or left position, as revealed by both
595 the **VPHJ** and the **PPHJ** tasks. A statistical comparison between the amplitude of the HAE assessed
596 in the three positions occupied by the adapted hand across experiments 2 and 4 revealed the effect
597 was present irrespective of differences in hand positions. Together, these results **support** that the
598 HAE reported here is both specific for the adapted hand and centred on the adapted hand.

599 In this experiment, we additionally assessed whether the shoulder could contribute to the AE
600 phenomenon, but found only a small and non-significant effect of PA on the perceived position of
601 the shoulder (1.06°). When adding all the measured aftereffects, considering also the slight shift of
602 the shoulder, the amount of the prisms optical deviation that we can account for ranges from 83%
603 (left hand position) to 93% (right hand position).

604

605 **6 General discussion**

606 *6.1 Hand After Effect a new (but old) measure of PA*

607 Here we showed that PA produces a new, previously overlooked aftereffect component, consisting
608 in the shift induced on proprioception at the level of the adapted hand. This Hand After Effect
609 emerged clearly and consistently across several experiments and testing procedures. We suggest to
610 call it HAE, precisely because, first it occurs independently from the used measure (either visual or
611 proprioceptive), second it appears to be specific for the adapted hand (not affecting the non-adapted
612 hand, or the shoulder) and third, it is hand-centred (its presence/amount not varying with the hand
613 position in space). Across four experiments and several types of measures, we found that the HAE
614 represents about 37% of the optical prism deviation (using 15° leftward prisms). This aftereffect
615 size is close to the ‘total shift’ aftereffect of PA, (about 40%), but in the opposite direction.

616 The change in arm position judgment following PA has been initially considered more than
617 50 years ago (Harris, 1963), though in a different way. In that original study, the aftereffect was
618 measured through the open loop pointing task, which has become a sort of standard, whereas the
619 change in the felt position of the hand was used as an explanatory concept, to account for the
620 misreaching of the target that was made visible by the AE. This explanatory concept was then
621 utilized in many other studies that, however, did not measure the proprioceptive change they
622 assumed to exist. Instead, they continued using the nowadays classical open loop pointing task
623 (Craske & Gregg, 1966; A. Efstathiou, Bauer, & Greene, 1967; Kornheiser, 1976). The first study
624 in which the hand position shift was measured, through a proprioceptive judgment task, is the one

625 by Craske (1966). Unfortunately, because of the procedure used, the absence of TS measure and the
626 lack of specification about the direction of the optical deviation induced by the specific prisms used,
627 it is not possible to gather a complete interpretation of both aftereffects. Nevertheless, he found an
628 HAE of 34% of the optical deviation. We have to wait until recently, when the effect of PA on
629 proprioception has been measured by Scarpina and colleagues (2015). They tested the adapted hand
630 position sense before and after leftward and rightward PA, performed with the left and right hand
631 (four groups). Their adaptation procedure was, however, relatively unusual, pointing movements
632 under prisms exposure being executed with the index finger of one hand toward the other hand's
633 fingers. They found that only the combination of leftward shifting prism using the left adapted hand
634 determined a significant change in proprioception of the adapted hand. There is a major difference
635 that could readily explain their lack of HAE for the right hand, repeatedly and consistently reported
636 here. The adaptation was performed with one hand pointing to the other: visual or proprioceptive
637 information used as target may actually bring to different sensitivity to PA (Bernier, Gauthier, &
638 Blouin, 2007). Conversely, our findings clearly show the existence and specificity of the HAE as a
639 distinct aftereffect. The comparison between aftereffects in experiment two underlines that this is
640 not merely another way of measuring a previously documented (head- or eye-centred) aftereffect,
641 but a new, previously unconsidered effect. Moreover, based on the findings of experiment two and
642 four, we conclude this so far largely neglected HAE is both specific for the adapted hand and
643 centred on this hand.

644

645 *6.2 HAE, the lost part of AE*

646 In Table 1, we have reported a summary of the studies on PA that took into account VS, PS and TS.
647 The total shift, even if it is somewhat sensitive to specific setups and procedures used, amounts
648 generally to about 40% of the optical shift induced by the prisms, and our findings indicate that
649 about the same amount can be attributed to the HAE. Most importantly, since the proprioceptive
650 shift of the hand is in the opposite direction of the TS, it could well represent the 'lost' part of the

651 AE. Feedforward adjustments have been suggested to drive rapid compensation of the initial phase
652 of the reach, resulting in the rapid reduction of endpoint errors typically observed early during
653 prism exposure (O’Shea et al., 2014, 2017; Pochopien, Spang, Stemmler, & Fahle, 2017). Also
654 depending on how cluttered/structured the visual working space appears to the subject, part of the
655 optical deviation may or may not be ‘visible’ through the closed loop pointing error, even in the
656 very first pointing trials. In a seminal paper, for example, the direct effect-error was maintained at
657 100% of the prisms deviation in the early pointing, thus testifying that the optical deviation has to
658 be taken into account fully for the adaptation to develop later on (Rossetti, Koga, & Mano, 1993).
659 Indeed, during the very first pointing movements in the adaptation phase (while wearing prisms)
660 subjects may misreach the target leftward by close to 100% of the optical deviation, then they
661 quickly correct this error (O’Shea et al., 2014, 2017; Pochopien, Spang, Stemmler, & Fahle, 2017;
662 Rossetti et al., 1993). As recalled above taking the example of a standard leftward adaptation in
663 healthy subjects (with base right prisms), when participants remove the prisms and point in an open
664 loop condition after adaptation, they misreach the alignment to the target rightward by about 40% of
665 the prism optical deviation. Yet, according to the known components of the AE, they should
666 misreach by the equivalent amount of the optical deviation. In the light of the present findings, we
667 postulate that this is the consequence of the existence of another AE component, the hand after
668 effect. The adapted hand is felt as if it were shifted about 40% leftward with respect to its real
669 position. Therefore, this amount of deviation should be added to the rightward shift that is measured
670 in PA studies through the open loop pointing and is normally called aftereffect (AE).

671 Our interest was here focused on the size of the TS and HAE, as compared to the total optical
672 shift of prisms. When summing the absolute values of the two aftereffects (HAE and AE), the total
673 amount reaches 86-94%, depending on the measure considered and the experimental design, thus
674 explaining the greater part of the optical shift (Figure 7).

675 One issue that deserves discussion is whether the specific change in hand position sense might
676 reflect another AE measure, namely the proprioceptive subjective straight-ahead, or PSSA. Most

677 typically, this AE is measured by asking participants to point with the adapted right hand moving in
678 front of them to indicate their subjective middle (or straight ahead) starting from the sternum, or
679 from a mid-sagittal starting point. If we now consider the observed HAE, the trajectory of the hand
680 while pointing straight ahead would start from a position which is felt significantly leftward with
681 respect to actual mid-sagittal plane. The landing position reached by the hand while pointing
682 straight ahead could thus be shifted to the right (Holmes, Snijders, & Spence, 2006). In this respect,
683 the HAE could contribute to the PSSA. However, our results do not support this possibility, because
684 the PSSA was smaller than the HAE and unrelated. To provide the most comparable measure, here
685 we measured the PSSA via a passive movement, as we did in the PPHJ task used to measure the
686 HAE, whereby the only difference was the reference point to be felt and reported: the subjective
687 straight ahead for PSSA, the hand position for the PPHJ. Even within these closely matched task
688 modalities, the two measures turned out to be quite different and unrelated, thus suggesting the
689 underlying processes are at least partially different. A similar consideration could be made between
690 OLP and VPHJ, in which a visual reference should be reported. Again, the two measures (HAE and
691 TS) are unrelated, suggesting their underlying processes are, at least in part, different.

692 With these new tasks (VPHJ and PPHJ), we repeatedly obtained a consistent and robust
693 measure of the HAE. We thus suggest this AE should be included into an updated sensori-motor
694 model of PA (see Fig.7). and inform recently advanced comprehensive theoretical PA frameworks
695 (e.g., (Petitet, O'Reilly, & O'Shea, 2018). Further studies are needed to elucidate the different and
696 still unknown aspects of HAE, both in healthy controls and in neurological patients.

697

698 *6.3 HAE and spatial neglect rehabilitation*

699 This study discloses that in the prismatic adaptation process, beside the long known visual and a
700 proprioceptive AE originating the supposedly 'total' shift, there is a new—though long suspected—
701 AE component that is hand centred. These findings imply that the PA model is actually more
702 complex than previously thought: the old concept of a change in hand proprioception following PA

703 (Harris, 1963; Kornheiser, 1976) needs to be reconsidered and included in PA models. This is
704 particularly important because, besides its sensorimotor effects, PA produces also visuospatial
705 perceptual changes in physiological conditions in healthy subjects (Schintu et al., 2017) and most
706 relevant, in pathological conditions in brain-damaged patients. Whether applied alone (Azouvi,
707 Jacquin-Courtois, & Luauté, 2017; Pisella, Rode, Farne, Tilikete, & Rossetti, 2006; Rode et al.,
708 2015), or in combination with brain neuromodulation or drugs (Calzolari, Bolognini, Casati,
709 Marzoli, & Vallar, 2015; Làdavas et al., 2015; Luauté et al., 2018; O’Shea et al., 2017), PA is
710 indeed one of the most promising rehabilitation techniques to improve several perceptual and motor
711 aspects of brain-damaged patients suffering from Unilateral Spatial Neglect (Champod, Frank,
712 Taylor, & Eskes, 2018; Facchin, Beschin, Toraldo, Cisari, & Daini, 2013a; Frassinetti, Angeli,
713 Meneghello, Avanzi, & Làdavas, 2002; Mizuno et al., 2011; Rode, Fourtassi, Pagliari, Pisella, &
714 Rossetti, 2017; Rossetti et al., 1998; Serino et al., 2007).

715 While the efficacy of prism adaptation in the rehabilitation of USN has been interpreted in
716 the light of several models (Bultitude et al., 2017; Clarke & Crottaz-Herbette, 2016; Martín-Arévalo
717 et al., 2016; Martín-Arévalo, Schintu, Farnè, Pisella, & Reilly, 2018; Pisella et al., 2006; Redding &
718 Wallace, 2006, 2010; Rossetti et al., 1998; Saevarsson & Kristjánsson, 2013; Schintu et al., 2016;
719 Striemer & Danckert, 2010) among which the recalibration – realignment model (Redding &
720 Wallace, 2006, 2010), these findings suggest that another feature of PA contributing to its efficacy
721 may rely on the changes in proprioception of the adapted hand. Following rightward PA (base left
722 prisms are typically used in USN), the adapted (right) hand would be felt rightward than its real
723 position. Thus, movements planned towards the left (such as in exploratory tasks) might result in a
724 larger leftward displacements, possibly contributing to neglect amelioration in visuo-motor
725 explorative tasks. Previous studies on PA in neglect patients reported normal TS (Facchin,
726 Bultitude, et al., 2019; Rode et al., 2015; Sarri et al., 2008), but a contamination of the VS and PS
727 measure from neglect itself (Bartolomeo & Chokron, 1999; Facchin et al., 2013a; Facchin,
728 Bultitude, et al., 2019; Facchin, Sartori, Luisetti, De Galeazzi, & Beschin, 2019; Farnè, Ponti, &

729 Ladavas, 1998; Pisella, Rode, Farne, Boisson, & Rossetti, 2002; Rode et al., 2015; Saj, Honoré,
730 Richard, Bernati, & Rousseaux, 2010; Sarri et al., 2008). Assessing the HAE in neglect patients, in
731 addition to VS, PS and TS, could provide valuable information possibly contributing to elucidate
732 differences in efficacy, or responder vs non-responder patients' profile. In this respect, we suggest
733 this novel aspect of PA should be considered in future studies of PA in neglect patients to better
734 inform models of PA that might allow for optimising patient-tailored PA procedures.

735

736 **Conflict of interest**

737 The authors declare no conflict of interest.

738

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1043

1044

1045 **Figure captions**

1046 Figure 1. Schematic of the procedures used in each experiments. **VPHJ** = Visual Proprioceptive
1047 **Hand Judgment**; **PPHJ** = Passive Proprioceptive **Hand Judgment**; OLP = Open Loop Pointing.

1048
1049 Figure 2. A) Total aftereffect (TS) measured by the open loop pointing (OLP) task. B)
1050 Proprioceptive shift of the felt position of the right index finger. All values are expressed in degrees.
1051 Positive values represent rightward bias and negative leftward. Bars represents +/- 1 S.E.M. * =
1052 $p < 0.05$; ** = $p < 0.005$; *** = $p < 0.0005$.

1053
1054 Figure 3. Cartoon showing the two tasks of hand position judgment. A) Visual Proprioceptive **Hand**
1055 **Judgment**, in which the participants reported the number on the seen ruler corresponding to the
1056 position where they felt their index finger was, by mentally projecting a vertical line from the finger
1057 to the ruler; B) Passive Proprioceptive **Hand Judgment**, in which participants said “Now” when
1058 their left index finger to correspond to the position where they felt their right index finger to be.

1059
1060 Figure 4. The graphs represent on the same scale in degrees, the shift found on the different
1061 measures of Experiment 2: A) Visual Subjective Straight Ahead; B) Visual Proprioceptive **Hand**
1062 **Judgment**; C) Open Loop Pointing; D) **Passive** Proprioceptive Subjective Straight Ahead; E)
1063 Passive Proprioceptive **Hand Judgment**. F) The graph represents the amount and the direction of the
1064 different aftereffects measured in Experiment 2. All values are expressed in degrees. Positive values
1065 represent rightward bias and negative leftward. Bars represents +/- 1 S.E.M. * = $p < 0.05$; ** =
1066 $p < 0.005$; *** = $p < 0.0005$.

1067
1068 Figure 5. The graphs (from A to F) represent the shift found in **VPHJ**, **PPHJ** and OLP as assessed
1069 for the left or right hand in experiment 3. Graphs are subdivided by hand (left and right) and task
1070 (**VPHJ**, **PPHJ** and OLP). All values are in the same scale in degree. Positive values represent
1071 rightward bias and negative leftward. Bars represent +/- 1 S.E.M. * = $p < 0.05$; ** = $p < 0.005$; *** =
1072 $p < 0.0005$.

1073
1074 Figure 6. The graphs on the left column show the HAE measured by **VPHJ** and **PPHJ** for the hand
1075 located in the left and right position. The graphs in the central column show the same tasks of
1076 proprioceptive judgment for the shoulder. The graphs in the right column represent a comparison
1077 for each task between the HAE in the two lateral position in experiment 4 and that observed in
1078 experiment 2. Data are in degrees. Positive values represent rightward bias and negative leftward.
1079 Bars represent +/- 1 S.E.M. * = $p < 0.05$; ** = $p < 0.005$; *** = $p < 0.0005$.

1080
1081 Figure 7. Graphical representation of the size of the optical prism deviation and the corresponding
1082 direction and size of TS and HAE.

1083

1084

<i>Reference</i>	<i>Prism Power</i>	<i>Base</i>	<i>Trial of adaptation</i>	<i>Feedback</i>	<i>VS</i>	<i>PS</i>	<i>TS</i>
(Held & Gottlieb, 1958)	11.3°	R	100	C			48%
(Held & Hein, 1958)	11.3°	LR	180	C			35%
(Harris, 1963)	11.3°	LR	90	C		48%	50%
(Hamilton, 1964)	11.3°	?	15'	C			31%
(Hay & Pick Jr, 1966)	11.3°	LR	6days	C	21%	25%	27%
(Craske & Gregg, 1966)	11.3°	R	Until 10 correct	C			35%
(A. Efstathiou et al., 1967)	8,7°	LR	3'	C			32%
(Cohen, 1967)	16.7°	LR	5'	CT			15%
(E. Efstathiou, 1969)	11°	LR	20'	C			46%
(Canon, 1970)	11.3°	LR	20'	C			19%
(Dewar, 1970)	12°	LR	42	C			73%
(Wilkinson, 1971)	12°	LR	40	T	13%	15%	28%
(Welch, 1971)	11.3°	R	95	T			62%
(Choe & Welch, 1974)	11,3°	LR	2'	CT	11%	30%	46%
(Welch, Choe, & Heinrich, 1974) Exp1	11.3°	R	30	T	16%	18%	50%
(Welch et al., 1974) Exp2	11.3°	R	30	T	14%	17%	41%
(Redding & Wallace, 1976)	11.3°	L	25'	C	4%	45%	51%
(Lackner & Lobovits, 1977)	11.3°		10'	n.s			23%
(Melamed, Beckett, & Halay, 1979)	11.3°	L	144	T	5%	43%	52%
(Redding & Wallace, 1988) Exp1	16.7°	L	60	T	13%	7%	23%
(Redding & Wallace, 1988) Exp2	16.7°	L	60	T	15%	5%	23%
(Redding & Wallace, 1988) Exp3	16.7°	L	60	T	17%	8%	23%
(Redding & Wallace, 1993)	11.3°	L	60	T	20%	25%	41%
(Redding & Wallace, 1996)	11.3°	L	60	T	9%	33%	42%
(Redding & Wallace, 1997b)	11.3°	L	60	T	10%	22%	35%
(Clower & Boussaoud, 2000)	5.7°	R	50	C			60%
(Martin, Norris, Greger, & Thach, 2002)	16.7°	R	50	T			38%
(Berberovic & Mattingley, 2003)	10°	LR	200	T		36%	
(Girardi, McIntosh, Michel, Vallar, & Rossetti, 2004) Exp1	15°	R	20	C	41%	17%	33%
(Girardi et al., 2004) Exp2	15°	R	20	C	47%	21%	43%
(Ferber & Murray, 2005)	10°	R	5'	C		27%	
(Striemer, Sablatnig, & Danckert, 2006)	15°	LR	15'	T		75%	
(Michel, Pisella, Prablanc, Rode, & Rossetti, 2007)	10°	R	84	T			40%
(Michel, Vernet, Courtine, Ballay, & Pozzo, 2008)	10°	LR	12'	C			39%
(Newport, Preston, Pearce, & Holton, 2009)	11.3°	R	80	T	1%	31%	
(Loftus, Vijayakumar, & Nicholls, 2009)	15°	LR	50	T			18%
(Wilms & Malá, 2010)	10°	L	90	T			46%
(Fortis, Goedert, & Barrett, 2011)	12,4°	LR	10'	T		13%	17%
(Herlihey & Rushton, 2012) Exp1	10°	R	204	C	2%	28%	
(Herlihey & Rushton, 2012) Exp2	10°	R	204	T	14%	16%	
(Bornschlegl, Fahle, & Redding, 2012)	8.5°	L	30	T	8%	19%	33%
(Michel et al., 2013)	15°	R	100	C			42%
(Facchin et al., 2013a)	11.3°	L	100	C		26%	33%
(Bultitude, Van der Stigchel, & Nijboer, 2013)	15°	LR	150	T			26%
(Fortis, Ronchi, Calzolari, Gallucci, & Vallar, 2013)	11.3°	L	90	T	6%	14%	28%
(Bultitude, Downing, & Rafal, 2013)	15°	R	150	T			34%
(Bultitude, List, & Aimola Davies, 2013)	14.2°	LR	90	T			32%
(Magnani, Mangano, Frassinetti, & Oliveri, 2013)	10°	LR	90	T			40%
(Magnani et al., 2014)	10°	L	90	T			51%
(Schintu et al., 2014)	15°	LR	150	T			47%
(O'Shea et al., 2014)	10°	L	100	C			49%
(Michel & Cruz, 2015)	15°	R	360				69%
(Schintu et al., 2016)	15°	R	150	T			47%
(Panico, Sagliano, Grossi, & Trojano, 2016)	11.3°	L	90	T			36%
(Patané, Farnè, & Frassinetti, 2016)	10°	LR	90	T			43%

(Pochopien et al., 2017)	14.2°	LR	60	T			33%	
(O'Shea et al., 2017)	10°	L	100	T			40%	
(Schintu et al., 2017)	15°	LR	150	T	30%		42%	
(Bracco, Veniero, Oliveri, & Thut, 2018)	10°	L	90	T			38%	
(Gaveau et al., 2018)	12°	L	50	C			37%	
(Facchin, Bultitude, et al., 2019)	11.3°	L	90	T	1%	20%	37%	
Mean						14%	26%	38%

1087 Table 1: Aftereffect size expressed as percentage of total optical shift in prismatic adaptation studies in healthy subjects.
1088 The column represent in order: Author reference, prism power in degree (Facchin, Beschin, Toraldo, Cisari, & Daini,
1089 2013b), the base of prism used (L = left; R = right), the trial of adaptation, the kind of adaptation used (C = concurrent;
1090 T = terminal; n.s. not specified), VS = visual shift, PS = Proprioceptive shift, TS = total shift. To uniform the results the
1091 different AE are reported in percentage of total optical shift.
1092

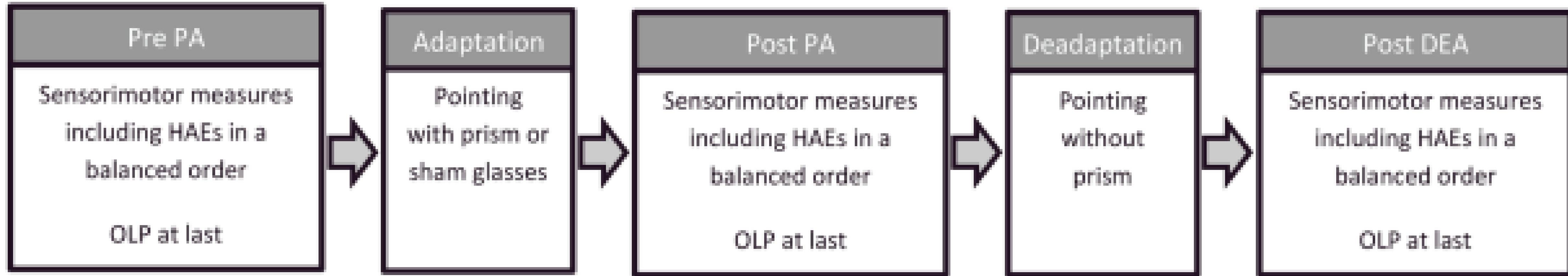
Experiment	Group	n.	M / F	Mean age (SD)
1	Prism	20	5/15	21.5 (2.14)
	Sham	20	6/14	21.0 (1.97)
2	Prism	16	2/14	24.0 (4.5)
	Sham	16	3/13	25.4 (3.2)
3	Prism	16	6/10	22.6 (4.5)
	Sham	16	5/11	28.19 (5.0)
4	Prism	16	3/13	25.3 (6.0)
	Sham	16	5/11	24.4 (5.0)

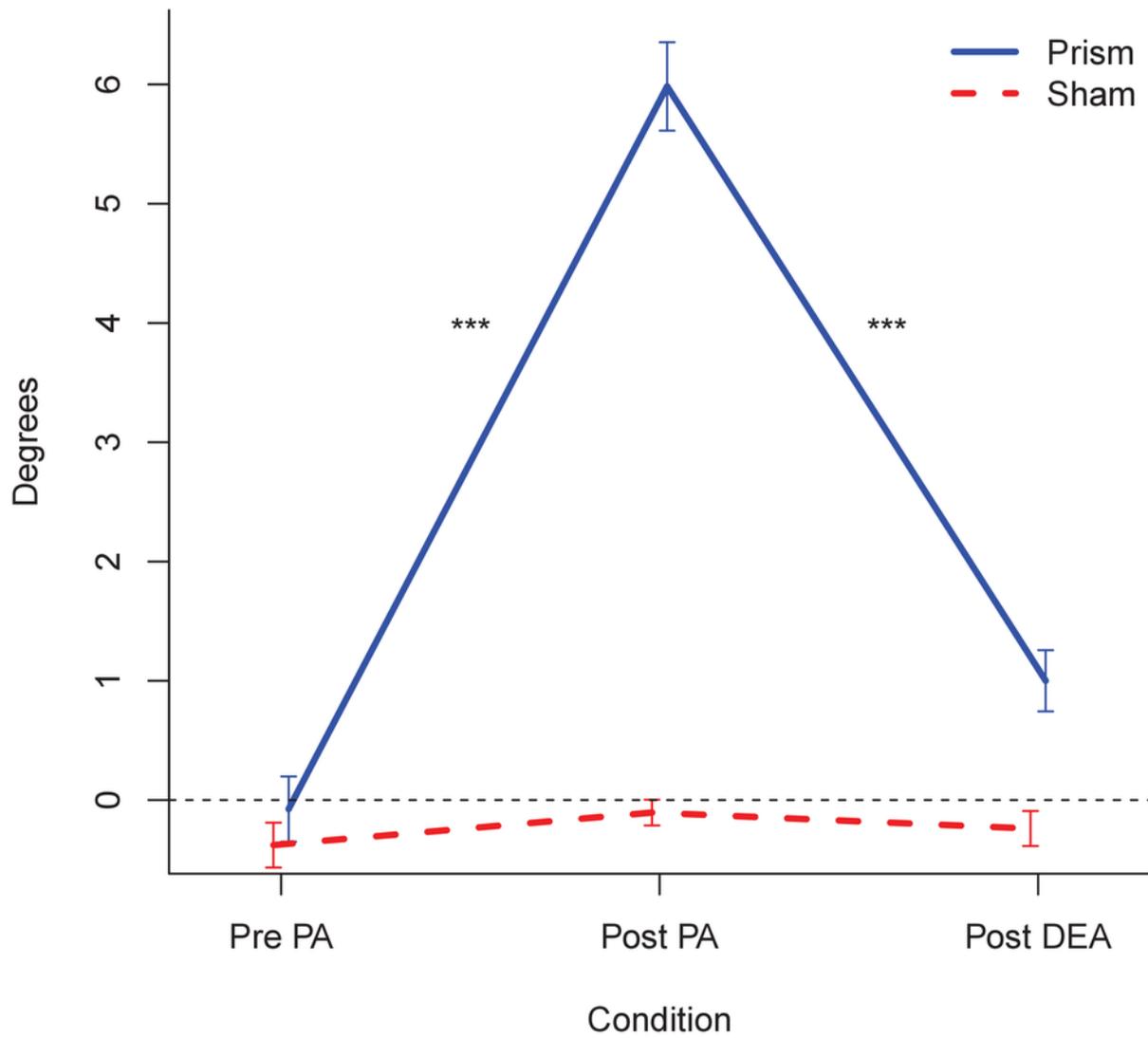
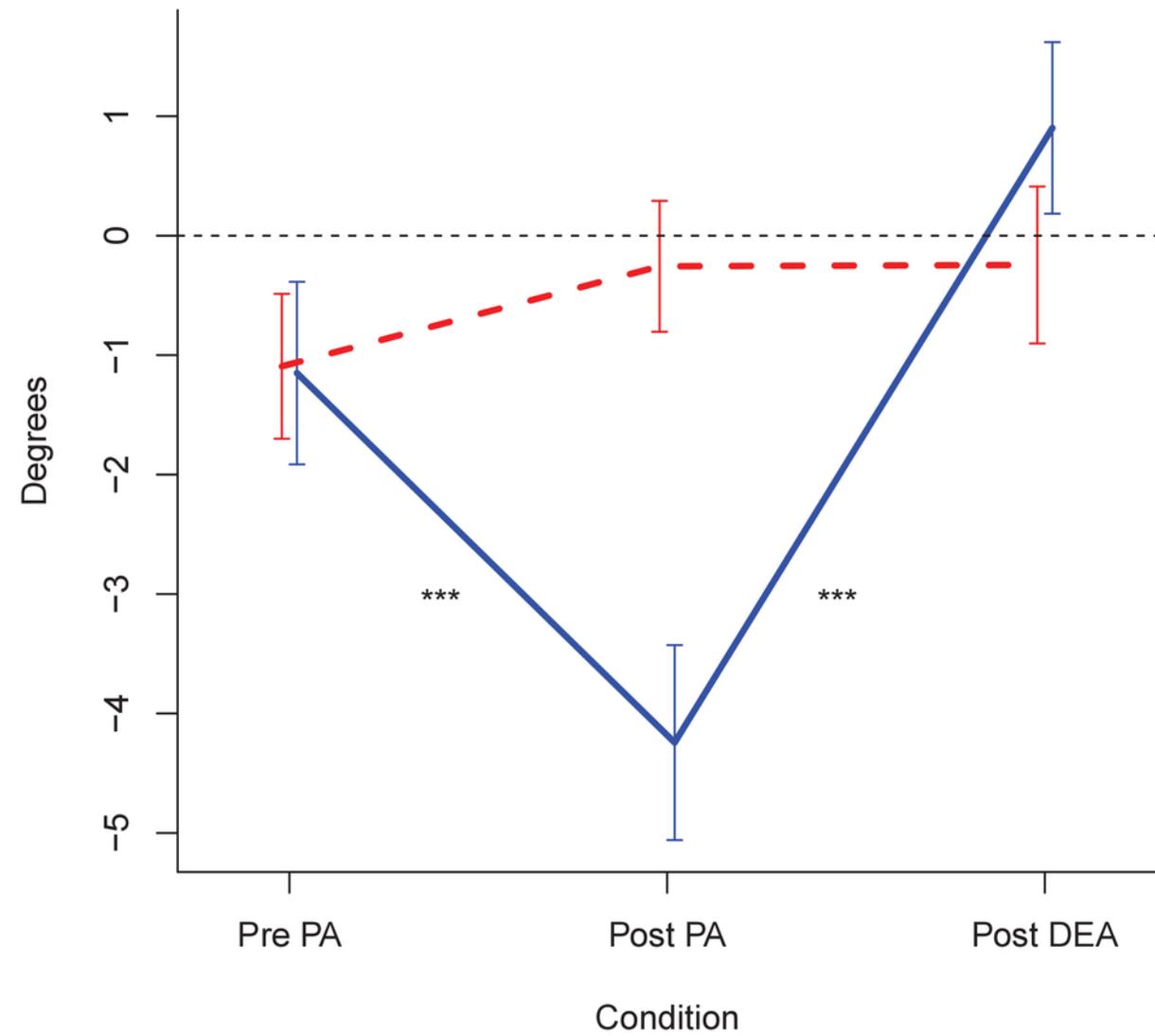
1093 Table 2. Demographic characteristics of the participants in the four experiments.

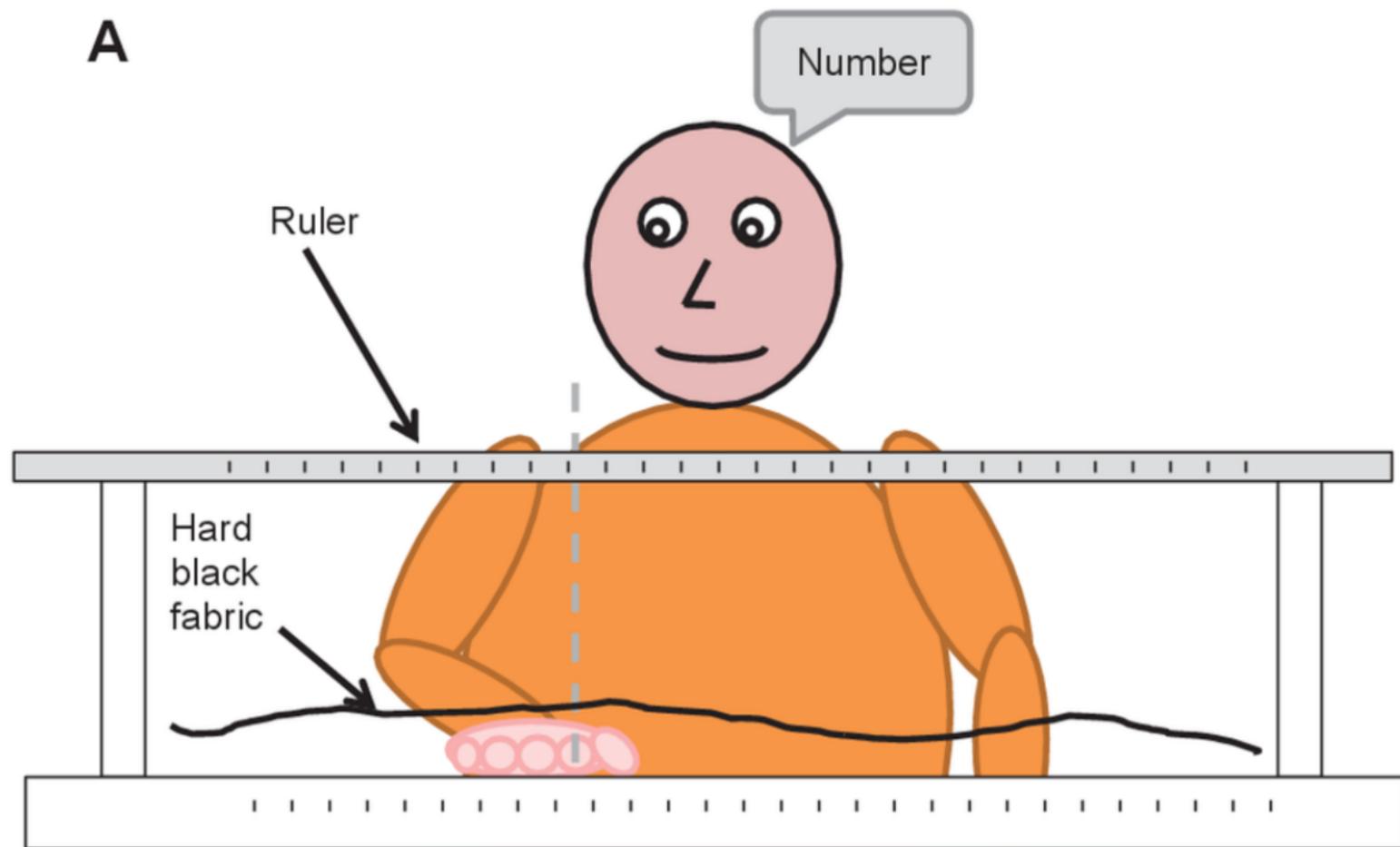
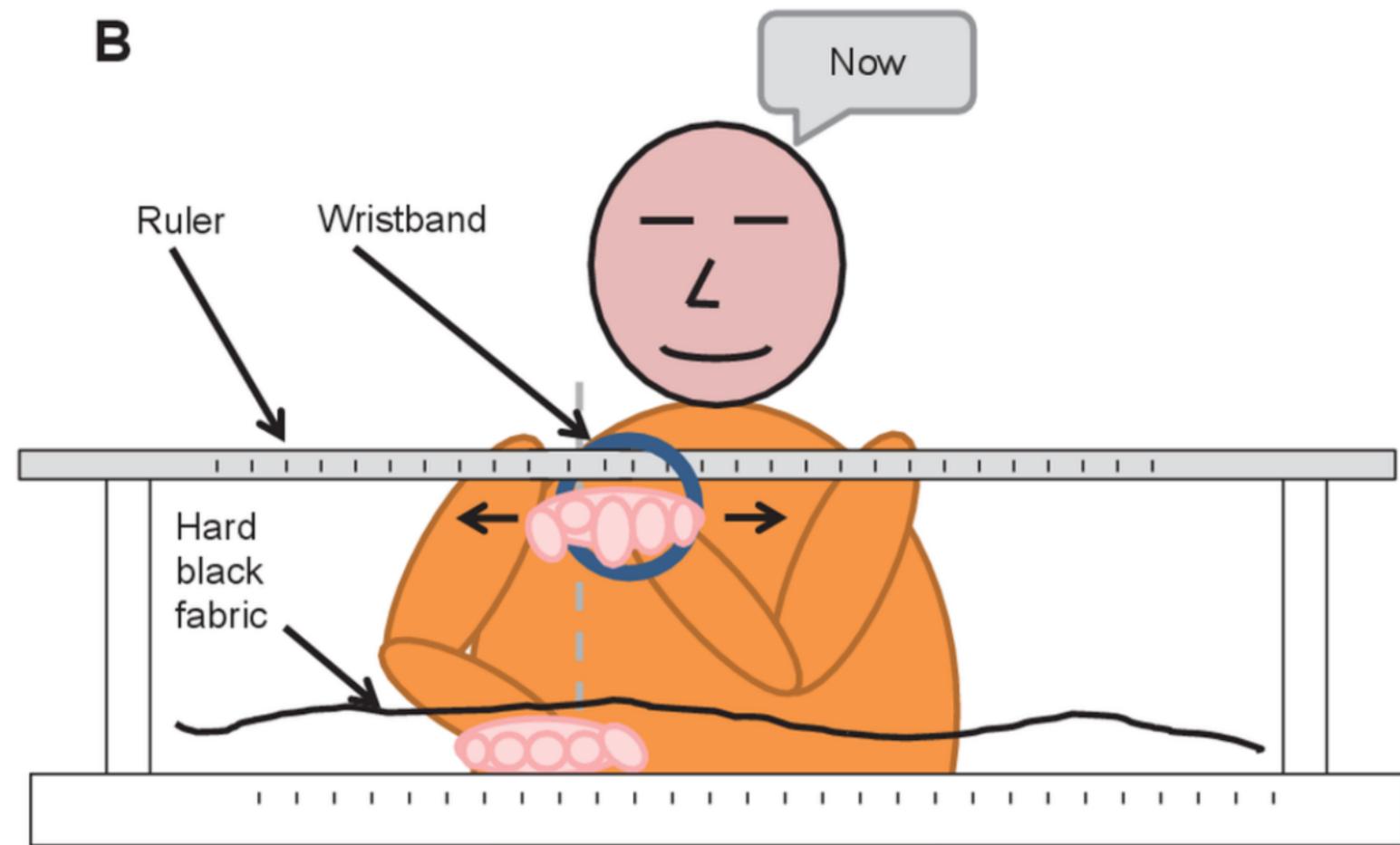
Experiment	VS	PS	TS	VPHJ	PPHJ	Total
Exp. 1			40%	21%		61%
Exp. 2	4%	18%	40%	36%	54%	76-94%
Exp. 3			36%	43%	33%	66-79%
Exp. 4			42%	43%	30%	76-86%

Table 3. Summary of the aftereffects obtained in the four experiments expressed in % as compared to the prism strength (15°).

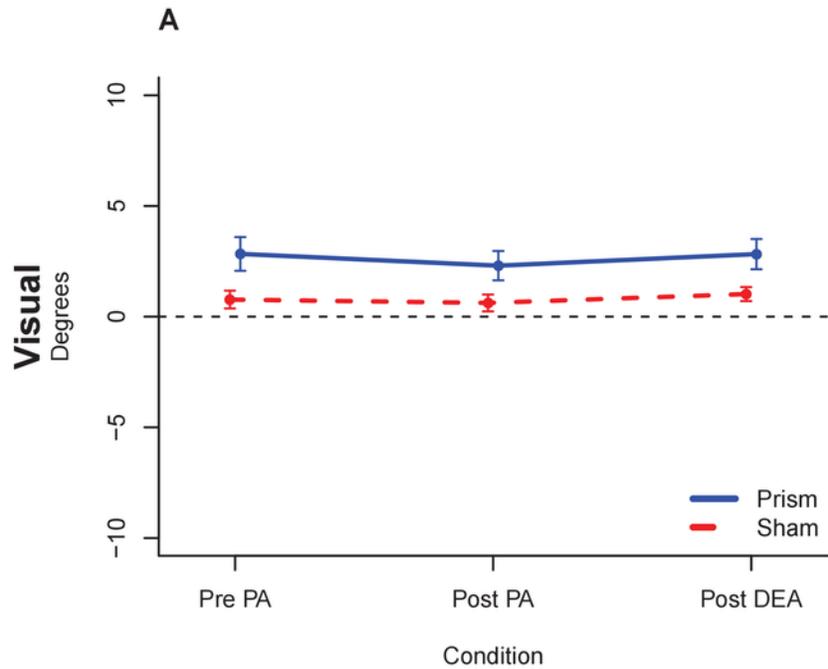
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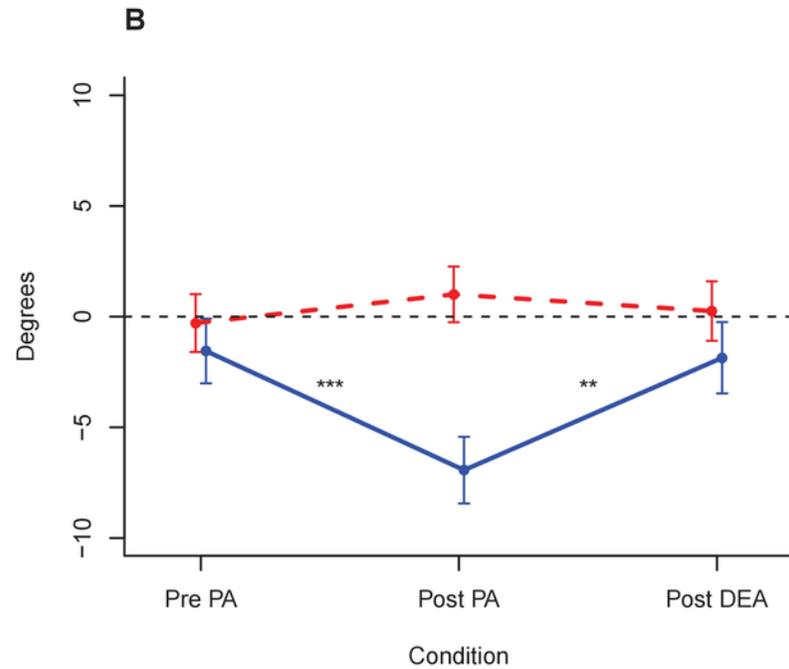
A**Open Loop Pointing****B****Proprioceptive Hand Judgement**

A**B**

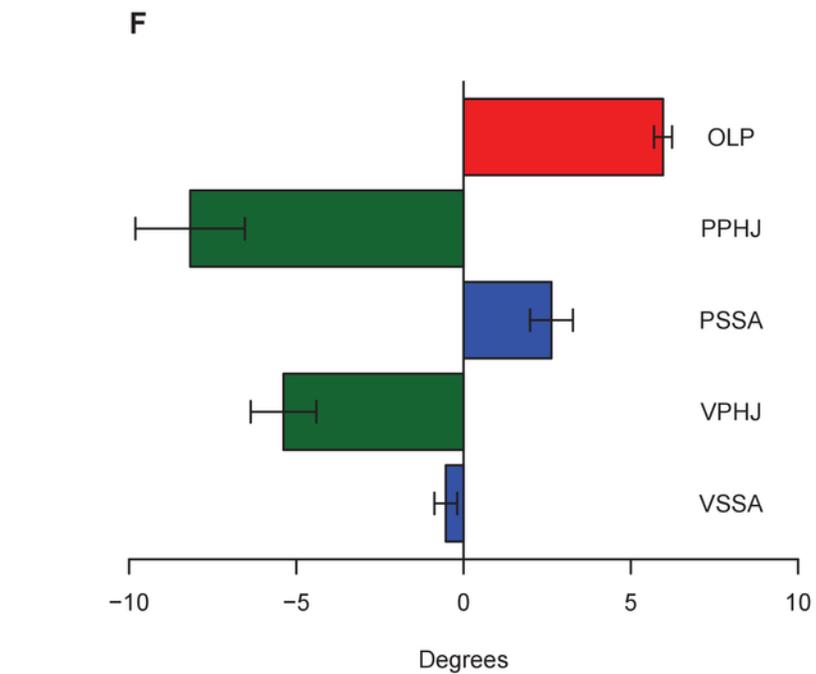
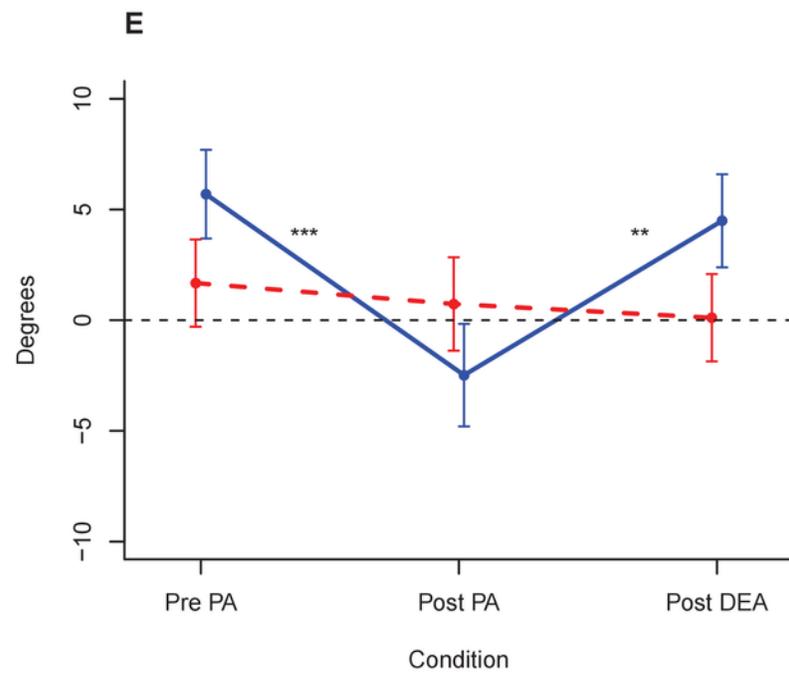
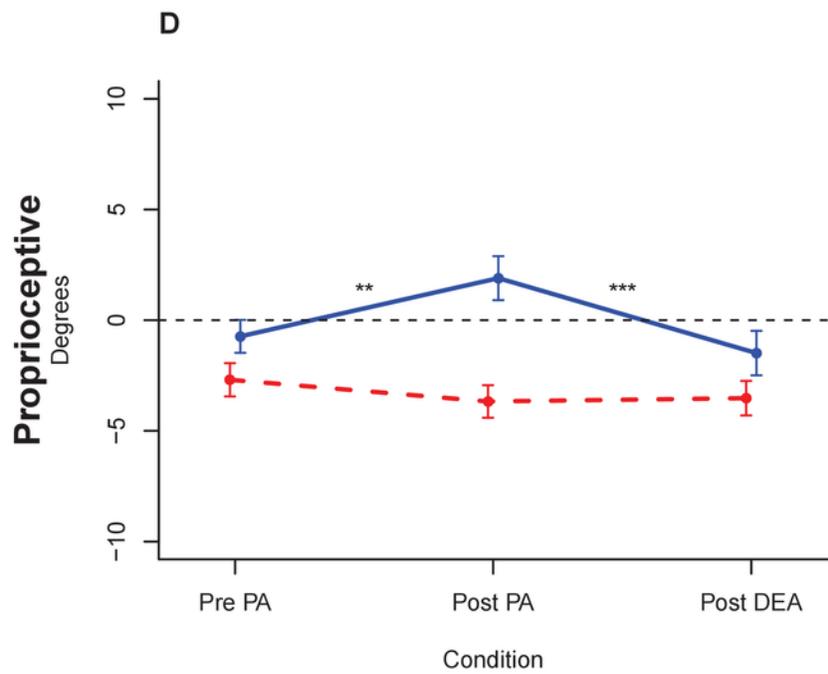
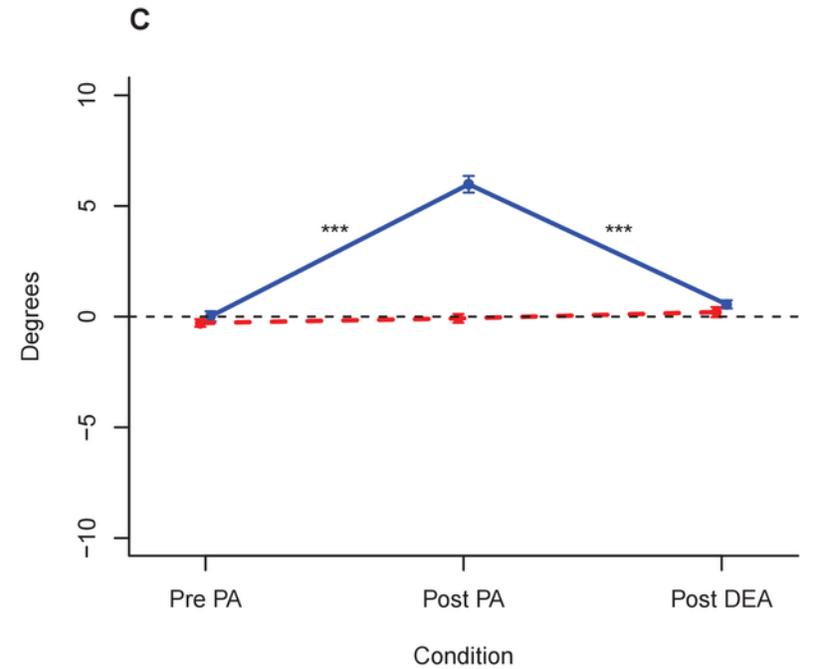
Subjective Straight Ahead



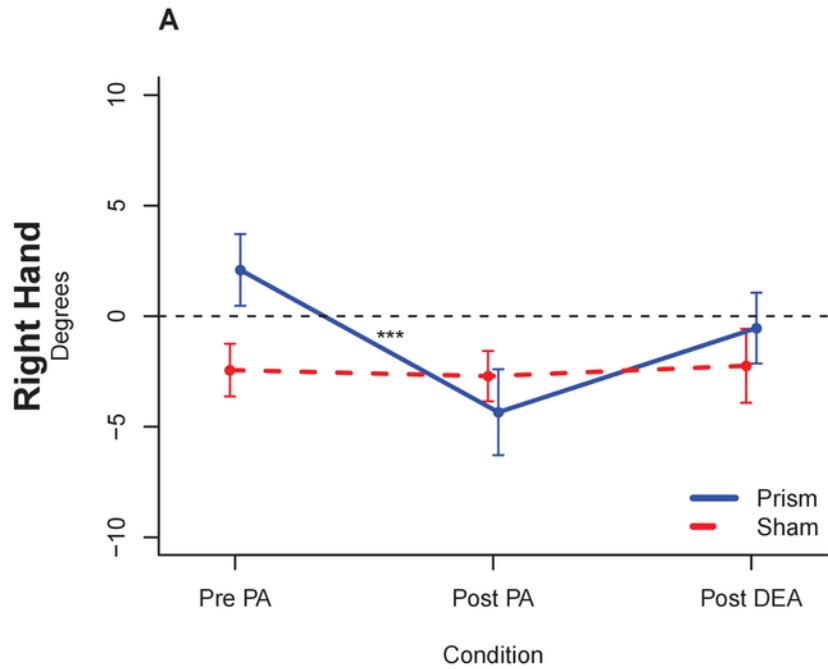
Proprioceptive Hand Judgement



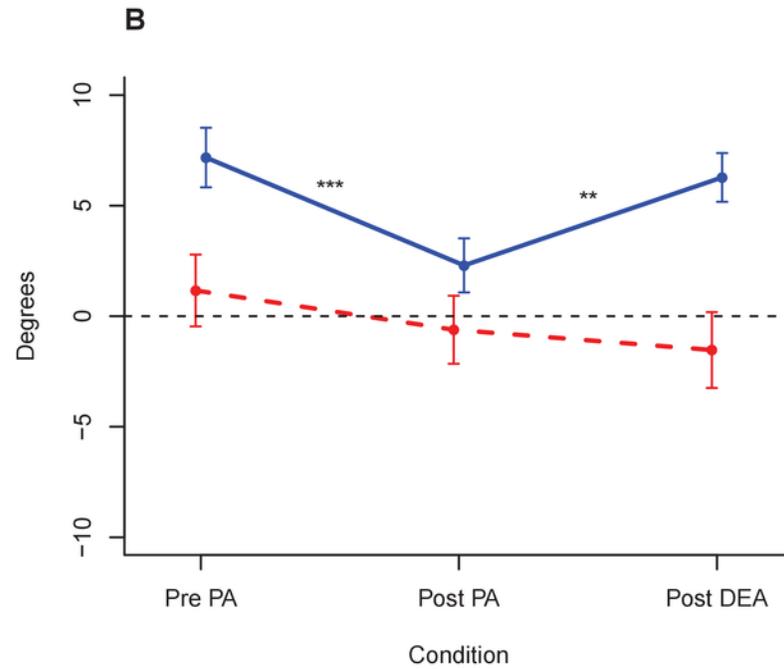
Open Loop Pointing



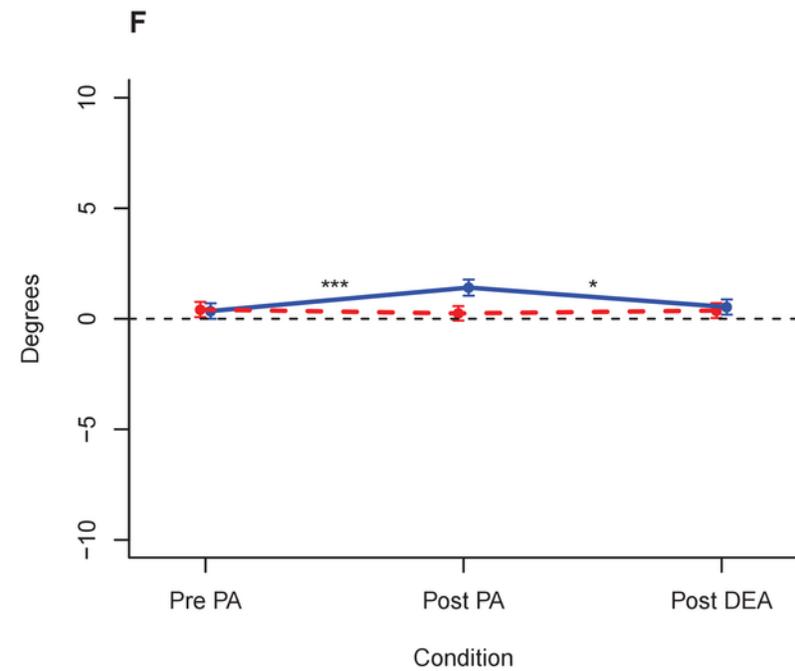
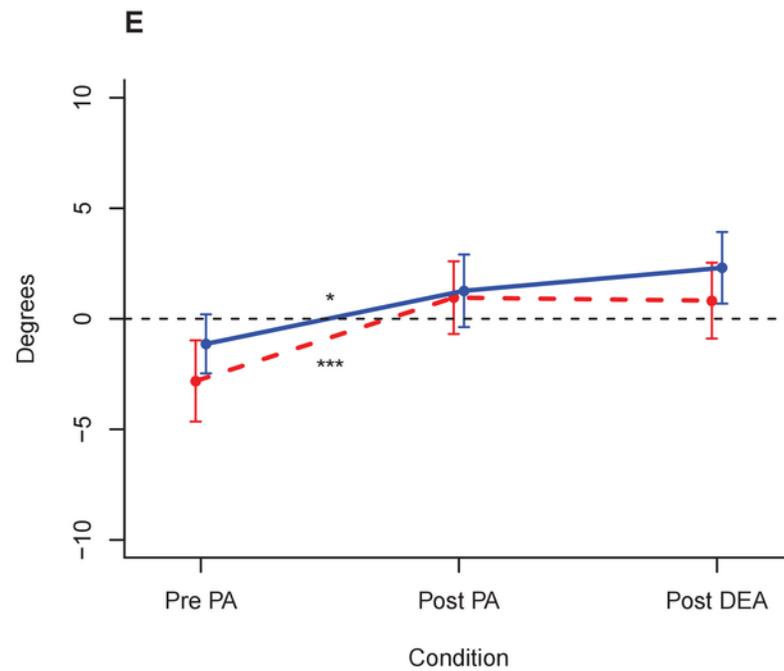
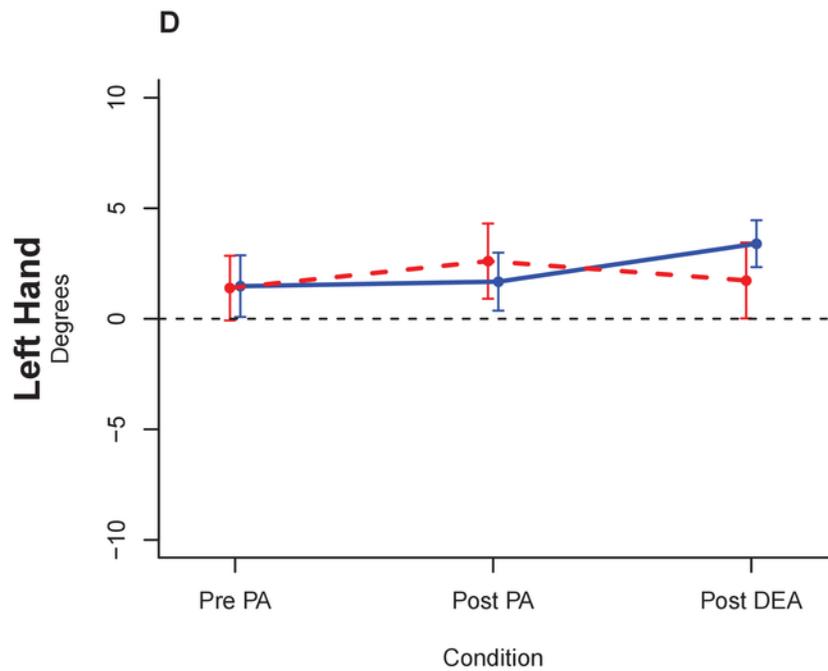
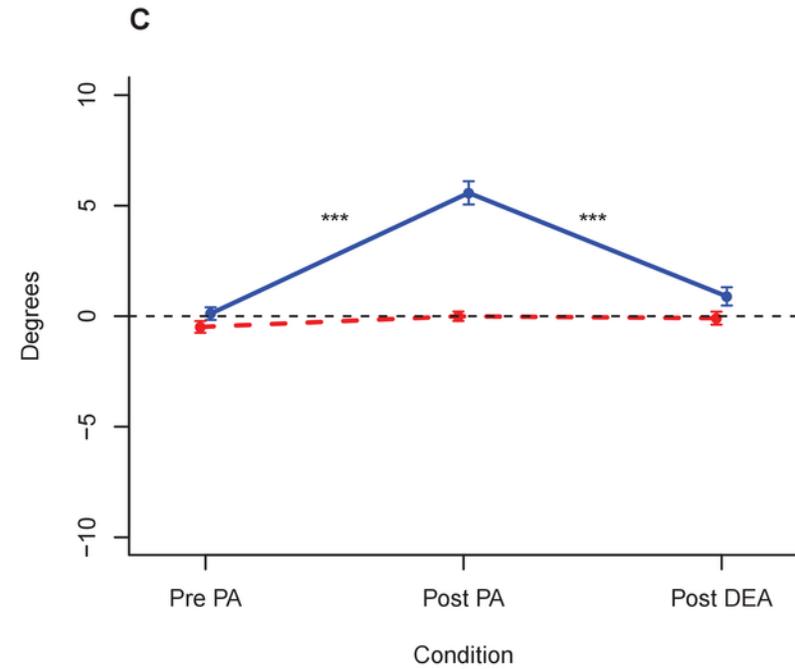
Visual Proprioceptive Judgment



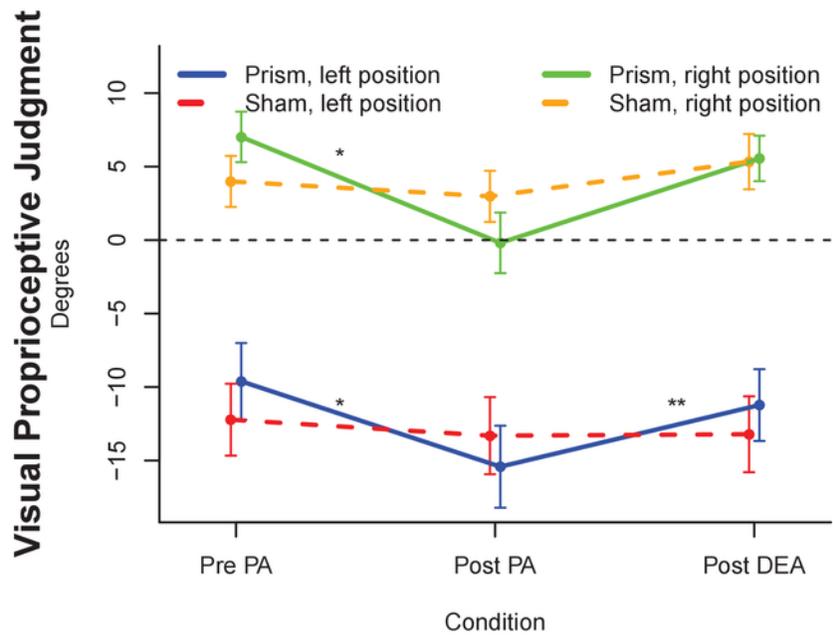
Passive Proprioceptive Judgement



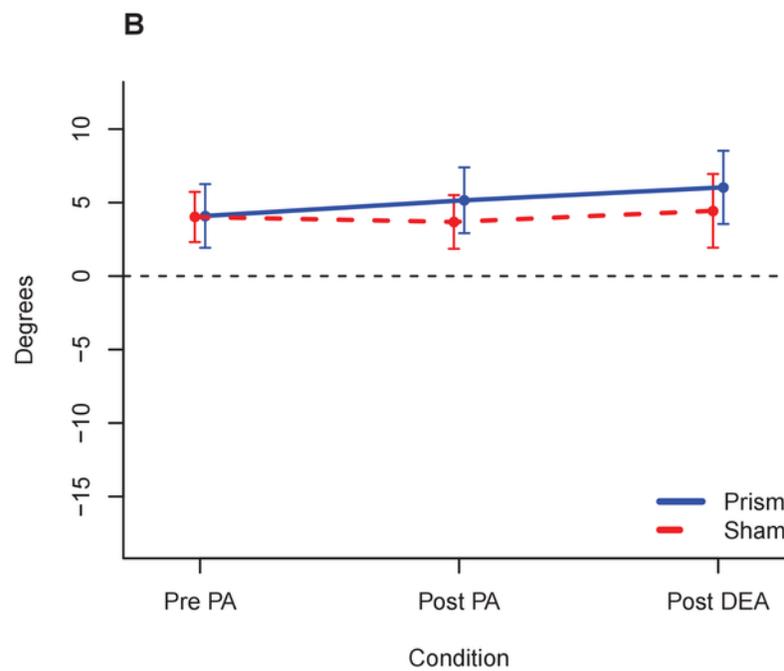
Open Loop Pointing



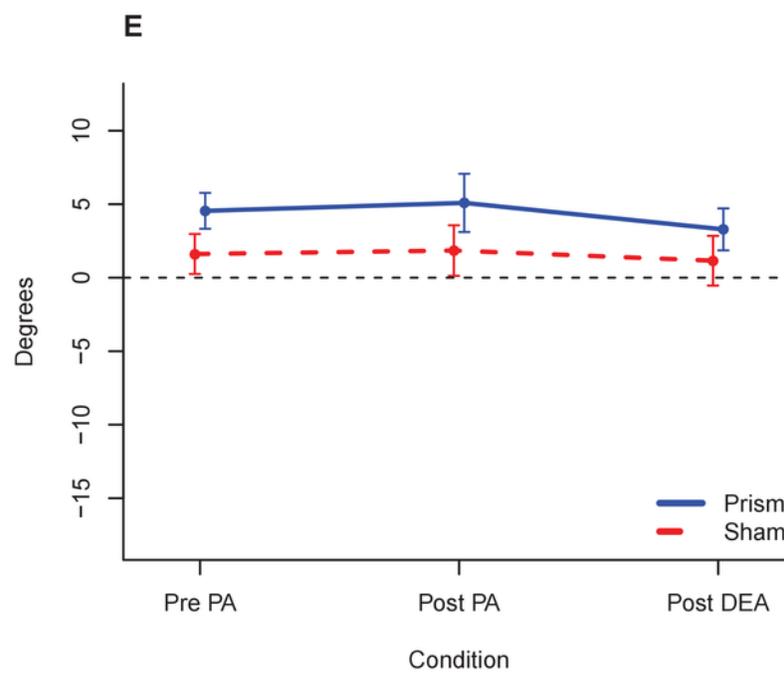
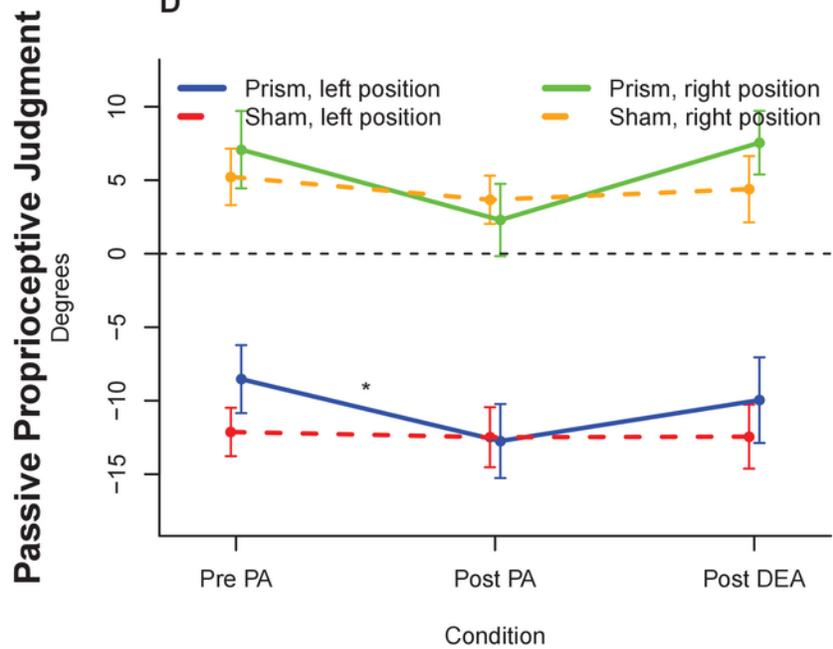
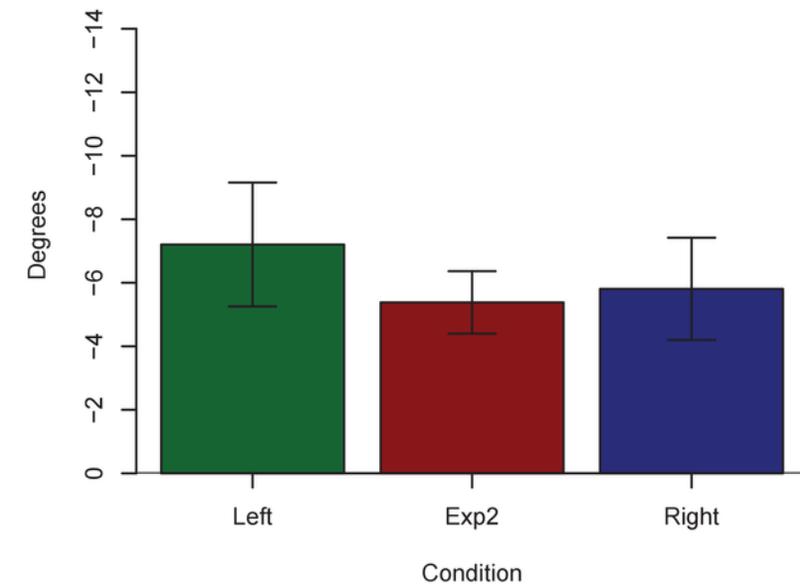
Hand, lateral positions



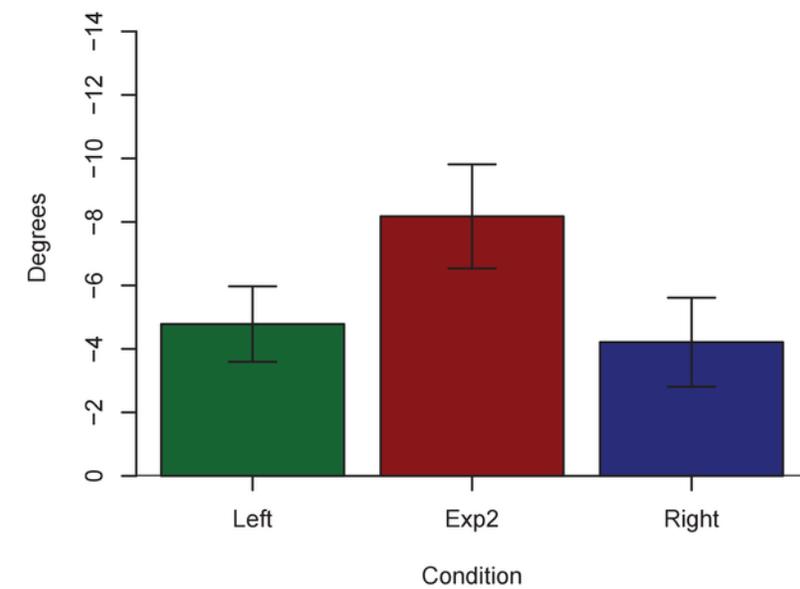
Shoulder



VPHJ



PPHJ



Prism optical deviation



TS



HAE