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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 ( $0.27^\circ$ ).

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  $6.05^\circ$  to the right (40.3% of optical shift) and the  
241 proprioceptive of hand aftereffect (HAE) was  $3.09^\circ$  (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  $9.14^\circ$ , 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 [ $F_{(2,60)} = 12.28, p < 0.0001, \eta^2_p$   
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 ( $1.06^\circ$ ). 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  $15^\circ$  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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743

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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)

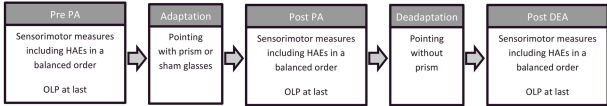
1093 Table 2. Demographic characteristics of the participants in the four experiments.

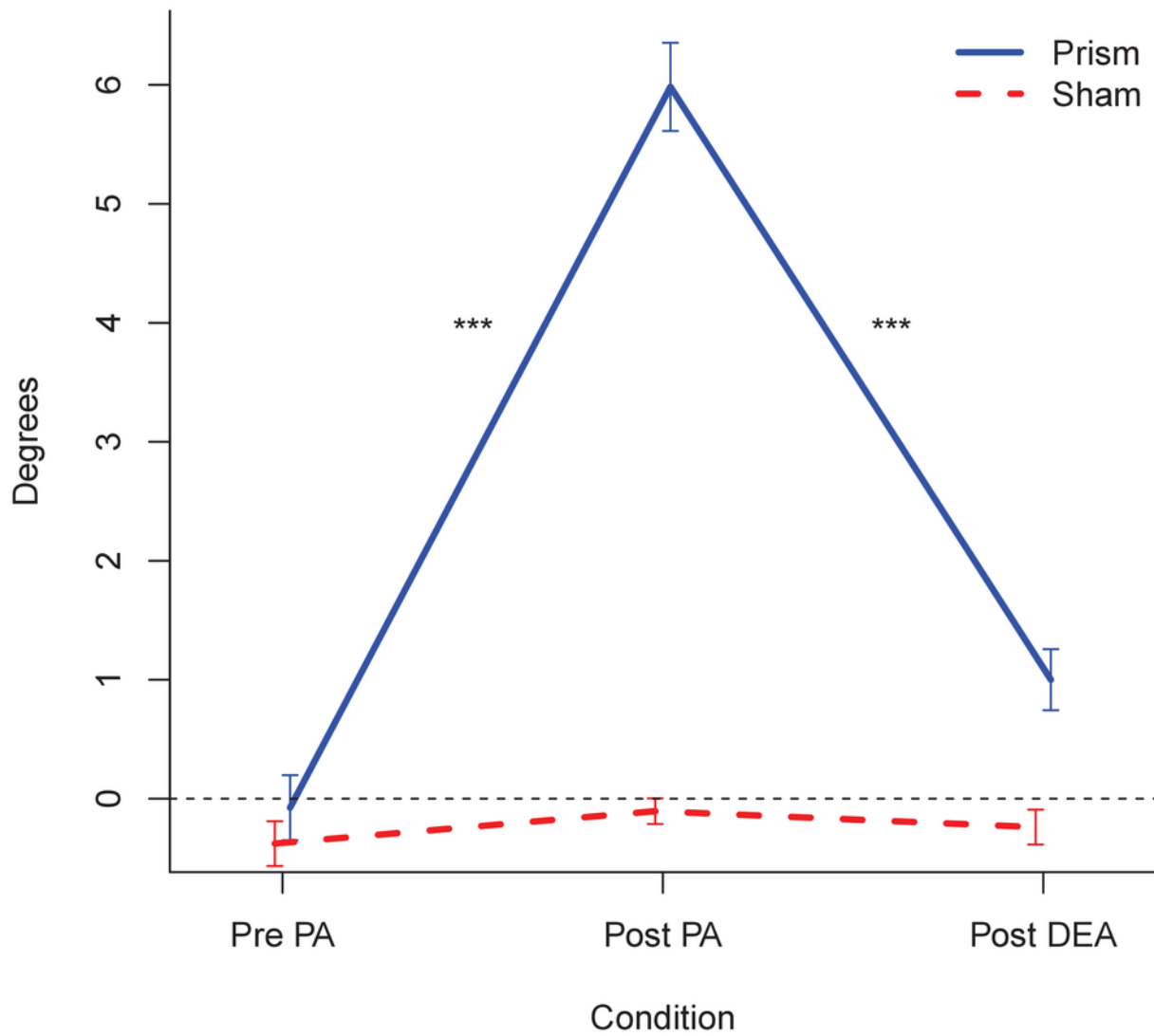
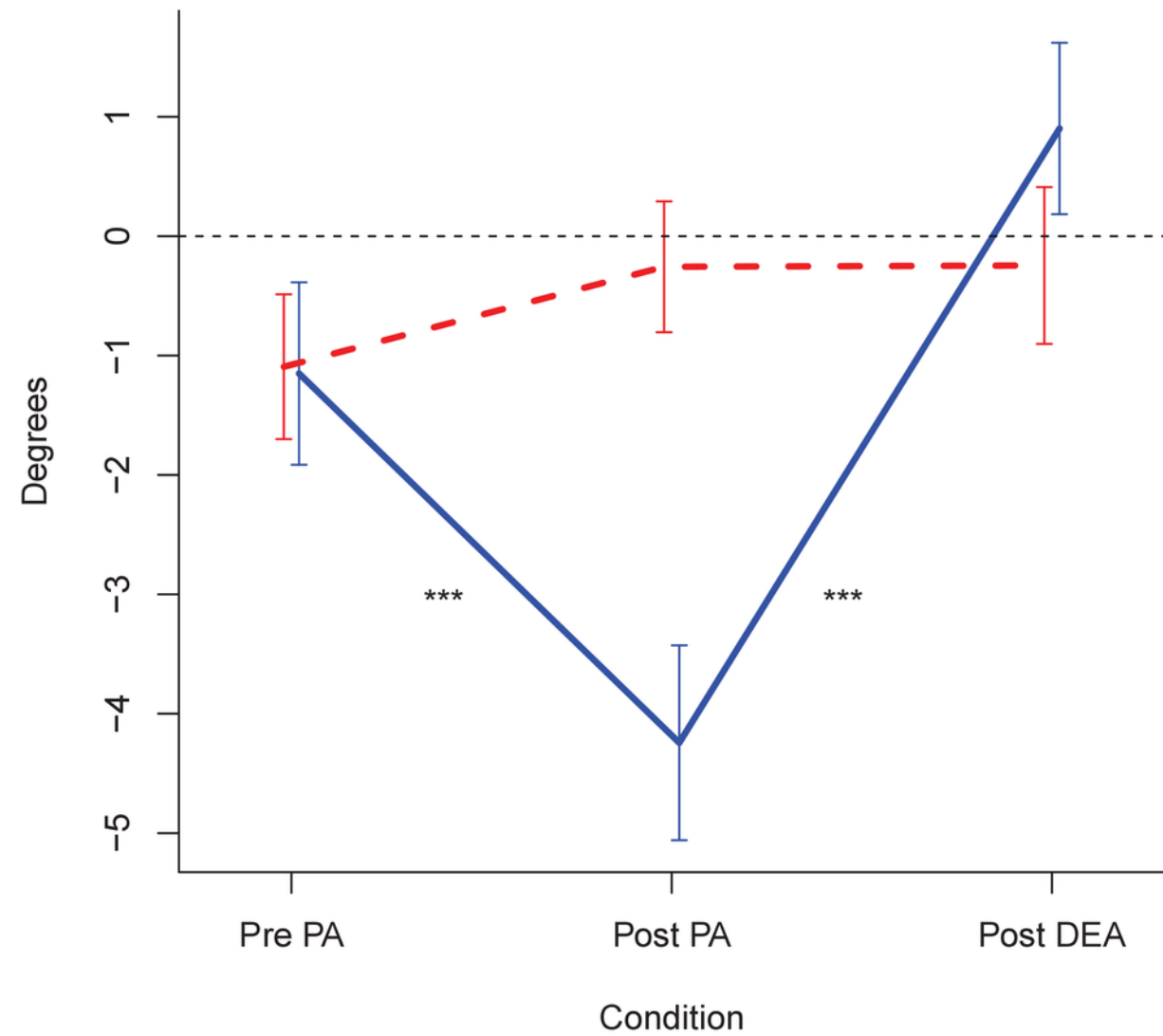


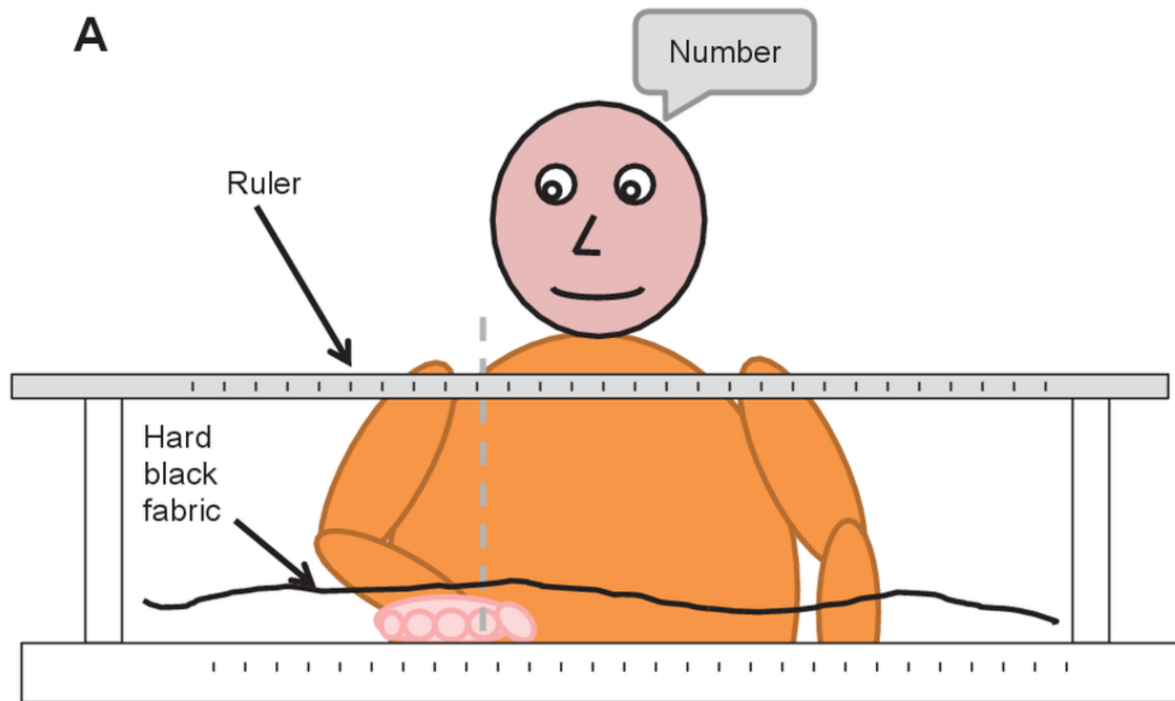
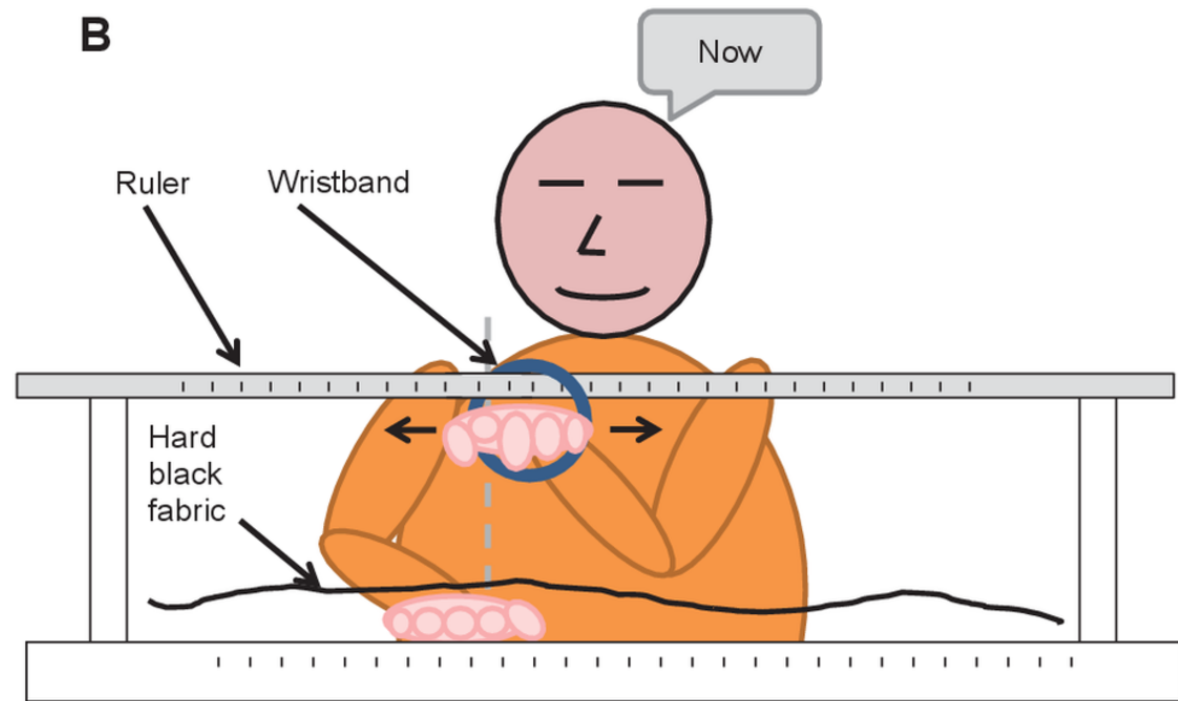
Experiment	VS	PS	TS	VPHJ	PPHJ	Total
Exp. 1			40%	21%		61%
Exp. 2	4%	18%	40%	36%	54%	76-94%
Exp. 3			36%	43%	33%	66-79%
Exp. 4			42%	43%	30%	76-86%

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

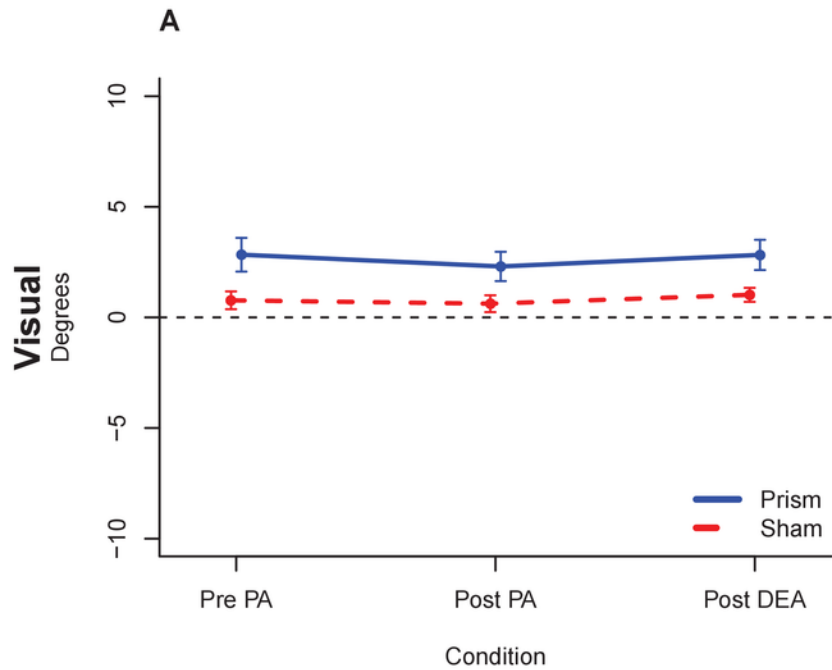
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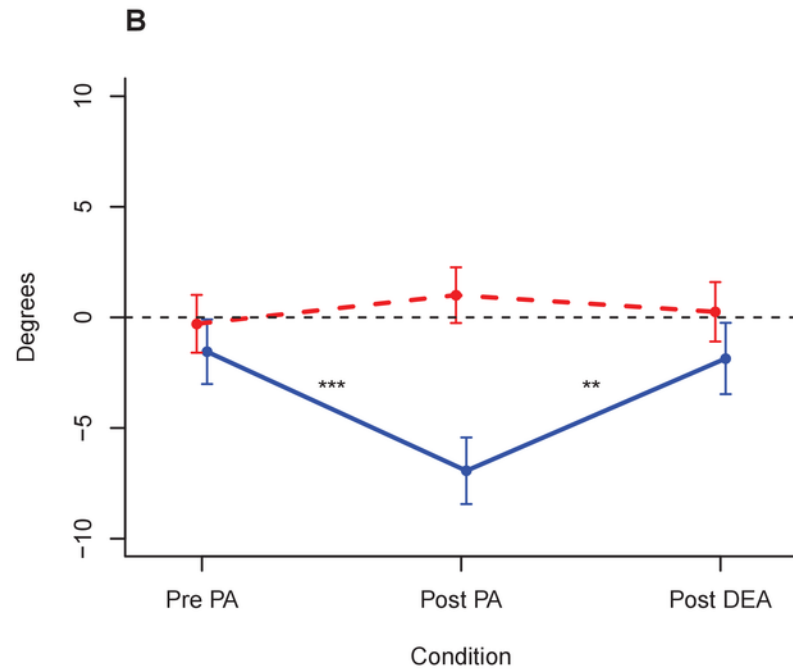
**A** Open Loop Pointing**B** Proprioceptive Hand Judgement

**A****B**

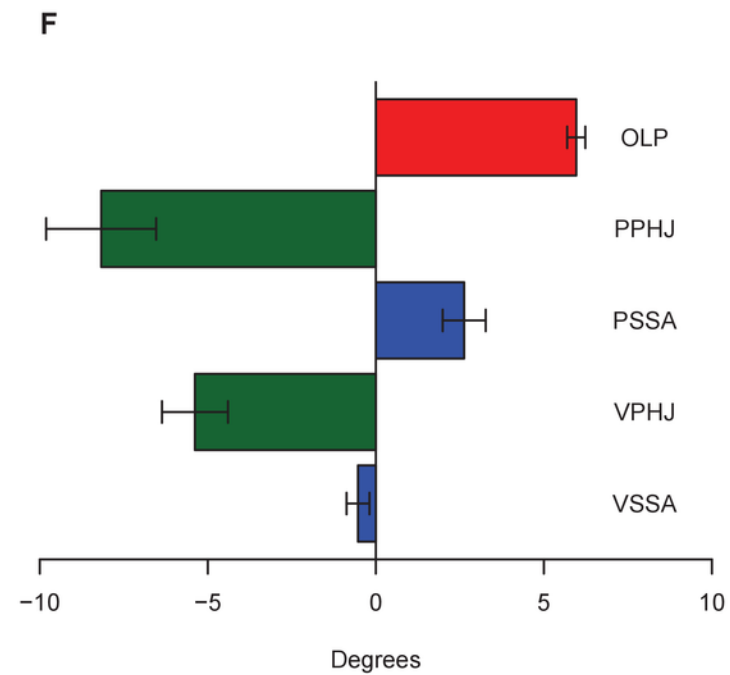
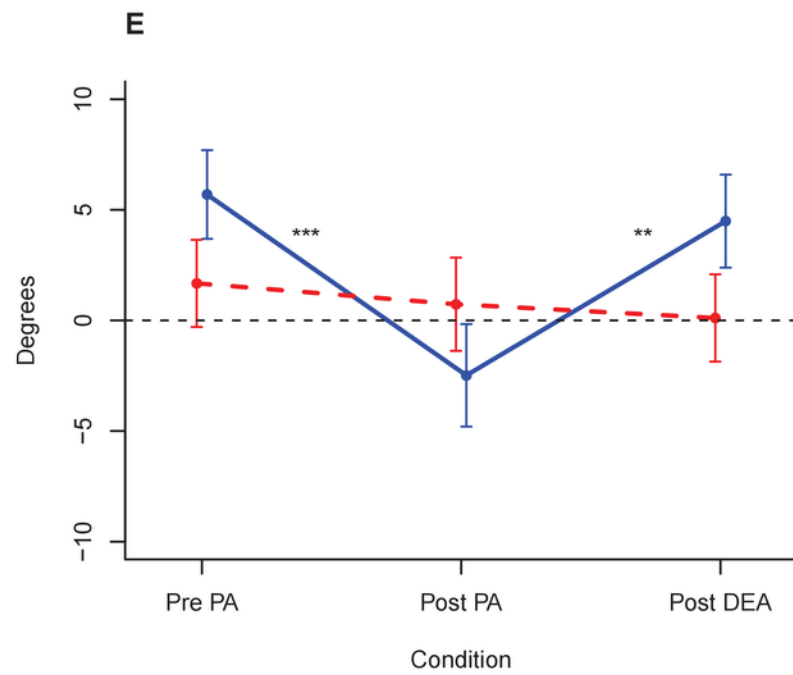
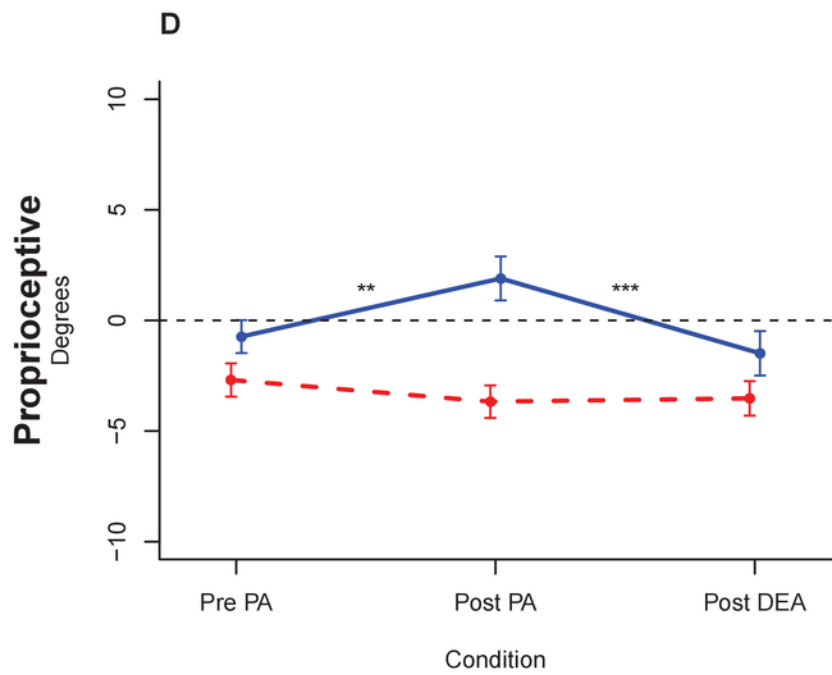
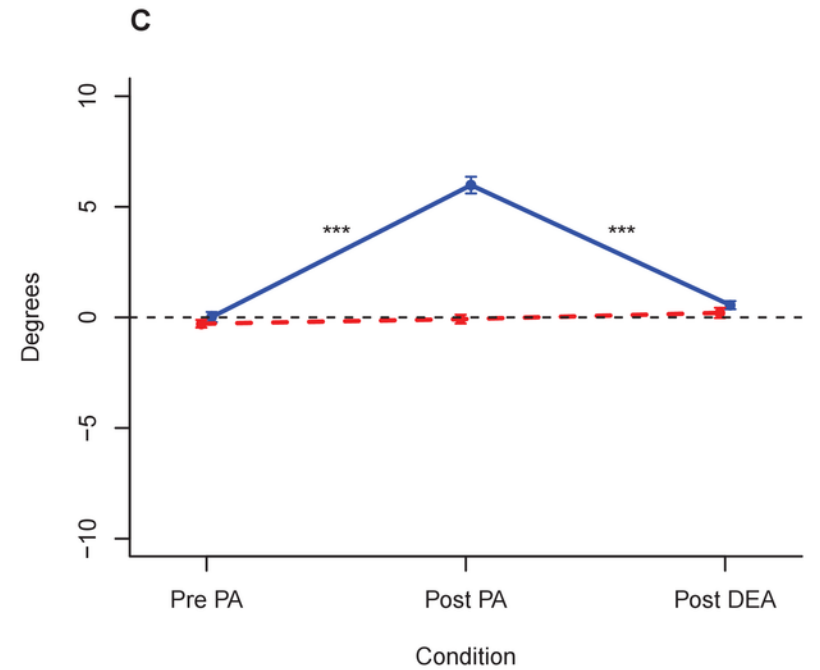
### Subjective Straight Ahead



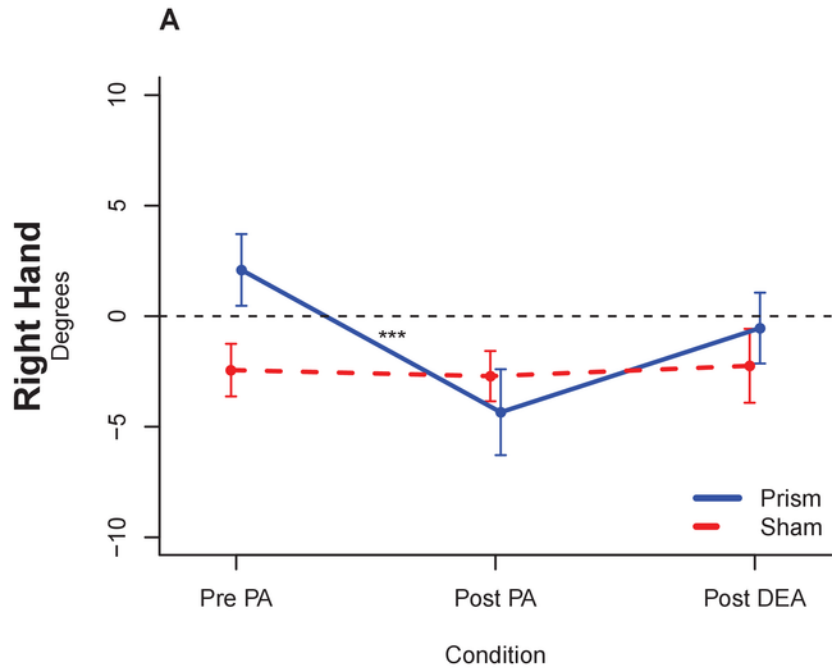
### Proprioceptive Hand Judgement



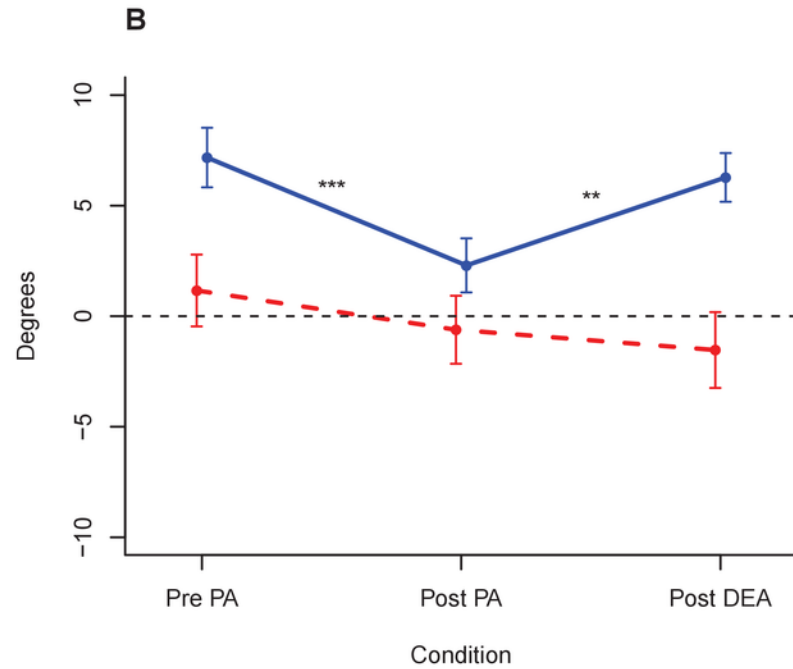
### Open Loop Pointing



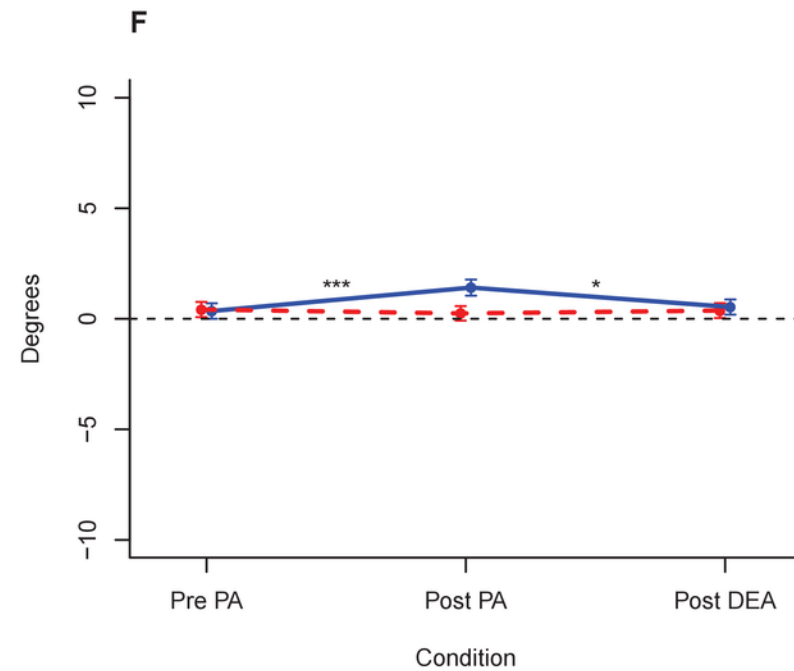
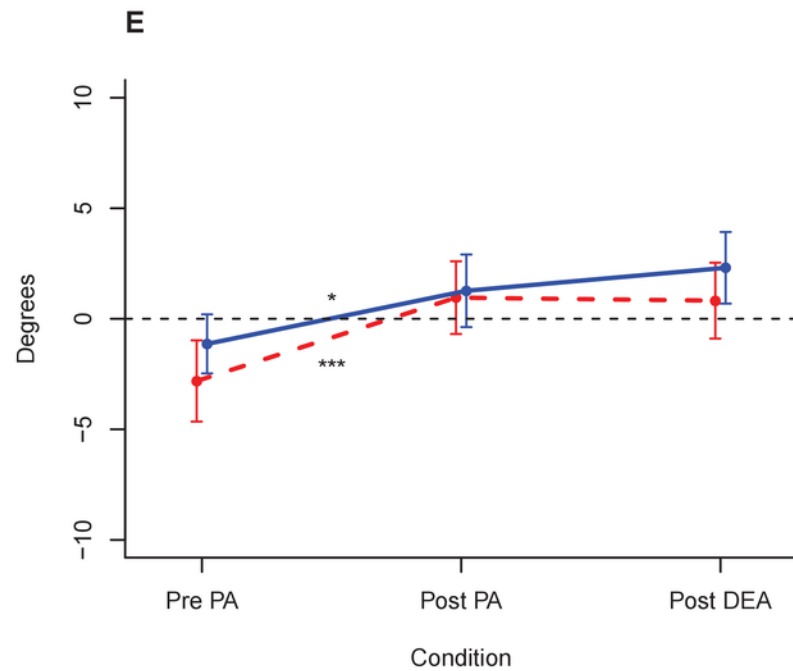
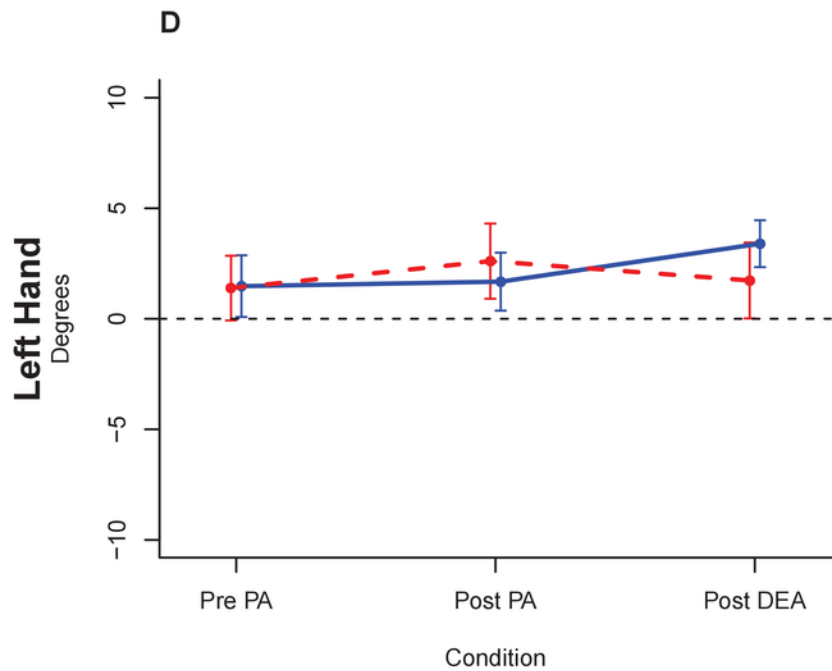
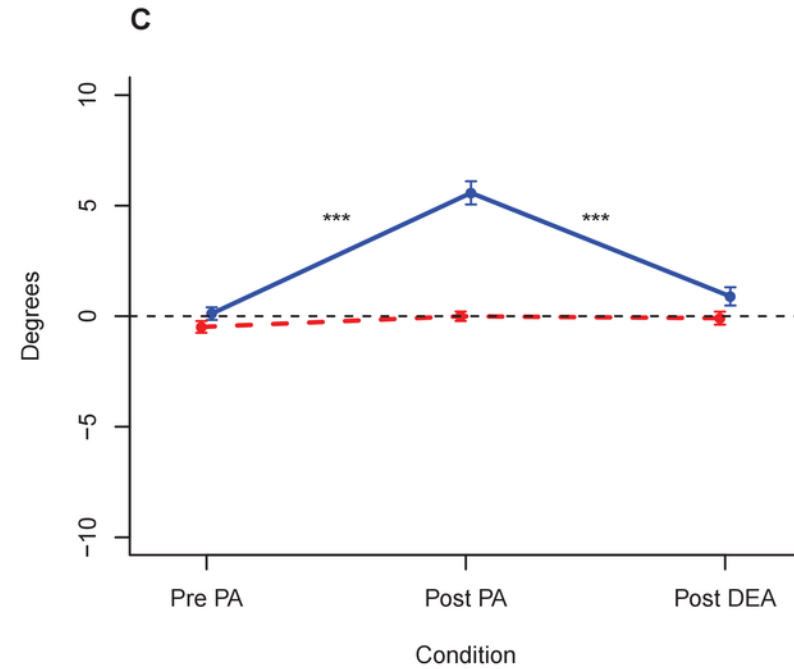
### Visual Proprioceptive Judgment



### Passive Proprioceptive Judgement

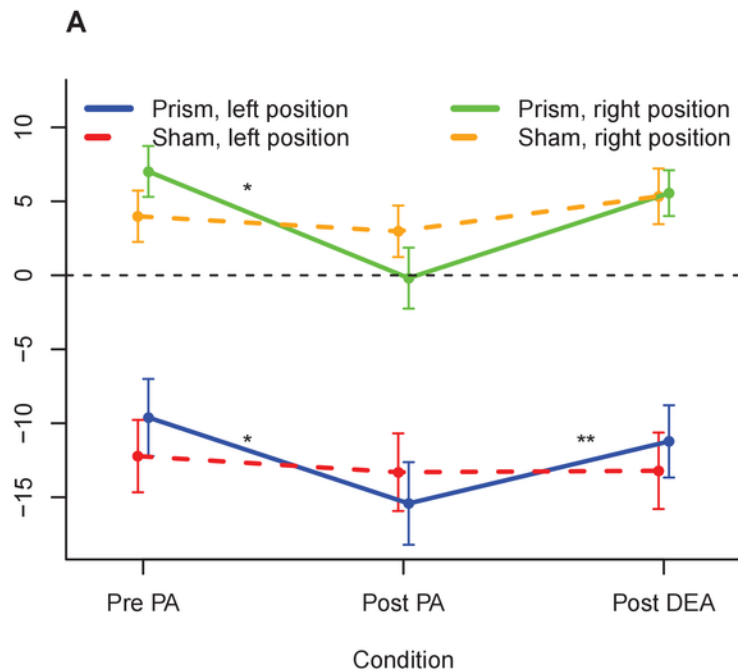


### Open Loop Pointing

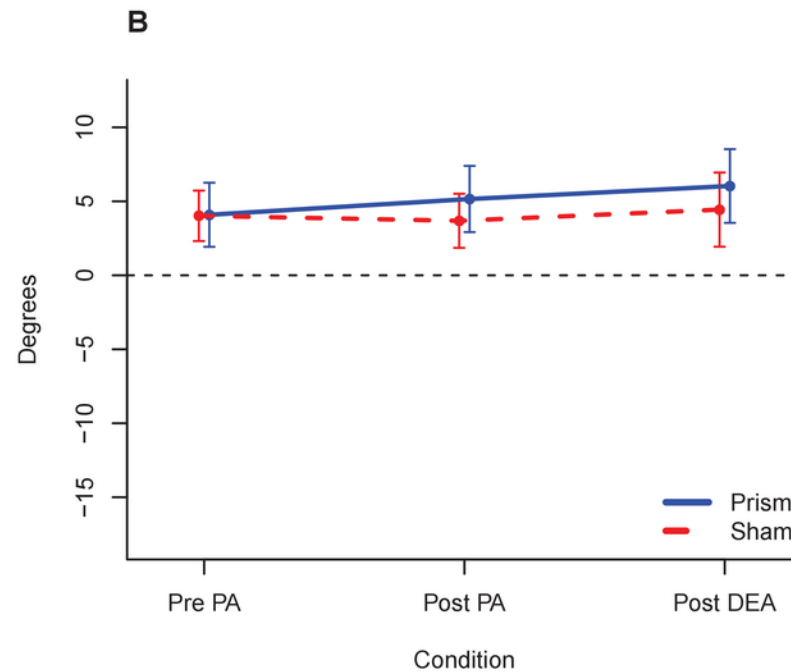


## Hand, lateral positions

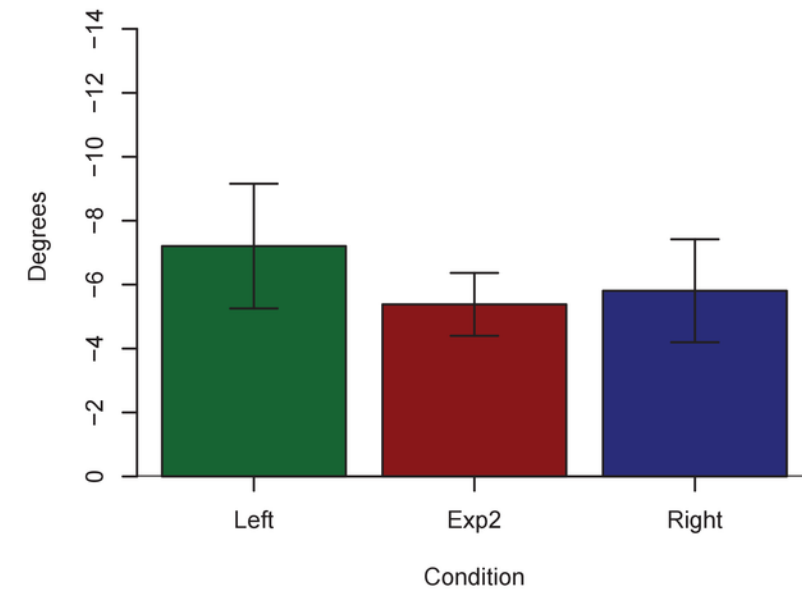
Visual Proprioceptive Judgment



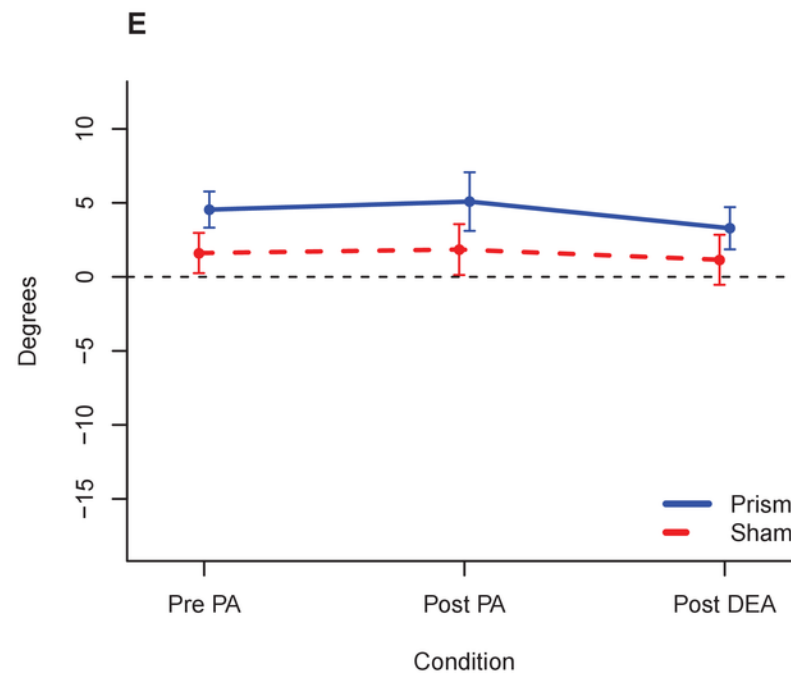
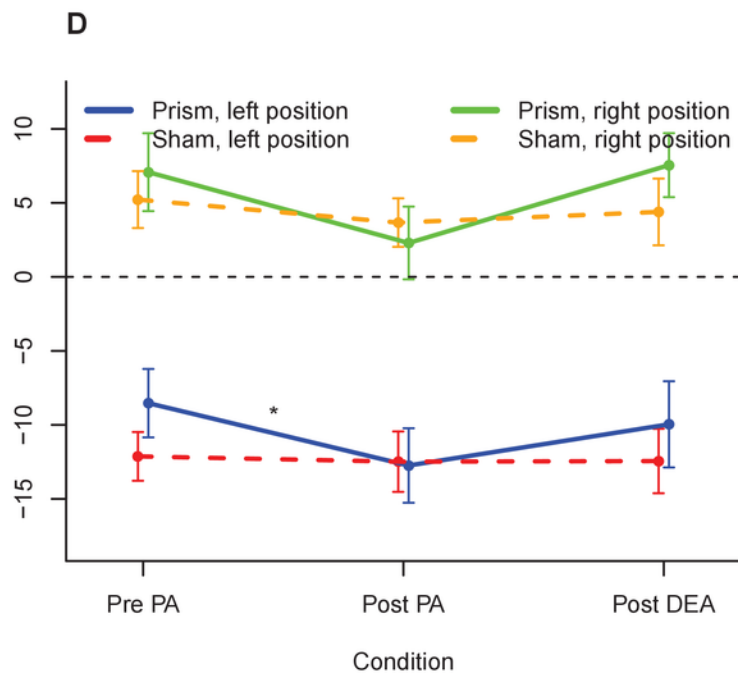
## Shoulder



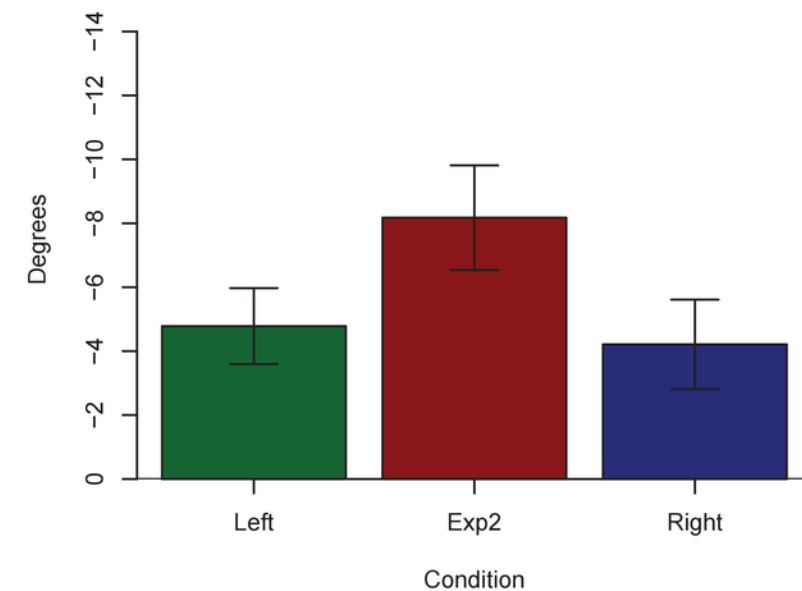
## VPHJ



Passive Proprioceptive Judgment



## PPHJ



# Prism optical deviation



**TS**



**HAE**