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

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A B S T R A C T

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

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with responder/non-responder patients' profile to inform integrated models of PA that might allow for optimising patient-tailored PA procedures.

1. Introduction

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

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

When considering the TS, which is the most often reported AE measure (see Table 1), one would expect that its quantity should reflect the amount of lateral deviation induced by prisms. During the prisms exposure phase, both healthy and most previously reported cases of brain-damaged patients (Michel, Bonnetain, & White, 2017) are indeed able to reduce the initial error to, virtually, zero with a slower rate of error correction (Facchin, Bultitude, Mornati, Peverelli, & Daini, 2019). Such an efficient error correction ability, which has sometimes been shown to predict neglect patients' improvement (Làdavas, Bonifazi, Catena, & Serino, 2011; Serino, Angeli, Frassinetti, & Làdavas, 2006), would imply that adaptation processes are in place to fully take into account the initial optical deviation. This, in turn, should predict that after prisms removal the fully corrected error would translate into a fully compensated behaviour, thus bringing to AE opposite in direction, but equivalent in amount, to the optical deviation induced by the prisms. In sharp contrast to such a straightforward prediction, the TS does not represent the total amount of prism deviation. Actually, it only explains about 38% of it (see Table 1). Depending on the used prisms, the optical deviation, the type of arm movements, the procedure used during adaptation and the specific setup, the AE ranges from 13% to 73% of the prisms deviation. Most of the reported studies found an aftereffect average of 38% of total prism deviation, while the sum of VS and PS is slightly higher than TS, reaching 40% of prism deviation (see Table 1 for details).

Why the AE does not express the entire prism deviation? In the present study, we address this question and hypothesize that the 'lost' part of the aftereffect has remained concealed for decades in a previously underestimated component: the change in the felt position of the hand after prism adaptation or Hand AE. Historically, the role of hand proprioception in prism adaptation has been taken into account mostly at the theoretical level. Harris (1963) used the change in the felt position of the hand as an explanatory concept for adaptation to laterally displacing prism. The same point of view was also considered in a review by Kornheiser (1976). Despite the fact that simple exposure (not adaptation) to prisms was already known to displace the judgment of the hand position based on proprioception (Folegatti, De Vignemont, Pavani, Rossetti, & Farnè, 2009; van Beers, Sittig, & Gon, 1999), there was sparse and scarce evidence that prism adaptation would also cause such a displacement (Craske, 1966; Craske & Gregg, 1966; Scarpina, Stigchel, Nijboer, & Dijkerman, 2015; Wallach & Huntington, 1973).

The results of a recent study, aimed at assessing the proprioceptive component of PA, provided some initial evidence that PA may induce a drift in the felt position of the hands, though apparently limited to certain combinations of pointing hand and prisms direction (Scarpina et al., 2015). Interestingly, the authors found that leftward PA seemed to affect hand proprioception in the direction of the optical deviation (leftward), thus opposite to the TS typically observed after PA. The role of hand proprioception is thus the focus of our interest here, for its potential to explain the puzzling result we are facing since the discovery of the effects of pointing through prims (von Helmholtz, 1910): if the felt hand position is displaced on the opposite direction of the TS, this could explain (at least some of) the lost part of AE compared to the full prism strength. In particular, if during (e.g., leftward) PA, hand proprioception is shifted in the same direction of the optical deviation (i.e., leftward) and opposite to the TS direction (i.e., rightward), the AE as measured by TS would consequently be smaller than the total deviation and the additional change in hand felt position could concur to account for the lost part of the AE. Moreover, the change in proprioception of the hand

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

Reference	Prism Power	Base	Trial of adaptation	Feedback	VS	PS	TS
Held and Gottlieb (1958)	11.3°	R	100	C			48%
Held and 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 and Pick (1966)	11.3°	LR	6days	C	21%	25%	27%
Craske and Gregg (1966)	11.3°	R	Until 10 correct	C			35%
(Efstathiou et al., 1967)	8,7°	LR	3′	C			32%
Cohen (1967)	16.7°	LR	5′	CT			15%
(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 and 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 and Wallace (1976)	11.3°	L	25′	C	4%	45%	51%
Lackner and Lobovits (1977)	11.3°		10′	n.s			23%
Melamed, Beckett, and 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 and Wallace (1993)	11.3°	L	60	T	20%	25%	41%
Redding and Wallace (1996)	11.3°	L	60	T	9%	33%	42%
Redding and Wallace (1997b)	11.3°	L	60	T	10%	22%	35%
Clower and Boussaoud (2000)	5.7°	R	50	C			60%
Martin, Norris, Greger, and Thach (2002)	16.7°	R	50	T			38%
Berberovic and 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 and Murray (2005)	10°	R	5′	C		27%	
Striemer, Sablatnig, and Danckert (2006)	15°	LR	15′	T		75%	
Michel, Pisella, Prablanc, Rode, and Rossetti (2007)	10°	R	84	T			40%
Michel, Vernet, Courtine, Ballay, and Pozzo (2008)	10°	LR	12′	C			39%
Newport, Preston, Pearce, and Holton (2009)	11.3°	R	80	T	1%	31%	
Loftus, Vijayakumar, and Nicholls (2009)	15°	LR	50	T			18%
Wilms and Malá (2010)	10°	L	90	T			46%
Fortis, Goedert, and 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, and Redding (2012)	8.5°	L	30	T	8%	19%	33%
Michel et al. (2013)	15°	R	100	C			42%
Facchin et al. (2013)	11.3°	L	100	C		26%	33%
Bultitude, Van der Stigchel, and Nijboer (2013)	15°	LR	150	T			26%
Fortis, Ronchi, Calzolari, Gallucci, and Vallar (2013)	11.3°	L	90	T	6%	14%	28%
Bultitude, Downing, and Rafal (2013)	15°	R	150	T			34%
Bultitude, List, and Aimola Davies (2013)	14.2°	LR	90	T			32%
Magnani, Mangano, Frassinetti, and 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 and Cruz (2015)	15°	R	360				69%
Schintu et al. (2016)	15°	R	150	T			47%
Panico, Sagliano, Grossi, and Trojano (2016)	11.3°	L	90	T			36%
Patané, Farnè, and Frassinetti (2016)	10°	LR	90	T			43%

(continued on next page)

Table 1 – (*continued*)

Reference	Prism Power	Base	Trial of adaptation	Feedback	VS	PS	TS
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, and 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%

could represent an additional frame of reference to be included into models of PA. On this basis, we designed a series of four experiments aimed at assessing, measuring, comparing and defining the effects of PA on hand proprioception.

2. Experiment 1

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

2.1. *Methods*

2.1.1. *Subjects*

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

2.1.2. *Experimental setup*

Participants sat at a table in a dark and sound-attenuated room, facing the experimental apparatus composed by a table covered by a semi-silvered mirror on a wooden frame. The wooden frame was open to the subject and to the examiner side and the participants' hand rested on the table under the mirror. Above the mirror, a ruler was positioned on two lateral supports, so that participants could see the numbers on it reflected at the same depth as their (unseen) hand on the table (about 40 cm). A light below the mirror allowed participants to have a vision of the hand and target during closed and open loop pointing movements. Conversely, when the light was off, the hand was unseen by participants and the reflected ruler become visible. The participants' proximal border of the mirror was black covered (by 5 cm) to prevent them from seeing the hand starting position when performing pointing movements. This setup was adapted from studies using the rubber hand illusion (Folegatti et al., 2009; Tsakiris & Haggard, 2005). In order to perform prism adaptation, a white panel was positioned on the table under the mirror. A tactile mark placed on the participant's side set the starting point for the participants' right index finger. Three coloured dots were marked on the distal edge of the panel (examiner side) corresponding to the subject body-midline at 0°, 10° leftwards and 10° rightwards. They represented the targets for the pointing movements: the midline one was used to perform the OLP task measuring the TS and the lateral dots were used for the adaptation procedure (both detailed below). Another ruler, visible only to the examiner on the vertical edge of the white panel, allowed him to measure the pointing error, to the nearest .5 cm. The distance between the participants' eyes and the targets was about 57 cm.

2.1.3. *Procedure*

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

2.1.4. *Visual proprioceptive hand judgment task*

In this task, participants were required to estimate the position of their hidden right index finger by means of a ruler reflected on the semi-silvered mirror covering their hand. Participants' right hand was positioned by the examiner on the table, 7.5 cm to the right of the body midline, at 40 cm of distance under the mirror, in a comfortable position. They had to report the number on the ruler corresponding to the position where they felt their index finger was, by mentally projecting a vertical line from the finger to the ruler. During the proprioceptive judgment task, the lights under the mirror were switched off, making the hand invisible and the ruler visible. Participants were required to repeat the

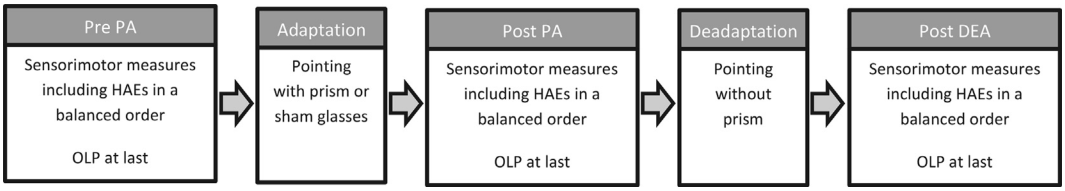

Fig. 1 – Schematic of the procedures used in each experiments. VPHJ = Visual Proprioceptive Hand Judgment; PPHJ = Passive Proprioceptive Hand Judgment; OLP = Open Loop Pointing.

proprioceptive judgment 6 times, with the ruler always presented with a random offset in order to avoid response strategies. The mismatch between the true position of the finger and the number indicated by the participant was calculated and resulted in a positive number if the displacement was rightward and a negative number if it was leftward. This measure was derived from rubber hand illusion studies, whereby one finger position is typically taken as a proxy for the hand felt position (Folegatti et al., 2009; Tsakiris & Haggard, 2005).

2.1.5. *Prism adaptation*

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

2.1.6. *Aftereffect–open loop pointing*

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

2.1.7. *Statistical analyses*

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

2.2. *Results*

2.2.1. *Aftereffect–open loop pointing*

To evaluate the total aftereffect (TS), a mixed ANOVA was performed with one between-subject factor Group (PA, SHAM) and one within-subject factor Condition (Pre PA, Post PA, Post DEA). The results showed a significant main effect of Group [$F_{(1,38)} = 76.75$, $p < .0001$, $\eta^2_p = .67$], Condition [$F_{(2,76)} = 241.32$, $p < .0001$, $\eta^2_p = .86$] and a significant interaction Group x Condition [$F_{(2,76)} = 206.19$, $p < .0001$, $\eta^2_p = .84$]. Post-hoc comparisons showed significant differences, only in the experimental PA group, between Pre and Post PA ($p < .0001$), between Post PA and Post DEA ($p < .0001$) and between Pre PA and Post DEA ($p < .005$). Results are depicted in Fig. 2A.

2.2.2. *Visual proprioceptive hand judgment task*

To assess differences in the proprioceptively felt position of the hand, a mixed ANOVA was performed with the same factors as above. Results showed significant effects for the main factor Condition [$F_{(2,76)} = 28.46$, $p < .0001$, $\eta^2_p = .42$] and the interaction Group x Condition [$F_{(2,76)} = 30.70$, $p < .0001$, $\eta^2_p = .45$]. As shown in Fig. 2B, Post-hoc comparisons showed significant differences, only in the experimental PA group, between Pre and Post PA ($p < .0001$), between Post PA and Post DEA ($p < .0001$) and between Pre PA and Post DEA ($p < .005$).

2.3. *Discussion*

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

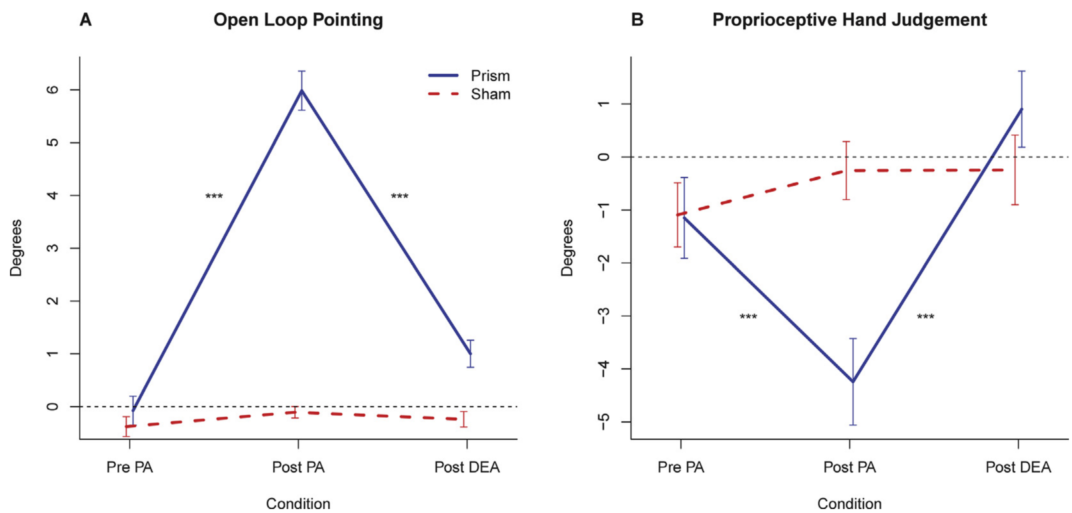

Fig. 2 — A) Total aftereffect (TS) measured by the open loop pointing (OLP) task. B) Proprioceptive shift of the felt position of the right index finger. All values are expressed in degrees. Positive values represent rightward bias and negative leftward. Bars represents ± 1 S.E.M. * = *p* < .05; ** = *p* < .005; * = *p* < .0005.**

experimental group showed typical processes of adaptation and de-adaptation, the control group did not show any significant shift in any of the conditions. Most interestingly, we observed that only in the experimental group the felt position of the hand was shifted −leftward- after PA (Fig. 2B). Similarly to the effects induced by de-adaptation on TS, the leftward hand proprioceptive shift was also reduced after de-adaptation, though not returning precisely to baseline values, but with some degree of rightward shift. Again, no significant differences were observed between conditions in the control group (see Fig. 2B). This effect was strong, significant and not observable in the control group, which only showed a little, not significant, rightward drift (.27°).

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

3. Experiment 2

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

3.1. *Methods*

3.1.1. *Subjects*

Based on the results obtained in Experiment 1, we performed a power analysis in order to check the smallest sample size to obtain a significant effect. Taking into account the planned experimental design, considering the 80% power for detecting an effect size of .45 (Exp1) with an alpha of .05, we estimated at least 10 participants were necessary. To obtain robust results across all the following experiments, several of them including newly developed tasks, we chose to set the sample size at 16 participants per group. Sixteen right-handed healthy subjects (assessed by Edinburgh questionnaire, 14 females, mean age 24.0 years SD = 4.5, Experimental group) and 16 right-handed healthy subjects (13 females, mean age 25.4 years SD = 3.2, Sham group; W = 173 *p* = n.s.), all naive to the prism adaptation procedure, participated in this experiment.

3.1.2. *Experimental setup*

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

3.1.3. *Procedure*

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

3.1.4. *Visual subjective straight ahead (VSSA)*

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

3.1.5. *Visual proprioceptive hand judgment (VPHJ)*

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

3.1.6. *Proprioceptive subjective straight ahead (PSSA)*

In order to best match the different sensorimotor measures, the evaluation of proprioceptive subjective straight ahead was performed in a slight different way than the classical pointing technique. The passive proprioceptive mid-sagittal judgment (Hatada, Miall, & Rossetti, 2006; Michel, Gaveau, Pozzo, & Papaxanthis, 2013) consisted in passively moving the participant's arm from right to the left and vice versa, using the ruler as a guide. Participants were blindfolded and put their right hand into a cloth wristband that was displaced by the experimenter from the right to the left till about shoulders. The experimenter first displaced the participants' hand from right to left with a continuous movement (approximately 2 cm/sec). Participants had to say "Now" when they felt their index finger perfectly aligned in front of their mid-sagittal plane. The movement ended only when the hand was in front of their left shoulder. Subsequently, the procedure was repeated from left to right, acquiring another judgment. Measurements on the two opposite directions were measured 3 times each, giving a total of 6 measures.

3.1.7. *Passive Proprioceptive Hand Judgment (PPHJ)*

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

3.2. Results

3.2.1. *Aftereffect–open loop pointing*

Results showed a significant effect of Condition [$F_{(2,60)} = 217.3$, $p < .0001$, $\eta^2_p = .88$], a significant effect of Group [$F_{(1,30)} = 60.1$, $p < .0001$, $\eta^2_p = .67$] and a significant interaction Condition x Group.

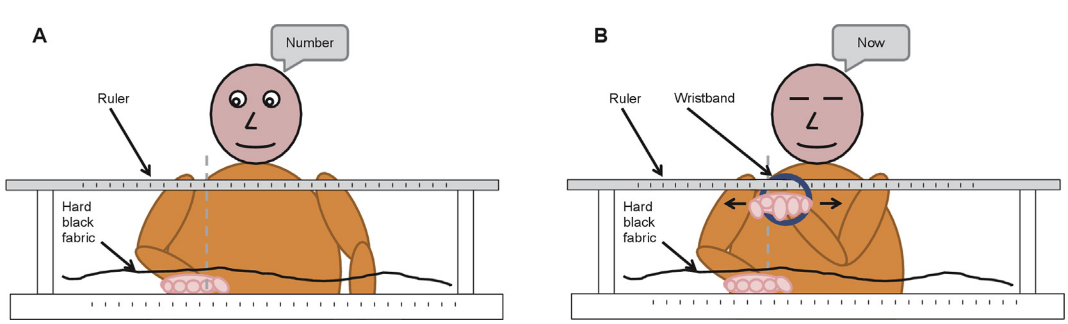

Fig. 3 – Cartoon showing the two tasks of hand position judgment. A) Visual Proprioceptive Hand Judgment, in which the participants reported the number on the seen ruler corresponding to the position where they felt their index finger was, by mentally projecting a vertical line from the finger to the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

$[F_{(2,60)} = 217.6$, $p < .0001$, $\eta^2_p = .88]$. Post-hoc comparisons showed significant differences, in the experimental PA group, between Pre and Post PA ($p < .0001$), between Post PA and Post DEA ($p < .0001$) and between Pre PA and Post DEA ($p < .05$). In the control group, there was only a significant difference between Pre PA and Post DEA ($p = .05$). Results are illustrated in Fig. 4C.

3.2.2. *Visual subjective straight ahead (VSSA)*

Results showed a significant main effect of Group $[F_{(1,30)} = 6.27$, $p < .05$, $\eta^2_p = .17]$. Condition was not significant ($p = .17$) and the interaction Condition x Group was not significant ($p = .75$). Results are visible in Fig. 4A.

3.2.3. *Proprioceptive subjective straight ahead (PSSA)*

The main effect of Condition had a significant effect $[F_{(2,60)} = 6.49$, $p < .005$, $\eta^2_p = .18]$, also Group had a significant effect $[F_{(1,30)} = 8.83$, $p = .01$, $\eta^2_p = .23]$ and there was a significant interaction Condition x Group $[F_{(2,60)} = 10.54$, $p < .0005$, $\eta^2_p = .26]$. Post-hoc comparisons showed significant differences, only for the experimental PA group, between Pre and Post PA ($p < .005$), as well as between Post PA and Post DEA ($p < .0001$). Results are displayed in Fig. 4D.

3.2.4. *Visual proprioceptive hand judgment (VPHJ)*

There was a significant effect of Condition $[F_{(2,60)} = 6.73$, $p < .005$, $\eta^2_p = .18]$, Group had a significant effect $[F_{(1,30)} = 4.12$, $p = .05$, $\eta^2_p = .18]$ and there was a significant interaction Condition x Group $[F_{(2,60)} = 15.1$, $p < .0001$, $\eta^2_p = .33]$. Post-hoc comparisons showed significant differences, only in the experimental PA group, between Pre and Post PA ($p < .0005$) and between Post PA and Post DEA ($p < .005$). Results are depicted in Fig. 4B.

3.2.5. *Passive Proprioceptive Hand Judgment (PPHJ)*

Results showed a significant effect of Condition $[F_{(2,60)} = 11.35$, $p < .0005$, $\eta^2_p = .28]$ and a significant interaction of Condition x Group $[F_{(2,60)} = 9.53$, $p < .001$, $\eta^2_p = .24]$. Post-hoc comparison revealed significant difference only in the PA group between Pre PA and Post PA ($p < .0005$) and between Post PA and Post DEA ($p < .005$). Results are depicted in Fig. 4E.

To compare the two modalities in which the HAE was assessed (VPHJ-PPHJ), a paired *t*-test was performed on the aftereffect of PJ (Post-minus Pre-). Results did not show significant difference between the two measures [VPHJ = −5.38 (3.93); PPHJ = −8.17 (6.55); $t_{(15)} = 1.8$, $p = .09$]. To ascertain if HAE is a different measure from PSSA, the size of PSSA and proprioceptive judgements of hand were compared. Two separate paired sample *t*-test showed significant differences between PSSA and VPHJ ($t_{(15)} = 7.09$, $p < .0001$, d = 1.77) and between PSSA and PPHJ ($t_{(15)} = 6.05$, $p < .0001$, d = 1.63). Pearson correlation between the previous measures did not show any significant relationship ($r < .16$, $p > .55$). In order to ascertain if the HAE is a different measure from TS, two correlations were performed between the TS and the HAE as assessed by VPHJ and PPHJ. In either case, the results were not significant ($r < .21$, $p > .4$).

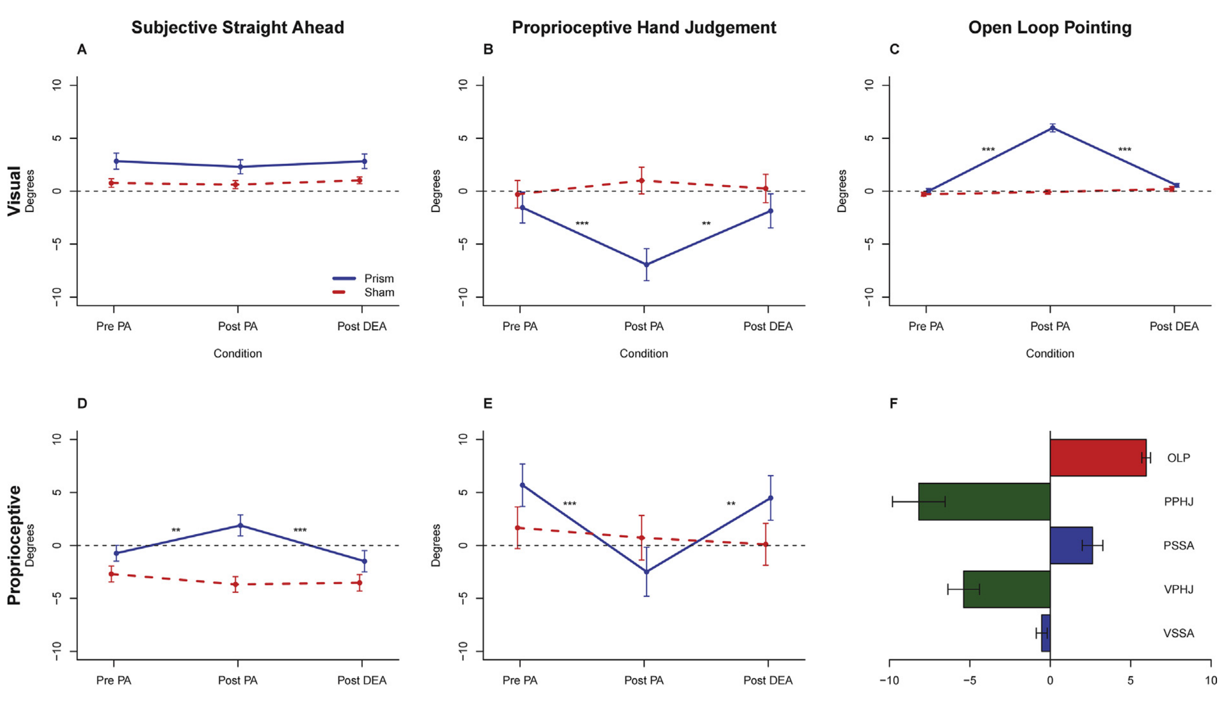

Fig. 4 — The graphs represent on the same scale in degrees, the shift found on the different measures of Experiment 2: A) Visual Subjective Straight Ahead; B) Visual Proprioceptive Hand Judgment; C) Open Loop Pointing; D) Passive Proprioceptive Subjective Straight Ahead; E) Passive Proprioceptive Hand Judgment. F) The graph represents the amount and the direction of the different aftereffects measured in Experiment 2. All values are expressed in degrees. Positive values represent rightward bias and negative leftward. Bars represents ± 1 S.E.M. * = $p < .05$; ** = $p < .005$; *** = $p < .0005$.

3.3. Discussion

To ensure that our proprioceptive judgment tasks does indeed measure a different aftereffect, specific for the hand, in Experiment 2 we compared the HAE with most classical sensorimotor measures of PA pertaining to other modalities and reference frames. First of all, we observed the expected adaptation and de-adaptation effects using the OLP task to measure the TS aftereffect. Second, although the VSSA was not affected by PA (as it was the case elsewhere using similar procedures, see Schintu et al., 2017), visual inspection of Fig. 4A indicates that the small and non-significant shift was in the leftward direction, as should be expected following leftward PA. Also in agreement with previous work, the proprioceptive subjective straight-ahead judgment, as measured with our passive technique, showed a typical PS in the direction opposite to the prism deviation (Michel et al., 2013; Redding et al., 2005). Most interestingly, the results of the VPHJ task confirmed the effects found at the level of the hand aftereffect in Experiment 1. In addition, using a purely proprioceptive and passive task (PPHJ), the presence of a significant and leftward shift of the hand position was also confirmed. Thus, despite using a different setup and different measures, the presence of the HAE is replicated and extended. Experiment 2, besides providing this replication, indeed makes sure that the HAE is not a different way of measuring the VS or TS, but it is specific for the hand. Moreover, having collected complementary sensorimotor measures of PA, based on different frames of reference, allows us to report two classes of directional aftereffects: the AE based on the head, which was toward the right (PS and TS; respectively D and C in Fig. 4) and the AE centred on the hand, which was toward the left (VPHJ and PPHJ; respectively B and E in Fig. 4).

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

4. Experiment 3

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

4.1. Methods

4.1.1. Subjects

Sixteen right-handed healthy subjects (assessed by Edinburgh questionnaire, 10 females, mean age 22.6 years SD = 4.5, Experimental group) and 16 right-handed healthy subjects (11 females, mean age 28.19 years SD = 5.0, Sham group; W = 220.5 p = .0005), all naïve to the PA procedures, were participated in this experiment.

4.1.2. Experimental setup

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

4.1.3. Procedure

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

4.2. Results

4.2.1. Aftereffect—open loop pointing RH & LH

Results for the right hand showed a significant effect of Condition [$F_{(2,60)} = 181.3$, $p < .0001$, $\eta^2_p = .85$], a significant effect of Group [$F_{(1,30)} = 27.8$, $p < .01$, $\eta^2_p = .48$] and a significant interaction Condition x Group [$F_{(2,60)} = 140.7$, $p < .0001$, $\eta^2_p = .82$]. Post-hoc comparisons showed significant differences, only in the Prism group, between Pre and Post PA ($p < .0001$), between Post PA and Post DEA ($p < .0001$). Results are depicted in Fig. 5C.

Results for the left hand showed a significant effect of Condition [$F_{(2,60)} = 4.33$, $p < .01$, $\eta^2_p = .13$] and a significant interaction Condition x Group [$F_{(2,60)} = 8.14$, $p < .001$, $\eta^2_p = .21$]. In the prism Group, post-hoc comparisons revealed significant differences between Pre PA and Post PA ($p < .0005$) and between Post PA and Post DEA ($p < .01$). Results are displayed in Fig. 5F.

Redding and Wallace (2009) previously noticed that the sequence of tasks execution (RH-LH *vs* LH-RH) can affect the TS aftereffect size. To evaluate this variable in the Prism group of this experiment, we ran a mixed ANOVA with the between-subject factor task Sequence (RH-LH, LH-RH) and the within-subjects factors Hand (left, right) and Condition (Pre-PA, Post-Pa, Post-DEA). Results showed significant main effects of Hand [$F_{(1,14)} = 7.54$, $p < .05$, $\eta^2_p = .35$] and Condition [$F_{(2,28)} = 156.25$, $p < .0001$, $\eta^2_p = .91$]. The significant interaction Condition x Sequence [$F_{(2,28)} = 3.68$, $p < .05$, $\eta^2_p = .21$] confirmed that the order of presentation could influence the amplitude of the aftereffect: namely, the RH-LH order was followed by a slightly larger amount of AE. The Interaction Hand x Condition [$F_{(2,28)} = 158.28$ $p < .0001$, $\eta^2_p = .92$] was also significant, indicating a smaller TS for the left hand Post-PA, the sign of inter manual transfer.

4.2.2. Visual proprioceptive judgment RH & LH

For the right hand there was a significant effect of Condition [$F_{(2,60)} = 6.55$ $p < .005$, $\eta^2_p = .18$] and a significant interaction

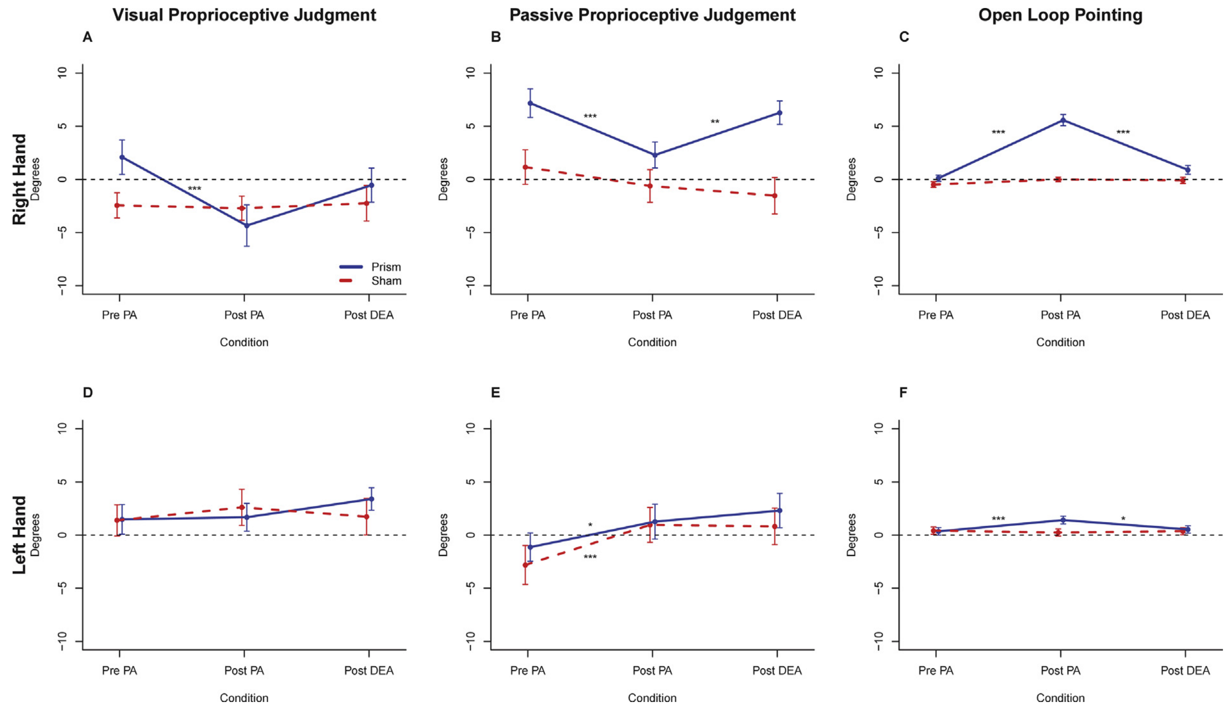

Fig. 5 – The graphs (from A to F) represent the shift found in VPHJ, PPHJ and OLP as assessed for the left or right hand in Experiment 3. Graphs are subdivided by hand (left and right) and task (VPHJ, PPHJ and OLP). All values are in the same scale in degree. Positive values represent rightward bias and negative leftward. Bars represent ± 1 S.E.M. * = $p < .05$; ** = $p < .005$; *** = $p < .0005$.

Group x Condition [$F_{(2,60)} = 5.41$ $p < .01$, $\eta^2_p = .15$]. Post-hoc comparisons showed significant differences between Pre PA and Post PA ($p < .0005$) again only in the prism Group. For the left hand, the results did not show any significant difference (all ps > .15). Results for each hand are displayed in Fig. 5A and D.

4.2.3. *Passive proprioceptive judgment RH & LH*

For the right hand, the results revealed a significant effect of Condition [$F_{(2,60)} = 11.16$, $p < .0001$, $\eta^2_p = .27$], a main effect of Group [$F_{(1,30)} = 8.89$, $p < .01$, $\eta^2_p = .23$] and a significant interaction Group x Condition [$F_{(2,60)} = 6.17$, $p < .005$, $\eta^2_p = .17$]. Post-hoc comparisons showed significant differences in the prism Group between Pre PA and Post PA ($p < .0005$) and between Post PA and Post DEA ($p < .001$).

For the left hand, the results showed a significant effect of Condition [$F_{(2,60)} = 12.28$, $p < .0001$, $\eta^2_p = .29$]. Post-hoc comparisons showed a significant difference between Pre PA and Post PA ($p < .005$) and Pre PA and Post DEA ($p < .0005$). Results for each hand are displayed in Fig. 5B and E.

4.3. Discussion

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

Overall, the results from the third experiment showed a certain amount of intermanual transfer of PA from the right (adapted) to the left (non-adapted) hand for the TS. However, the leftward HAE was significant only for the right adapted hand, as revealed by both the visual (VPHJ: 6.44° $p < .0005$) and the proprioceptive tasks (PPHJ: 4.88° $p < .0001$), but was absent for the non-adapted hand (Fig. 3), thus showing the HAE is specific for the adapted hand.

5. Experiment 4

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

5.1. Methods

5.1.1. Subjects

Sixteen right-handed healthy subjects (assessed by Edinburgh questionnaire, 13 females, mean age 25.3 years SD = 6.0, Experimental group) and 16 right-handed healthy subjects (11 females, mean age 24.4 years SD = 5.0, Sham group; W = 139 $p = .69$), all naïve to the PA procedures, participated in this experiment. A summary of participants is reported in Table 2.

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

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)

5.1.2. Procedure

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

5.1.3. Experimental setup

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

5.2. Results

5.2.1. Aftereffect–open loop pointing

Results showed a significant effect of Condition [$F_{(2,60)} = 161.9$, $p < .0001$, $\eta^2_p = .84$], a significant effect of Group [$F_{(1,30)} = 28.7$, $p < .0001$, $\eta^2_p = .49$] and a significant interaction Condition x Group [$F_{(2,60)} = 135.6$, $p < .0001$, $\eta^2_p = .82$]. Post-hoc comparisons showed significant differences, in the experimental PA group, between Pre and Post PA ($p < .0001$), between Post PA and Post DEA ($p < .0001$) and between Pre PA and Post DEA ($p < .05$).

To additionally assess whether there was any difference across experiments between the amount of adaptation, as measured through the OPL task across PA groups, we ran a repeated measure ANOVA with the between-subject factor Experiment (Exp. 1, 2, 3, 4) and the within-subject factor Condition (Pre PA, Post PA and Post DEA). There was a significant main effect of Condition [$F_{(2,128)} = 1032.44$, $p < .0001$, $\eta^2_p = .94$], but neither the main effect of Experiment [$F_{(3,64)} = .06$, $p = .97$] nor the interaction Condition x Experiment were significant [$F_{(6,128)} = 1.27$ $p = .28$]. Data are reported in Table 3.

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

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%

5.2.2. Visual proprioceptive hand judgment

To assess the difference between positions we ran a repeated measure ANOVA with the within-subject factor Position (LP, RP), the within-subject factor Condition (Pre-PA, Post-Pa, Post-DEA) and the between factor Group (Prism, Sham). Results showed a significant effect of Position [$F_{(1,30)} = 75.16$, $p < .0001$, $\eta^2_p = .72$], a significant effect of Condition [$F_{(2,60)} = 10.94$, $p < .0001$, $\eta^2_p = .27$], as well as a significant interaction of Condition x Group [$F_{(2,60)} = 5.24$, $p < .01$, $\eta^2_p = .015$], but no significant interaction between Position and Condition. In the Prism Group, concerning the RP, Post-hoc comparisons showed significant differences between Pre PA and Post PA ($p < .01$) and for LP, post-hoc comparisons showed significant differences between Pre PA and Post PA ($p < .01$) and between Post PA and Post DEA ($p < .005$; Fig. 6A).

A one-way ANOVA was performed to compare the amplitude of the HAE, as measured by the VPHJ task (Post-minus Pre-), in the three positions (Exp. 2 and 4). No significant difference emerged ($p = .69$; Fig. 6C).

5.2.3. Passive proprioceptive hand judgment

The same repeated measure ANOVA structure viewed for VPHJ reveal a significant effect of Position [$F_{(1,30)} = 137.47$, $p < .0001$, $\eta^2_p = .82$], a significant effect of Condition [$F_{(2,60)} = 6.20$, $p < .005$, $\eta^2_p = .17$], a significant interaction of Condition x Group [$F_{(2,60)} = 3.18$, $p < .05$, $\eta^2_p = .10$], but no significant interaction between Position and Condition. Only for LP Post-hoc comparisons showed significant differences between Pre PA and Post PA ($p < .05$; Fig. 6D).

Again, to compare this effect amplitude across the three different positions (Exp.2 and 4), we ran a one-way ANOVA on

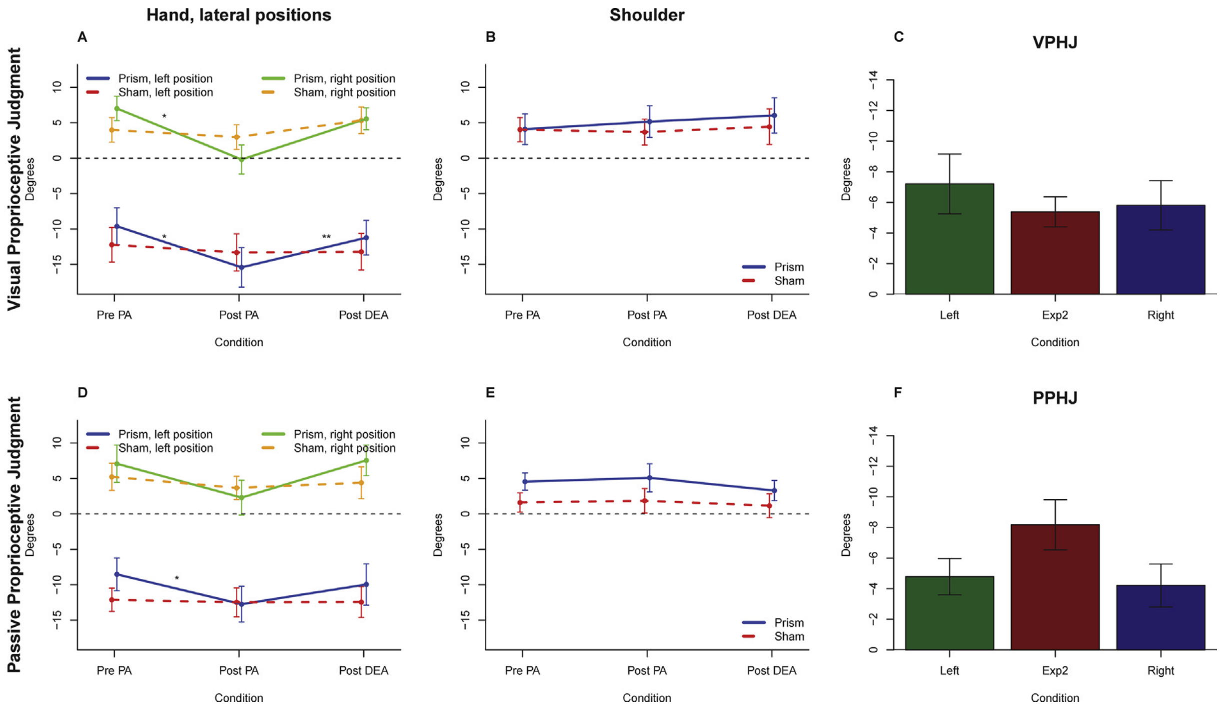

Fig. 6 – The graphs on the left column show the HAE measured by VPHJ and PPHJ for the hand located in the left and right position. The graphs in the central column show the same tasks of proprioceptive judgment for the shoulder. The graphs in the right column represent a comparison for each task between the HAE in the two lateral position in Experiment 4 and that observed in Experiment 2. Data are in degrees. Positive values represent rightward bias and negative leftward. Bars represent ± 1 S.E.M. * = $p < .05$; ** = $p < .005$; *** = $p < .0005$.

the amplitude effect (Post-minus Pre-). Results did not show significant differences between the amplitude of the HAE effect across positions ($p = .12$; Fig. 6F).

5.2.4. *Visual proprioceptive shoulder judgment*

Results did not show any significant effect (all ps > .26; see Fig. 6B).

5.2.5. *Passive proprioceptive shoulder judgment*

Results did not show significant effect (all ps > .16; see Fig. 6E).

5.3. *Discussion*

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

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

6. General discussion

6.1. *Hand after effect a new (but old) measure of PA*

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

The change in arm position judgment following PA has been initially considered more than 50 years ago (Harris, 1963), though in a different way. In that original study, the aftereffect was measured through the open loop pointing task, which has become a sort of standard, whereas the change in the felt position of the hand was used as an explanatory concept, to account for the misreaching of the target that was made visible by the AE. This explanatory concept was then utilized in many other studies that, however, did not measure the proprioceptive change they assumed to exist. Instead, they continued using the nowadays classical open loop pointing task (Craske & Gregg, 1966; A.; Efstathiou, Bauer, & Greene, 1967; Kornheiser, 1976). The first study in which the hand position shift was measured, through a proprioceptive judgment task, is the one by Craske (1966). Unfortunately, because of the procedure used, the absence of TS measure and the lack of specification about the direction of the optical deviation induced by the specific prisms used, it is not possible to gather a complete interpretation of both aftereffects. Nevertheless, he found an HAE of 34% of the optical deviation. We have to wait until recently, when the effect of PA on proprioception has been measured by Scarpina et al. (2015). They tested the adapted hand position sense before and after leftward and rightward PA, performed with the left and right hand (four groups). Their adaptation procedure was, however, relatively unusual, pointing movements under prisms exposure being executed with the index finger of one hand toward the other hand's fingers. They found that only the combination of leftward shifting prism using the left adapted hand determined a significant change in proprioception of the adapted hand. There is a major difference that could readily explain their lack of HAE for the right hand, repeatedly and consistently reported here. The adaptation was performed with one hand pointing to the other: visual or proprioceptive information used as target may actually bring to different sensitivity to PA (Bernier, Gauthier, & Blouin, 2007). Conversely, our findings clearly show the existence and specificity of the HAE as a distinct aftereffect. The comparison between aftereffects in experiment two underlines that this is not merely another way of measuring a previously documented (head- or eye-centred) aftereffect, but a new, previously unconsidered effect. Moreover, based on the findings of experiment two and four, we conclude this so far largely neglected HAE is both specific for the adapted hand and centred on this hand.

6.2. *HAE, the lost part of AE*

In Table 1, we have reported a summary of the studies on PA that took into account VS, PS and TS. The total shift, even if it is somewhat sensitive to specific setups and procedures used, amounts generally to about 40% of the optical shift induced by the prisms, and our findings indicate that about the same amount can be attributed to the HAE. Most importantly, since the proprioceptive shift of the hand is in the opposite direction of the TS, it could well represent the 'lost' part of the AE. Feedforward adjustments have been suggested to drive rapid compensation of the initial phase of the reach, resulting in the rapid reduction of endpoint errors typically observed early during prism exposure (O'Shea et al., 2017, 2014; Pochopien, Spang, Stemmler, & Fahle, 2017). Also depending on how cluttered/structured the visual working space appears to the subject, part of the optical deviation may or may not be 'visible' through the closed loop pointing error, even in the very first pointing trials. In a seminal paper, for example, the direct effect-error was maintained at 100% of the prisms deviation in the early pointing, thus testifying that the optical deviation has to be taken into account fully for the adaptation to develop later on (Rossetti, Koga, & Mano, 1993). Indeed, during the very first pointing movements in the adaptation phase (while wearing prisms) subjects may misreach the target leftward by close to 100% of the optical deviation, then they quickly correct this error (O'Shea et al., 2017, 2014; Pochopien et al., 2017; Rossetti et al., 1993). As recalled above taking the example of a standard leftward adaptation in healthy subjects (with base right prisms), when participants remove the prisms and point in an open loop condition after adaptation, they misreach the alignment to the target rightward by about 40% of the prism optical deviation. Yet, according to the known components of the AE, they should misreach by the equivalent amount of the optical deviation. In the light of the present findings, we postulate that this is the consequence of the existence of another AE component, the hand after effect. The adapted hand is felt as if it were shifted about 40% leftward with respect to its real position. Therefore, this amount of deviation should be added to the rightward shift that is measured in PA studies through the open loop pointing and is normally called aftereffect (AE).

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

One issue that deserves discussion is whether the specific change in hand position sense might reflect another AE measure, namely the proprioceptive subjective straight-ahead, or PSSA. Most typically, this AE is measured by asking participants to point with the adapted right hand moving in front of them to indicate their subjective middle (or straight ahead) starting from the sternum, or from a mid-sagittal starting point. If we now consider the observed HAE, the trajectory of the hand while pointing straight ahead would start from a position which is felt significantly leftward with respect to actual mid-sagittal plane. The landing position reached by the hand while pointing straight ahead could thus be shifted to the right (Holmes, Snijders, & Spence, 2006). In this respect, the HAE could contribute to the PSSA. However, our results do not support this possibility, because the PSSA was smaller than the HAE and unrelated. To provide the most comparable measure, here we measured the PSSA via a passive movement, as we did in the PPHJ task used to measure the HAE, whereby the only difference was the reference point to

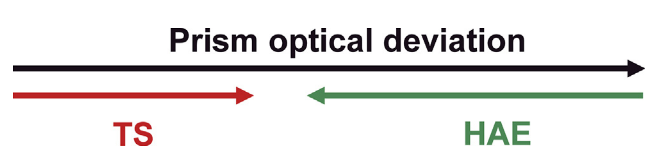

Fig. 7 – Graphical representation of the size of the optical prism deviation and the corresponding direction and size of TS and HAE.

be felt and reported: the subjective straight ahead for PSSA, the hand position for the PPHJ. Even within these closely matched task modalities, the two measures turned out to be quite different and unrelated, thus suggesting the underling processes are at least partially different. A similar consideration could be made between OLP and VPHJ, in which a visual reference should be reported. Again, the two measures (HAE and TS) are unrelated, suggesting their underling processes are, at least in part, different.

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

6.3. *HAE and spatial neglect rehabilitation*

This study discloses that in the prismatic adaptation process, beside the long known visual and a proprioceptive AE originating the supposedly ‘total’ shift, there is a new—though long suspected- AE component that is hand centred. These findings imply that the PA model is actually more complex than previously thought: the old concept of a change in hand proprioception following PA (Harris, 1963; Kornheiser, 1976) needs to be reconsidered and included in PA models. This is particularly important because, besides its sensorimotor effects, PA produces also visuospatial perceptual changes in physiological conditions in healthy subjects (Schintu et al., 2017) ad most relevant, in pathological conditions in brain-damaged patients. Whether applied alone (Azouvi, Jacquin-Courtois, & Luauté, 2017; Pisella, Rode, Farne, Tilikete, & Rossetti, 2006; Rode et al., 2015), or in combination with brain neuromodulation or drugs (Calzolari, Bolognini, Casati, Marzoli, & Vallar, 2015; Làdavas et al., 2015; Luauté et al., 2018; O'Shea et al., 2017), PA is indeed one of the most promising rehabilitation techniques to improve several perceptual ad motor aspects of brain-damaged patients suffering from Unilateral Spatial Neglect (Champod, Frank, Taylor, & Eskes, 2018; Facchin, Beschin, Toraldo, Cisari, & Daini, 2013; Frassinetti, Angeli, Meneghello, Avanzi, & Làdavas, 2002; Mizuno et al., 2011; Rode, Fourtassi, Pagliari, Pisella, & Rossetti, 2017; Rossetti et al., 1998; Serino et al., 2007).

While the efficacy of prism adaptation in the rehabilitation of USN has been interpreted in the light of several models (Bultitude et al., 2017; Clarke & Crottaz-Herbette, 2016; Martín-Arévalo et al., 2016; Martín-Arévalo, Schintu, Farnè, Pisella, & Reilly, 2018; Pisella et al., 2006; Redding & Wallace, 2006, 2010; Rossetti et al., 1998; Saevarsson & Kristjánsson, 2013; Schintu et al., 2016; Striemer & Danckert, 2010) among which the recalibration – realignment model (Redding & Wallace, 2006, 2010), these findings suggest that another feature of PA contributing to its efficacy may rely on the changes in proprioception of the adapted hand. Following rightward PA (base left prisms are typically used in USN), the adapted (right) hand would be felt rightward than its real position. Thus, movements planned towards the left (such as in exploratory tasks) might result in a larger leftward displacements, possibly contributing to neglect amelioration in visuo-motor explorative tasks. Previous studies on PA in neglect patients reported normal TS (Facchin, Bultitude, et al., 2019; Rode et al., 2015; Sarri et al., 2008), but a contamination of the VS and PS measure from neglect itself (Bartolomeo & Chokron, 1999; Facchin et al., 2013; Facchin, Bultitude, et al., 2019; Facchin, Sartori, Luisetti, De Galeazzi, & Beschin, 2019; Farnè, Ponti, & Ladavas, 1998; Pisella, Rode, Farne, Boisson, & Rossetti, 2002; Rode et al., 2015; Saj, Honoré, Richard, Bernati, & Rousseaux, 2010; Sarri et al., 2008). Assessing the HAE in neglect patients, in addition to VS, PS and TS, could provide valuable information possibly contributing to elucidate differences in efficacy, or responder vs non-responder patients' profile. In this respect, we suggest this novel aspect of PA should be considered in future studies of PA in neglect patients to better inform models of PA that might allow for optimising patient-tailored PA procedures.

Conflicts of interest

The authors declare no conflict of interest.

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