



HAL
open science

Saccades to both vision and touch are modified following adaptation but cross-modal transfers are asymmetrical.

Ali Batikh, Valérie Gaveau, Muriel Panouillères, Éric Koun, Romeo Salemme, Alessandro Farnè, Denis Péliesson

► **To cite this version:**

Ali Batikh, Valérie Gaveau, Muriel Panouillères, Éric Koun, Romeo Salemme, et al.. Saccades to both vision and touch are modified following adaptation but cross-modal transfers are asymmetrical.. Journal of Neurophysiology, In press. hal-04689294

HAL Id: hal-04689294

<https://hal.science/hal-04689294v1>

Submitted on 5 Sep 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Public Domain

1 RESEARCH ARTICLE

2 RUNNING HEAD: Cross-modal transfer of saccadic adaptation.

3 Saccades to both vision and touch are modified following
4 adaptation but cross-modal transfers are asymmetrical.

5 Ali Batikh¹ <https://orcid.org/0000-0002-0306-8903> , Valérie Gaveau¹
6 <https://orcid.org/0000-0002-2255-5766> , Muriel T.N. Panouillères¹ <https://orcid.org/0000-0003-0264-2093> ,
7 Éric Koun¹ <https://orcid.org/0000-0003-3624-3701> , Roméo Salemme¹
8 <https://orcid.org/0000-0003-1075-540X> , Alessandro Farnè^{1§} <https://orcid.org/0000-0001-5769-3491> ,
9 Denis Péliçon^{1§} <https://orcid.org/0000-0002-9114-7758>

10

11 ¹IMPACT Team of Lyon Neuroscience Research Center INSERM U1028 CNRS UMR5292 University Claude
12 Bernard Lyon 1, France.

13 [§] These authors contributed equally to this work.

14

15 Correspondence: *Ali Batikh* (ali.batikh.97@gmail.com).

16

17 **ABSTRACT**

18 Adaptation of reactive saccades (RS), made toward the sudden appearance of stimuli in our
19 environment, is a plastic mechanism thought to occur at the motor level of saccade generation. As
20 saccadic oculomotor commands integrate multisensory information in the parietal cortex and superior
21 colliculus, adaptation of RS should occur not only towards visual but also tactile targets. In addition,
22 saccadic adaptation in one modality (vision or touch) should transfer cross-modally. To test these
23 predictions, we used the double-step target paradigm to adapt rightward saccades made at two
24 different eccentricities toward the participants' index and middle fingers, identified either visually
25 (Experiment1) or tactually (Experiment2). In each experiment, the rate of adaptation induced for the
26 adapted modality and the rate of adaptation transfer to the non-adapted modality were compared to
27 that measured in a control (no adaptation) session. Results revealed that touch-triggered RS can be
28 adapted as well as visually triggered ones. Moreover, the transfer pattern was asymmetric: visual
29 saccadic adaptation transferred fully to tactile saccades, whereas tactile saccadic adaptation, despite full
30 generalization to non-adapted fingers, transferred only partially to visual saccades. These findings
31 disclose that in the case of tactile saccades, adaptation can be elicited in the absence of post-saccadic
32 visual feedback. In addition, the asymmetric adaptation transfer across sensory modalities suggests that
33 the adaptation locus for tactile saccades may occur in part upstream of the final motor pathway
34 common to all saccades. These findings bring new insights both on the functional loci(us) and on the
35 error signals of RS adaptation.

36 **NEW & NOTEWORTHY**

37 The present study revealed that, as predicted from a large literature, adaptation of visual reactive
38 saccades transfers to tactile saccades of the same as well as neighboring amplitudes. Furthermore, in a

39 modified double-step target paradigm, tactile saccades exposed to repeated errors adapt with similar
40 rate and spatial generalization as visual saccades, but this adaptation only slightly transfers to visual
41 saccades. These findings bring new information on saccadic adaptation processes.

42 **Keywords:** Saccadic adaptation; Touch; Vision; Cross-modal transfer.

43

44 INTRODUCTION

45 We perform over 100,000 saccades per day to bring the image of objects of interest onto the fovea, the
46 highest acuity part of our retina. Saccadic eye movements triggered by the sudden appearance of an
47 object are classified as reactive (or reflexive) (RS), whereas those produced based on our internal goals
48 are defined as voluntary saccades (VS). The latter relies on the activation of a wider neural network in
49 comparison with the former (1).

50 Not only visual but also auditory (i.e., the sound of car brakes nearby) as well as somatosensory
51 stimuli (i.e., a bee landing on our hand), can trigger saccadic eye movements. Compared to visual
52 saccades, auditory saccades are less accurate, their latency decreases with increasing amplitude and
53 they display a lower peak velocity (2). Similarly to auditory saccades, tactile (or somatosensory) saccades
54 are less precise, less accurate, and display longer latency and lower velocity peak than visual saccades of
55 the same amplitude (3–5). Consequently, due to their lower speed and longer duration, saccades toward
56 a non-visual target show a curved trajectory more often than visual saccades, reminiscent of feedback-
57 or feedforward-based on-line correction (6).

58 Importantly, the categorization into reactive or voluntary also applies to tactile saccades. Amlôt
59 and Walker (7) studied the latency of pro-saccades (RS directed toward a target) and anti-saccades (VS
60 to the opposite direction of a target) in response to visual or tactile targets and found that, in both
61 modalities, the latency of pro-saccades is shorter than the latency of anti-saccades. Also, an equivalent
62 of the visual grasp reflex (the failure of the oculomotor system to inhibit an erroneous pro-saccade
63 toward the visual target in anti-saccades trials) was observed for tactile anti-saccades, with a very similar
64 erroneous pro-saccades rate in the tactile (11.04%) and visual modality (13.13%). Whether voluntary or
65 reflexive, the increased latency of somatosensory saccades relative to visual saccades can be attributed
66 in large part to the additional processing step of coordinate transformation, as evidenced by Neggers
67 and Bekkering (8). In their study of goal-directed eye and hand movements toward visual and tactile
68 targets delivered on the participants' knee, these authors found that across subjects correlations
69 between saccadic and hand reaction time (RT) were higher for somatosensory than visual targets. They
70 argued that the information elicited by tactile stimulation of the knee, initially encoded in a leg-
71 reference frame, had to be translated into an adequate reference frame for both the eye and arm motor
72 responses, leading to correlated RT. In contrast, the information elicited by the visual target, initially
73 encoded in an adequate reference frame for the saccadic system, thus needs to be translated into
74 another reference frame only for the arm movement, yielding a weaker correlation between eye and
75 hand RTs.

76 The additional cost of coordinate transformation on somatosensory saccades is further
77 evidenced by the so-called crossed versus uncrossed hand paradigm (9). The reaction time of saccades
78 toward a tactile target on the hand is longer when hands are crossed over the midsagittal plane than in
79 the uncrossed hands condition. This cost is thought to be related to a conflict between the somatotopic
80 (anatomical) representation of the stimulated hand locus and its external (spatial) representation. In

81 addition, in the crossed condition some tactile saccades follow a curved trajectory: these ‘turnaround’
82 saccades start in the direction dictated by the anatomical coding of the target and then are corrected in
83 flight toward the actual, spatial location of the target. This phenomenon can be used to timestamp the
84 underlying coordinate transformation between the anatomical and spatial representations of tactile
85 targets. Indeed, firstly, the latency of the turnaround point relative to the tactile stimulation (332 ± 30
86 ms) was similar to the reaction time of straight saccades in the crossed hands posture (319 ± 25 ms); and
87 secondly, the reaction time of turnaround saccades was similar to that of (straight) saccades executed
88 when the arms are uncrossed (6).

89 The superior colliculus (SC) plays an important role in the convergence of somatosensory and
90 visual signals. Groh and Sparks (10) found that among 86 neurons exhibiting saccade-related activity in
91 the monkey SC, all but one additionally responded both to tactile and visual input. Interestingly, just like
92 visuo-saccadic neurons, these multisensory saccadic neurons have a saccadic movement field, meaning
93 their motor discharge is tuned to the amplitude and direction of the impending saccade and not to its
94 endpoint relative to the body. Therefore, at the SC level, the somatosensory signals have already been
95 transformed into saccadic signals encoded in an eye-centered coordinate reference frame. To test
96 whether this transformation takes place within the SC, the researchers also recorded the target-related
97 activity of 34 SC somatosensory neurons while monkeys performed saccades toward visual or tactile
98 stimulations delivered to their hands. They found that the discharge of 74% of those cells varies with
99 initial eye position and is therefore not solely encoded in a somatotopic reference frame, suggesting
100 that somatosensory signals reaching the SC have already been remapped, at least in part, in upstream
101 structures (11).

102 One critical feature of the oculomotor system is its plasticity. Saccades are the fastest
103 movements that we can produce. Due to their high speed, and besides the exceptions already
104 mentioned above, saccades usually cannot be modified in flight, but nonetheless, their precision is
105 maintained throughout life. Sensorimotor adaptation mechanisms correct for saccade errors caused by
106 fatigue, aging, or neurological diseases. Errors eliciting such so-called saccadic adaptation occur when
107 the saccade landing position repeatedly overshoots (hyper-metria) or undershoots the target position
108 (hypo-metria), leading respectively to an adaptive decrease or increase of saccade amplitude. In the
109 laboratory, saccadic adaptation is most often elicited by the double-step target paradigm introduced by
110 McLaughlin (12). This method consists of stepping a visual target (1st step) to elicit the saccadic response
111 and, when the eyes are in-flight, stepping it again either backward or forward relative to the on-going
112 saccade (2nd step) to elicit a post-saccadic error. Although the intrasaccadic step is usually not
113 consciously perceived by subjects, the resulting post-saccadic error elicits, shortly after the primary
114 saccade, a corrective saccade bringing the eye back to the stepped target. When repeated across
115 identical double-step trials, the post-saccadic error is interpreted by the brain as a saccade programming
116 error and leads adaptation mechanisms to reduce (for backward steps) or increase (for forward steps)
117 the primary saccade amplitude, reaching a steady state level after some 10th to 100th of trials in humans
118 (for review see, (13–15)).

119 Saccadic adaptation has been initially thought to result from motoric changes unfolding at the
120 level of the cerebellum and brainstem (for review see (14, 15)). However, further studies disclosed that
121 this mechanism additionally affects visual perception and relies also on higher cerebral areas. Studies
122 combining fMRI with the double-step target paradigm have identified several cerebral or/and cerebellar
123 areas whose activation can be related to the different subprocesses of saccadic adaptation: the

124 detection and the processing of the motor error, the learning process itself, the modifications in
125 corrective saccades metrics (16–20).

126 Behavioral studies have also mitigated the pure motoric hypothesis of adaptation, but mainly
127 for VS. First, studies comparing the effect of RS adaptation onto non-adapted VS (RS-to-VS transfer) to
128 the effect of VS adaptation onto non-adapted RS (VS-to-RS transfer) found an asymmetric pattern of
129 transfer of adaptation with a stronger transfer from VS to RS than the other way around, suggesting the
130 existence of partially segregated adaptation sites for these two types of saccades (21, 22). Second, RS
131 and VS also show different patterns of adaptation transfer to hand-pointing movements and anti-
132 saccades. Indeed, adaptation of VS, but not of RS, transfers to hand pointing movements performed
133 under gaze fixation condition (23), suggesting that only the former type of adaptation involves a sensory
134 level. In addition, the adaptation of RS along a single horizontal direction transfers toward anti-saccades
135 performed in the same (adapted) direction but not to those directed away (un-adapted direction)
136 whereas in the case of VS, unidirectional adaptation transfers to both adapted and un-adapted
137 directions. As in anti-saccades tasks the sensory and the motor vectors are dissociated, these results
138 suggest that RS adaptation takes place at a motor level, whereas VS adaptation recruits both motor and
139 sensory loci (24). Altogether, these studies strongly suggest that backward adaptation of RS acts at an
140 oculomotor level. In contrast, as forward adaptation (of both VS and RS) has been much less
141 investigated, its corresponding neural substrates are still debated. Forward adaptation is generally
142 harder to induce than backward adaptation and the underlying mechanisms were suggested to differ
143 between these two types of adaptation (25, 26). For these reasons, we focused the present study on RS
144 backward adaptation mechanisms.

145 This hypothesis that RS backward adaptation takes place at a motor level implies that backward
146 adaptation of visually triggered RS should transfer toward RS triggered by stimuli in other sensory
147 modalities. In agreement with this prediction, Frens and van Opstal (27) showed that adaptation of
148 visually guided RS transferred to ‘auditory saccades’ of the same vector (see also (28)). However, no
149 empirical evidence from tactile saccades is available to support the notion of a motor locus of
150 adaptation for RS. Indeed, neither the possibility to induce adaptation of touch-triggered saccades, nor
151 the cross-modal transfer of adaptation to and from tactile saccades, have ever been investigated so far.

152 Thus, the present study seeks to further characterize the mechanisms involved in RS adaptation
153 by addressing these two questions. To this twofold aim, we performed two experiments where
154 backward saccadic adaptation was induced by the double-step target paradigm. In Experiment 1, we
155 adapted RS toward visual targets (LEDs placed on the fingers of the participants’ right hand) and tested
156 the effect of such adaptation on RS toward both visual and tactile targets (electrocutaneous stimulations
157 of the participant’s fingers). In Experiment 2, we exposed participants to adaptation of RS toward tactile
158 stimuli thanks to a tactile double-step paradigm and tested the effect of such potential adaptation again
159 on RS toward both visual and tactile targets. We predicted in both experiments, first a significant
160 decrease of adapted RS amplitude due to the adaptation exposure and second, a significant
161 generalization of this adaptation to non-adapted RS toward nearby targets as well as a significant
162 transfer to RS in the non-adapted modality.

163 EXPERIMENT 1: TRANSFER OF VISUAL SACCADES ADAPTATION TO 164 TACTILE SACCADES.

165 MATERIALS AND METHODS

166 1. Participants

167 Sample size was calculated via the open access software G*Power 3.1.9.7 (effect size = 0.4, alfa = 0.05,
168 Power = 0.8 and correlation among repeated measures = 0.6). There was no previous study investigating
169 the transfer of adaptation from visual to tactile saccades, therefore we relied on the high visual to
170 auditory transfer of adaptation reported in the literature (28) to select an effect size = 0.4. Twenty-one
171 naïve volunteers (all right-handed, 8 males and 13 females, mean age 27.5 ± 4.2 ranging between 22 and
172 37 years old) participated in the first experiment. Fifteen participants were involved in a session where
173 adaptation was elicited (ADAPT session), and fifteen participants were involved in another session
174 where control saccades were performed (CTRL session) (nine of them had participated in the ADAPT
175 session).

176 Participants' vision was normal or corrected-to-normal. Exclusion criteria were simultaneous
177 participation in other experiments involving sensorimotor adaptation, a history of neurological or
178 psychiatric disorders, cognitive disorders preventing the comprehension of the instructions,
179 consumption of psychotropic drugs or alcohol, and severe sleep deprivation during the last 24 hours.
180 Participants were asked not to wear makeup or to remove it before the experiment (to prevent any
181 problem with the eye tracker).

182 Both experiments of this study were done in two separate phases. The initial sample sizes for
183 Experiment 1 and 2 were 10 and 16 respectively. Around eight months later and following the reviewers
184 suggestions on the first submitted version of the manuscript, sample sizes were increased to 15
185 participants in the first experiment and 30 participants in the second one.

186 2. Ethical Statement

187 Both Experiment 1 and Experiment 2 of the present study conformed with the Code of Ethics of the
188 World Medical Association (Declaration of Helsinki 1964) and were approved by the ethics committee of
189 INSERM U1028 (IRB00003888; decision n° 21-762 dated 19/01/2021). An informed consent was received
190 from every participant prior to each experiment.

191 3. Experimental setup

192 Participants were sitting in total darkness with their head stabilized using a chinrest. They faced a
193 vertical panel situated 30 cm from their eyes which maintained their right hand in a vertical position by
194 a strap surrounding their wrist and rings surrounding the second phalanx of their fingers. In this position,
195 the pinky, ring, middle, index, and thumb fingers were respectively at 5, 10, 15, 20, and 25 degrees of
196 visual angle in the horizontal axis relative to the participant's midline (see Figure 1A). Six red light-
197 emitting diodes (LED, diameter 2 mm) were positioned on the panel: one LED used as a fixation point
198 (FP) was located at the participant's gaze level and 5 degrees to the left of the participant's midline; the
199 five other LEDs were embedded in the rings maintaining the fingers. LEDs located on the index, middle,
200 and ring fingers were horizontally aligned with the FP, the pinky and thumb LEDs were located below
201 this line. The LEDs were attached on the front face of 5 wooden rings fixed on a vertical wooden board,
202 allowing to maintain each finger aligned with its corresponding LED. In addition, rings and board were
203 painted black and, before inserting their fingers in the rings, participants wore a black fabric glove.

204 Finally, the LEDs' intensity was kept low enough to prevent any lightning of the black gloves or rings.
205 Therefore, the participants could never see the location of their fingers or hand during the experiment.
206 For tactile stimulation, two electro-dermal electrodes with opposite polarities (Neuroline 7000, Ambu,
207 Denmark) were placed on each finger underneath each LED, at the level of the distal (anode) and middle
208 (cathode) phalanxes. The supra-threshold (100% detection accuracy) electrocutaneous stimulus felt like
209 tingling, resulting from a squared wave pulse delivered by constant-current stimulators (Iso-Flex,
210 A.M.P.I., Israel). A horizontal ruler was positioned on the top of the vertical panel (50 mm above the
211 middle finger position), allowing to measure, at the beginning and end of each session, the participants'
212 perceptual estimate of the middle finger position of their unseen hand (see below:
213 section4/Procedures). Eye movements were recorded with an infrared eye tracker (EyeLink 1000, SR
214 Research, Canada) at a frequency of 1000 Hz with an accuracy of 0.1°. Eye velocity was calculated online
215 using a two-point central difference algorithm (29) and the time of saccade onset, used to trigger intra-
216 saccadic target step or target extinction during rightward saccades, was based on a velocity threshold of
217 30°/s.

218 Each experimental session started with a calibration of the eye tracker, with participants being
219 asked to fixate a central LED as well as four other LEDs placed on the panel (up, down, to the right, and
220 the left of the central LED). A drift correction was performed after each experimental block and,
221 whenever the eye drifted more than two degrees from the central LED, a calibration of the eye tracker
222 was repeated.

223 4. Procedures

224 As experiments were conducted in a completely dark room, we took into consideration the fact
225 that our conscious perception of hand position drifts toward our body midline (so-called proprioceptive
226 drift) (30). We thus measured this drift before and after ADAPT and CTRL sessions, by asking participants
227 to indicate which number on the visible ruler best matched the position of their occluded middle finger
228 (measured 9 times, randomly sliding the ruler each time to avoid response strategies (31)).

229 ADAPT and CTRL sessions each involved five steps: a PRE proprioceptive location assessment, a
230 saccade PRE-exposure phase, a saccade Exposure phase, a saccade POST-exposure phase, and a POST
231 proprioceptive location assessment. We detail the time course of the saccade trials below (see Figure
232 1B).

233 During PRE-exposure the baseline performance of visual saccades and tactile saccades was
234 evaluated: participants performed one block of 75 rightward saccades directed toward visual targets
235 (visual block) and one block of 75 rightward saccades directed toward tactile targets (tactile block). All
236 trials were initiated with the participants staring at the FP for a random duration (2000 to 3000 ms).
237 Then, the FP was turned off and one of the five (visual or tactile) peripheral stimuli was presented
238 randomly. Participants were instructed to saccade toward the location of the target as rapidly and as
239 precisely as possible. During the saccadic response, the (visual or tactile) stimuli were terminated, but
240 participants nonetheless had to maintain fixation on the now-absent target until the reappearance of
241 the FP. At the end of the trial, the Fixation LED was turned on again, indicating the participant to get
242 prepared for the next trial. Participants were asked to blink on their way back to the fixation point to
243 reduce the amount of blinking that can occur during the saccades.

244 In the Exposure phase, participants performed 120 visual saccades randomly directed toward
245 the index or the middle finger. As in PRE-exposure, each trial started with a fixation period which ended
246 with the simultaneous appearance of the visual stimulus and the disappearance of the FP. In the ADAPT
247 session, saccade onset detection triggered a 5 deg leftward intra-saccadic displacement of the target

248 (from the index to the middle finger or from the middle to the ring finger), this backward shift being
249 aimed at inducing an adaptive shortening of saccade amplitude (12). During the CTRL session, aimed at
250 measuring any potential change of saccade metrics unrelated to adaptation mechanisms, the target
251 remained at its initial location (index or middle finger) for the duration of the trial.

252 The POST-exposure was identical to the PRE-exposure phase. Comparisons of saccade gain
253 between these 2 phases allowed evaluating the after-effect of visual saccades adaptation and the
254 transfer of adaptation to tactile saccades.

255 The order of the two saccade blocks (visual and tactile) performed in each PRE- and POST-
256 exposure phase was counterbalanced between participants: half of them performed the visual block
257 followed by the tactile block in the PRE-exposure, then the tactile followed by the visual block in the
258 POST-exposure (Vis-Tact/Tact-Vis) and the other half vice versa (Tact-Vis/Vis-Tact).

259 The nine participants who performed both experimental sessions (ADAPT and CTRL) were tested
260 with at least one week washout delay in-between to avoid any cross-over effects related to the
261 retention of adaptation (32).

262 5. Analysis

263 Horizontal and vertical eye positions were analyzed offline using software developed in MATLAB by our
264 team. Saccades onset and offset were identified based on a velocity threshold of $15^\circ/\text{s}$. Saccade
265 amplitude was measured as the difference between eye positions 50 ms before the saccade onset and
266 50 ms after the saccade offset. The following dependent variables were then extracted for each saccade:
267 1) gain: ratio between the saccade amplitude and the target initial eccentricity (difference between the
268 target position and saccade starting position), this parameter was used to investigate the effect of the
269 double-step adaptation exposure on saccade size as it presents the advantage, over saccade amplitude,
270 of being expressed relative to the target distance, thus allowing to measure the mean accuracy of
271 saccades toward targets of different eccentricities pooled together (see (14), (13)); 2) latency: time
272 between the appearance of the initial target (T1) and the saccade onset; 3) duration: time between
273 saccade onset and saccade offset; 4) peak velocity: maximum eye velocity reached during the saccade.
274 Trials where saccades were made toward the pinky were discarded from further analyses; indeed, this
275 closest target from fixation (10°) was the most difficult for our participants to localize through tactile
276 saccades, resulting in the highest saccade amplitude variability among all fingers; in addition, restricting
277 our analyses to the ring and thumb allowed us to perform our generalization tests to the two
278 symmetrical locations around the index and middle fingers used for adaptation. Trials where the
279 saccadic gain fell outside the range defined by the mean gain $\pm 2 \times$ standard deviations (calculated and
280 applied for each participant across each session, phase, modality and target location separately), trials
281 where the saccade latency was lower than 80 ms or higher than 700 ms, and trials where a blink
282 occurred during the primary saccade were excluded from the analysis (exclusion of 9.57% of the trials in
283 total).

284 Two additional parameters were then calculated. First, in the exposure phase, the slope of the
285 linear relationship between saccadic gain and trial number was calculated for visual saccades toward the
286 middle and the index fingers, separately. Second, we calculated, for each finger and separately in the
287 adapted and the non-adapted modality, the following ratio of saccadic gain change between the pre-
288 and post-exposure phases: Gain change ratio = $(\text{Gain PRE} - \text{Gain POST}) / \text{Gain PRE}$. Therefore a positive
289 gain change ratio indicates a decrease in saccadic gain in the POST-exposure phases compared to the
290 PRE-exposure (compatible with backward adaptation) while a negative gain change ratio indicates an

291 increase in saccadic gain (for example, a gain change ratio of +0.3 corresponds to a 30% decrease of gain
292 in post-exposure relative to pre-exposure).

293 6. Statistical analyses

294 Statistical analyses were done using IBM SPSS statistics 29.0.0.0. First, to check if the double-step
295 exposure successfully elicited adaptation of visual RS, the slope of the linear relationship between
296 saccadic gain and trial number was submitted to a repeated measures ANOVA with the factor 'Target
297 position' (middle finger vs index finger) as within-subjects factor and the factor 'Session' (ADAPT vs
298 CTRL) as between-subjects factor. In addition, the gain change ratio of RS in the visual (adapted)
299 modality, used as a measure of adaptation after-effect, was also submitted to the same repeated
300 measures ANOVA Target position (middle and index fingers) x Session (ADAPT vs CTRL). Second, to
301 investigate whether adaptation of visual RS generalized to targets near the adapted locations, the gain
302 change ratio of visual saccades toward non-adapted fingers was submitted to a repeated measures
303 ANOVA with 'Target position' (ring and thumb fingers) as within-subjects factor and 'Session' (ADAPT vs
304 CTRL) as between-subjects factor. A similar ANOVA was performed on the gain change ratio of tactile
305 saccades toward all 4 fingers to investigate the transfer of adaptation to the other modality, except this
306 time the within-subjects factor 'Target position' had 4 levels (ring, middle, index and thumb fingers). We
307 included in this analysis of transfer only participants who showed a significant level of adaptation (14
308 subjects out of 15), i.e. showing a significant decrease of visual RS gain (independent-samples t-test
309 comparisons between PRE and POST phases) at least for the index or the middle finger.

310 Third, we submitted the proprioceptive assessments to a repeated measures ANOVA with the
311 factor 'Phase' (PRE vs POST) as within-subjects factor and 'Session' as between-subjects factor.

312 We also analyzed separately the latency, duration, and peak velocity, for both visual and tactile
313 saccades in the 14 significantly adapted participants using a 3-way repeated measures ANOVA with
314 'Phase' (PRE vs POST), 'Modality' (Visual vs Tactile) and 'Target position' (index vs middle finger) as
315 within-subjects factors and 'Session' (ADAPT vs CTRL) as between-subjects factor (see supplemental
316 material for the results of this analysis).

317 RESULTS

318 1. The adaptation of visual RS

319 As stated in the Methods, the existence of visual RS adaptation was addressed by two analyses of visual
320 RS performed toward the index and the middle fingers, first, on the slope of the gain change during the
321 exposure phase, then on the ratio of gain change between PRE and POST phases. Examples of gain
322 values for individual saccades performed toward the index and the middle fingers in the PRE- and POST-
323 exposure phases (visual and tactile saccades) as well as during the Exposure phase (visual saccades) are
324 plotted in Figure 2.

325 a. Gain slope during Exposure phase

326 The gain change during the Exposure phase of the ADAPT session can be seen in supplemental figure 1
327 for all significantly adapted participants (see Methods). The mean slopes of the gain change during the
328 exposure block are illustrated in Figure 3A. The repeated measures ANOVA revealed a main effect of the
329 factor Session ($F(1, 28) = 20.061, p < 0.001$) (mean slope \pm s.d.: ADAPT = -0.000549 ± 0.000528 , CTRL =
330 0.000164 ± 0.000319). No other significant effect or interactions were found (all $F \leq 3.212$, all $p \geq 0.084$).
331 These results suggest that the double-step paradigm was successful in reducing the size of visual

332 saccades similarly for both adapted locations and that this decrease was significantly larger than in the
333 CTRL (no step) paradigm.

334 b. Gain change ratio between PRE and POST phases

335 As illustrated in Figure 3B, the mean gain change ratio for visual RS performed toward the index and the
336 middle fingers was larger in the ADAPT session than in the CTRL session. Indeed, the 2-way ANOVA
337 revealed a significant main effect of the factor Session ($F(1, 28) = 139.45$, p -value < 0.001) (mean gain
338 change ratio \pm standard deviation: ADAPT = 0.1238 ± 0.04 , CTRL = -0.0207 ± 0.025) as well as a
339 significant Session \times Target position interaction ($F(1, 28) = 5.05$, $p = 0.033$). There was no significant
340 main effect of the factor Target position ($F(1, 28) = 0.569$, p -value = 0.457). Post hoc pairwise Bonferroni
341 comparisons showed a significant difference between the ADAPT and CTRL session for both middle
342 fingers (p -value < 0.001) and index finger (p value < 0.001); it also revealed a significant difference
343 between the index and the middle fingers (mean difference index - middle = -0.018 ± 0.008 , p value =
344 0.043) in the ADAPT session but not in the CTRL (mean difference index - middle = 0.009 ± 0.008 , p value
345 = 0.300). These results indicate that visual RS gain after-effects were significantly larger in the ADAPT
346 session than in the CTRL session, showing that exposure to the double-step paradigm successfully
347 induced adaptation of visual saccades.

348 We next verified whether the order of visual and tactile blocks, despite their counterbalancing
349 (see Procedures section), could affect the above results. To this aim, we submitted the gain change ratio
350 to the same ANOVA but with the additional between-subjects factor 'Block order' (Tact-Vis/Vis-Tact vs
351 Vis-Tact/Tact-Vis). This analysis showed that there was neither a main effect of Block order nor any
352 interaction with the other factors (Session and Target position, all $F \leq 2.730$, all p values ≥ 0.111). In
353 sum, these results strengthen our conclusion that exposure to the double step paradigm successfully
354 induced adaptation of visual saccades.

355 2. Transfer analysis

356 This analysis includes only the 14 participants who were significantly adapted in the ADAPT session for
357 at least one of the two 'adapted' fingers (middle and/or index finger) (see Methods).

358 As shown in Figure 4A, visual RS adaptation generalized to nearby locations. Indeed, the
359 repeated measure ANOVA performed on the gain change ratio of non-adapted visual RS showed a
360 significant main effect of the Session factor ($F(1, 26) = 51.778$, p -value < 0.001) (mean gain change ratio
361 \pm standard deviation: ADAPT = 0.114 ± 0.050 , CTRL = -0.013 ± 0.043) with no other significant main
362 effect or interaction (all $F \leq 1.664$, all p values ≥ 0.208). This result indicates a significantly larger gain
363 decrease for visual non-adapted saccades in the ADAPT in comparison to CTRL session, irrespective of
364 the target location.

365 We tested a possible effect of the order of visual blocks in the experimental protocol, by
366 submitting the gain change ratio to the above ANOVA with the additional 'Block order' factor (Tact-
367 Vis/Vis-Tact vs Vis-Tact/Tact-Vis). Results showed neither significant main effect of Block order, nor
368 significant interaction with the other factors of the ANOVA (all $F \leq 1.821$, all p values ≥ 0.190).

369 As shown in Figure 4B, the visual RS adaptation transferred to tactile RS. Indeed, the repeated
370 measures ANOVA performed on the gain change ratio of non-adapted tactile RS showed a significant
371 main effect of the Session factor ($F(1, 26) = 15.766$, p -value < 0.001) (mean gain change ratio \pm standard
372 deviation: ADAPT = 0.167 ± 0.108 , CTRL = -0.017 ± 0.136) with no other significant main effect or
373 interaction (all $F \leq 1.447$, all p values ≥ 0.243). This result indicates a significantly larger gain decrease for

374 tactile non-adapted saccade in the ADAPT in comparison to CTRL session, irrespective of the target
375 location.

376 As for the previous analysis, we tested a possible effect of the order of visual and tactile blocks,
377 by submitting the gain change ratio to the above ANOVA with the additional 'Block order' factor (Tact-
378 Vis/Vis-Tact vs Vis-Tact/Tact-Vis). Results showed neither significant main effect of Block order, nor
379 significant interaction with the other factors of the ANOVA (all $F \leq 1.681$, all p values ≥ 0.192).

380 In summary, these results indicate that the gain of visual RS to non-adapted targets (ring and
381 thumb fingers) as well as the gain of all non-adapted tactile RS decreased significantly more in the
382 ADAPT session than in the CTRL session, therefore showing that visual RS adaptation generalized to
383 nearby locations and transferred to tactile RS.

384 3. Proprioceptive drift

385 As shown in Figures 5, participants underestimated their unseen middle finger location. This
386 proprioceptive drift was larger in the POST phase in comparison to the PRE phase (Figure 5B) but
387 importantly, this pattern of change did not differ between the CTRL and the ADAPT sessions (Figure 5A).
388 Indeed, the repeated measure ANOVA disclosed a significant main effect of the factor Phase ($F(1, 28) =$
389 24.78 , $p < 0.001$) (mean estimations (in degree) \pm s.d.: PRE = 11.96 ± 3.06 , POST = 8.7 ± 3.33), but no
390 significant main effect of Session, and no significant Session \times Phase interaction (all $F \leq 0.237$, all $p \geq$
391 0.630). Therefore, the proprioceptive drift of the hand increased to a comparable extent during the
392 ADAPT and CTRL exposures. Thus, changes in proprioceptive drift differ from, and hence are not likely
393 responsible for, the changes in tactile RS gain reported above.

394 **EXPERIMENT 2: INVESTIGATING THE ADAPTATION OF TACTILE** 395 **SACCADES AND ITS TRANSFER TO VISUAL SACCADES.**

396 Results from Experiment 1 indicate that the adaptation of visual RS transfers fully to non-adapted
397 saccades in the same modality. Most notably, they additionally reveal that visual RS adaptation also
398 transfers to tactile RS, irrespective of whether they were directed toward adapted or non-adapted finger
399 locations. Importantly, this transfer across modalities is independent of the proprioceptive drift, as the
400 latter was equally present in the CTRL condition where neither adaptation nor transfer were observed.

401 In keeping with the previously reported visual-to-auditory adaptation transfer (27), this visual-
402 to-tactile adaptation transfer is consistent with the hypothesis that RS adaptation modifies the saccade
403 motor command, thus acting downstream, at a level of the final common pathway where multisensory
404 information about the target has already been transformed into a motor, oculocentric, reference frame.
405 To further support this hypothesis, we designed Experiment 2 to determine, first, whether saccades to
406 tactile targets can be adapted and, second, whether saccadic adaptation transfer is bidirectional, i.e.,
407 also from tactile to visual saccades. To this twofold aim, we adapted the double-step paradigm to
408 electrocutaneous stimulation of the fingers during the tactile saccade execution, to repeatedly expose
409 tactilely triggered saccades to a backward aiming error. Then, similarly to Experiment 1, we assessed the
410 effectiveness of this tactile saccade adaptation and measured its effect on both visual and tactile
411 saccades performed toward different target eccentricities.

412 MATERIALS AND METHODS

413 1. Participants

414 Sample size was estimated via G*Power 3.1.9.7 (effect size = 0.25, α = 0.05, Power = 0.8, correlation
415 among repeated measures = 0.6). As in Experiment 1, previous studies investigating tactile saccades
416 adaptation were lacking, therefore we based our choice of a moderate effect (effect size = 0.25) on the
417 well-established low precision (high standard deviation of the gain) of tactile saccades (4). Thirty
418 volunteers (3 left-handed, 22 females and 8 males, mean age = 26.8 ± 4.7 , ranging between 19 and 37
419 years old) participated in Experiment 2 (all but one, the experimenter, were naïve to the objectives of
420 this study). Inclusion and exclusion criteria were the same as in Experiment 1. All participants performed
421 an ADAPT and a CTRL session separated by at least 7 days, in a counterbalanced order (15 participants
422 started with the CTRL session, and the other 15 started with the ADAPT session).

423 2. Experimental setup

424 The experimental setup was the same as for Experiment 1. Eye movements were recorded at a 1000 Hz
425 frequency using the remote configuration of the EyeLink® 1000 plus infrared Eye Tracker (SR Research,
426 Canada).

427 3. Procedures

428 The design was the same as in Experiment 1, except that all subjects performed both ADAPT and CTRL
429 sessions (within-subject design). Each session consisted of the same 5 steps as in Experiment 1: a PRE
430 proprioceptive location assessment, a saccade PRE-exposure phase, a saccade exposure phase, a
431 saccade POST-exposure phase, and a POST proprioceptive location assessment. The testing order of
432 tactile and visual saccades blocks in the PRE-exposure and POST-exposure phases were counter-
433 balanced between participants: half of them performed visual saccades before tactile saccades in the
434 PRE-exposure then tactile saccades before the visual ones in the POST-exposure (Vis-Tact/Tact-Vis), the
435 other half were assigned the reverse order (Tact-Vis/Vis-Tact).

436 The PRE- and POST- exposure blocks differed from those of Experiment 1 only by the duration of
437 the visual and tactile targets, here 100 ms, to make the tactile stimulations more comfortable for
438 participants, and by a slightly reduced intensity of the LED to provide a more comfortable contrast.

439 For the exposure phase in the ADAPT session, a tactile target double-step paradigm was
440 implemented, as follows. Participants first fixated on the FP for a random duration similar to Experiment
441 1, then a tactile stimulation was applied for 100 ms to their index or middle finger. Participants had to
442 look as rapidly and as precisely as possible toward their stimulated finger and as soon as their saccadic
443 eye movement was detected, a second tactile stimulation of 100 ms was delivered on the middle finger
444 or the ring finger, respectively (inducing in every trial a 5° tactile backward step). Participants were
445 asked to fixate on the last felt position of the tactile stimulation until the FP reappeared. In the CTRL
446 session, the sequence of events was identical except that the second tactile stimulation was applied to
447 the same, initially stimulated, finger (no target step).

448 4. Analyses

449 As in Experiment 1 saccades performed toward the pinky finger were discarded from the analysis. The
450 same exclusion criteria were used as in Experiment 1, which resulted in the exclusion of 12.9% of trials.
451 As in Experiment 1, we calculated the following parameters for all visual and tactile saccades: latency,
452 amplitude, gain, duration, and peak velocity; then, the slope of the relationship between tactile saccade

453 gain and trial number of the exposure phase was computed separately for the ADAPT and CTRL sessions
454 and for the middle and the index fingers. We finally computed the gain change ratio.

455 5. Statistical analyses

456 A data quality check showed that some participants systematically performed very hypometric
457 tactile saccades in the PRE-exposure phase of both the ADAPT and CTRL sessions. Thus, using K-Means
458 clustering methods, we checked if we could detect significantly different sub-groups in our sample of 30
459 participants based on their mean tactile saccades gain in the PRE-exposure phase. The number of sub-
460 groups was determined using the elbow method (3 sub-groups) then fed to the K-Means clustering
461 revealing that all three subgroups differ statistically from each other's according to their mean tactile RS
462 gain: group 1 (5 subjects, mean gain = 0.374, range 0.342 to 0.471), group 2 (11 participants, mean gain
463 = 0.676, range 0.623 to 0.752) and group 3 (14 participants, mean gain = 0.9915, range 0.847 to 1.205).
464 As this study focused on the adaptive amplitude reduction of saccades, we decided to exclude group 1,
465 resulting in a final sample size of 25 participants. This decision was based on the fact that the strong
466 hypo-metricity of tactile saccades in group 1 would have led 1) to a biased and underestimated
467 adaptation capacity (amplitude reduction adaptation is limited when baseline saccade gain is already
468 low), and 2) even if those participants would nonetheless be adapted, to a biased and underestimated
469 transfer of such adaptation to the visual modality because the adapted tactile saccades vectors would
470 differ too much from the non-adapted visual saccades vectors.

471 Using the same method we checked if we could identify participants with very hypometric
472 saccades in Experiment 1. We were able to identify 2 best fitted subgroups of participants according to
473 their mean tactile RS gain, however, none of them qualified to have very hypometric saccades (mean
474 gain \pm standard deviation: Group 1 (7 participants) = 0.589 ± 0.116 , Group 2 (8 participants) = $0.9392 \pm$
475 0.093) which might be related to the smaller sample size in Experiment 1 compared to Experiment 2.

476 We then followed the same analysis strategy as in Experiment 1. First, the slope of the linear
477 relationship between saccadic gain and trial number during exposure was submitted to a two-way
478 repeated measures ANOVA with the within-subjects factors 'Session' (ADAPT vs CTRL) and Target
479 position (middle vs index fingers). Then, the gain change ratio of tactile (adapted modality) RS, used as a
480 measure of adaptation after-effect, was submitted to the same repeated measures Target position
481 (index and the middle fingers) x Session (ADAPT vs CTRL) ANOVA. Second, we investigated a possible
482 generalization and/or transfer of adaptation. To this aim, we submitted the gain change ratio of non-
483 adapted tactile and visual RS to two separate 2-way repeated measures ANOVA with 'Target position'
484 and 'Session' (ADAPT vs CTRL) as within-subjects factors. The 'Target position' factor had 2 levels in the
485 first ANOVA (ring vs thumb fingers) and 4 in the second ANOVA (ring, middle, index and thumb fingers).
486 We included in this last analysis only participants who showed a significant level of adaptation (13
487 subjects out of 25), i.e. showing a significant decrease of tactile RS gain (independent-samples t-test
488 comparisons between PRE and POST phases) at least for the index or the middle finger. Third, we
489 submitted the proprioceptive assessments to a two-way repeated measures ANOVA with the within-
490 subjects factors 'Session' (ADAPT vs CTRL) and 'Phase' (PRE vs POST).

491 As in Experiment 1, we also analyzed separately the latency, duration, and peak velocity, for
492 both visual and tactile saccades in adapted participants only (see supplemental material for the results
493 of this analysis).

494 RESULTS

495 1. The adaptation of tactile RS

496 As in Experiment 1, we present below examples of gain values for individual saccades performed toward
497 the index and the middle fingers in the PRE- and POST-exposure phases (tactile and visual saccades), as
498 well as during the Exposure phase (tactile saccades), plotted in Figure 6.

499 a. Gain Slope during exposure phase

500 The gain change during the Exposure phase of the ADAPT session can be seen in supplemental figure 2
501 for all significantly adapted participants (see Methods). The mean slopes of gain change during the
502 exposure phase are illustrated in Figure 7A. The repeated measures ANOVA revealed a significant main
503 effect of the factor Session ($F(1, 24) = 4.971, p = 0.035$) (ADAPT = -0.000942 ± 0.001145 , CTRL = $-$
504 0.000154 ± 0.001196). No other significant main effect or interaction was found (all $F \leq 0.772$, all $p \geq$
505 0.388). These results suggest that the target double step paradigm was successful in reducing the size of
506 tactile saccades similarly for both adapted locations and that this decrease was significantly larger than
507 in the CTRL (no-step) paradigm.

508 b. Gain change ratio between PRE and POST phases

509 The results of this analysis, illustrated in Figure 7B, revealed that the gain change ratios of tactile RS
510 performed toward the two trained targets (index and middle fingers) were larger in the ADAPT session
511 than in the CTRL session. Indeed, the two-way repeated measures ANOVA showed a significant main
512 effect of the factor Session ($F(1, 24) = 10.614, p\text{-value} = 0.003$) (mean gain change ratio \pm standard
513 deviation: ADAPT = 0.0877 ± 0.1594 , CTRL = -0.0272 ± 0.2102). No further main effects or interactions
514 were found (all $F \leq 1.758$, all p values ≥ 0.197). Thus, the significantly larger after-effect in the ADAPT
515 session than in the CTRL session suggests that the double step paradigm exposure successfully induced
516 adaptation of tactile saccades.

517 We then tested the effects of block order and of session order by adding to the previous
518 repeated measures ANOVA the following two between-subjects factors: 'Block order' (Tact-Vis-Vis-Tact
519 vs Vis-Tact-Tact-Vis) and 'First session' (ADAPT vs CTRL). This analysis showed neither main effect of
520 these two additional factors, nor significant interactions between them or with the other factors
521 (Session and Target) (all $F \leq 3.163$, all p values ≥ 0.09). These results show that the blocks order did not
522 affect our previous conclusion.

523 2. Transfer analysis.

524 As in Experiment 1, this analysis includes only the 13 participants who were significantly adapted in the
525 ADAPT session for at least one of the two 'adapted' fingers (middle and/or index finger)(see Methods).

526 The 2-way repeated measures ANOVA performed on the gain change ratio of tactile non-
527 adapted RS showed significant main effect of the factor Session ($F(1, 12) = 8.198, p\text{-value} = 0.014$) as
528 well as a significant Session \times Target location interaction ($F(1, 12) = 6.127, p\text{-value} = 0.029$). Post hoc
529 pairwise Bonferroni comparisons performed to assess this interaction showed significant differences
530 between sessions for both the ring ($p\text{-value} = 0.014$) and thumb ($p\text{-value} = 0.031$) fingers (mean \pm
531 standard deviation for ring finger: ADAPT = 0.222 ± 0.202 , CTRL = 0.016 ± 0.221 , Thumb finger: ADAPT =
532 0.186 ± 0.087 , CTRL = 0.106 ± 0.116). It revealed neither significant difference between Target locations
533 in the ADAPT session ($p\text{-value} = 0.473$) nor in the CTRL session ($p\text{-value} = 0.086$). There was no
534 significant main effect for the factor Target location ($F(1, 12) = 0.436, p\text{-value} = 0.521$). These results

535 (plotted in Figure 8A) suggest that the adaptation of tactile RS generalized to tactile RS toward nearby
536 non-adapted locations.

537 We then tested the potential effects of block order and session order by an ANOVA with two
538 additional between-subjects factor 'Block order' (Tact-Vis-Vis-Tact vs Vis-Tact-Tact-Vis) and 'First
539 session' (ADAPT vs CTRL). This analysis showed neither significant main effect of Block order and First
540 session, nor significant interaction between these two factors or with the other within-subjects factors
541 (all $F \leq 3.018$, all p -values ≥ 0.116)."

542 The 2-way repeated measures ANOVA performed on the gain change ratio for visual non-
543 adapted RS showed a significant main effect of the factor Session ($F(1, 12) = 13.462$, p -value = 0.003)
544 (mean \pm standard deviation: ADAPT = 0.034 ± 0.062 , CTRL = -0.008 ± 0.048). No other main effects or
545 interaction were found in this ANOVA (all $F \leq 2.444$, all p -values ≥ 0.113). These results (plotted in Figure
546 8B) suggest that the adaptation of tactile RS transferred to visual RS performed toward all tested
547 locations.

548 We also tested the potential effects of block order and session order by a similar ANOVA with
549 two additional between-subjects factor 'Block order' (Tact-Vis-Vis-Tact vs Vis-Tact-Tact-Vis) and 'First
550 session' (ADAPT vs CTRL). This analysis showed neither significant main effect of Block order and First
551 session, nor significant interaction between these two factors or with the other within-subjects factors
552 (all $F \leq 1.606$, all p -values ≥ 0.237).

553 In summary, the current analysis indicates that the gain of tactile RS to non-adapted targets
554 (ring and thumb fingers) as well as the gain of all non-adapted visual RS decrease specifically in the
555 ADAPT session, therefore showing that tactile RS adaptation generalized to nearby locations and
556 transferred to visual RS.

557 3. Proprioceptive drift

558 As shown in Figure 9, participants underestimated the location of their unseen middle finger location.
559 This proprioceptive drift increases with time from PRE to POST phase (Figure 9B), but importantly, it did
560 so similarly in both the ADAPT and the CTRL sessions (Figure 9A). Indeed, the repeated measure ANOVA
561 indicates a significant main effect of the factor Phase ($F(1, 24) = 18.59$, $p < 0.001$) (mean estimations (in
562 degree) \pm s.d.: PRE = 9.49 ± 3.1 , POST = 7.9 ± 3.9), but no significant main effect of the factor Session,
563 and no significant Session \times Phase interaction (all $F \leq 1.453$, all $p \geq 0.240$). Therefore, the decrease of
564 saccadic gain observed for tactile RS in the ADAPT session (see previous sections) appears unrelated to
565 the proprioceptive drift.

566 DISCUSSION

567 In this study, we sought to determine whether RS adaptation operates at the motor level, i.e., modifying
568 the saccadic command. To test this hypothesis we adapted, separately, reactive visual or tactile
569 saccades and we investigated the transfer of adaptation to the non-adapted modality, the reasoning
570 being that if motor, then saccadic adaptation should also transfer to saccades triggered by other sensory
571 modalities. We found in Experiment 1 that adaptation of reactive visual saccades strongly transferred to
572 tactile saccades and we reported for the first time in Experiment 2, experimental support for the
573 existence of adaptation of tactile saccades, although this adaptation transferred to visual saccades only
574 slightly. In the following sections, we discuss the results obtained in this study in respect to the existing
575 literature on saccadic adaptation.

576 Within the visual modality, saccadic adaptation has been shown to transfer to non-adapted
577 saccades according to a spatial gradient known as the adaptation field (13, 27). This means that
578 adaptation of a given saccade fully transfers to all saccades with the same vector, i.e., direction and
579 amplitude, irrespective of their initial/final position and that, conversely, the rate of transfer
580 progressively decreases as the amplitude and/or the direction of the tested saccades deviates from the
581 adapted vector. When the deviation of direction between the two saccade vectors reaches 90° no
582 transfer of adaptation is observed at all, but with a deviation of 45° a transfer of about 50% occurs,
583 reflecting a large adaptation field. The visual adaptation field is also quite extended along the saccade
584 amplitude dimension and is asymmetric (33), with a higher rate of adaptation transfer to saccades larger
585 than the adapted saccade compared to smaller-sized saccades.
586 Here, while we replicate the adaptation field finding (Experiment 1) for the visual modality, we reveal
587 for the first time (Experiment 2) the existence of adaptation for tactile saccades (discussed below). In
588 addition, we further disclose that tactile saccades adaptation also displays an adaptation field. Indeed,
589 after the adaptation of tactile saccades toward the middle and the index finger a generalization of
590 adaptation has been shown to non-adapted tactile saccades toward the ring and the thumb fingers.
591 Moreover, the high amount of adaptation spatial generalization seen for both sensory modalities in the
592 present experiments fits with the existence of wide adaptation fields and can further be attributed to
593 the simultaneous training of two slightly different saccade vectors (to the middle and the index finger).
594 Importantly, this spatial generalization further argues that the decrease in tactile saccades gain during
595 the exposure phase of the adaptation session in Experiment 2 is not related to a strategy followed by
596 participants to saccade directly toward the second tactile stimulation but rather to a plastic gain
597 reduction resulting from backward adaptation mechanisms. This interpretation is also compatible with
598 the significant after-effect on the saccade gain observed in the POST-exposure phase in comparison to
599 the PRE-exposure phase.

600 The transfer of visual saccades adaptation to saccades in a different modality has been reported
601 so far for auditory saccades only, as indicated in the introduction (27, 28). With Experiment 1, we were
602 able to show that an adaptation transfer exists also from visual to tactile saccades. These cross-modal,
603 visual-to-auditory, and visual-to-tactile, transfers of adaptation argue for a motor functional locus of RS
604 backward adaptation common for saccades in all modalities and possibly situated at the cerebello-
605 brainstem level. Furthermore, this hypothesis would also predict a significant cross-modal transfer of
606 adaptation in the reverse direction, i.e., from tactile saccades to visual saccades. Indeed, Experiment 2
607 provided evidence for the existence of such transfer, which however, turned out to be much smaller
608 than the visual-to-tactile transfer of adaptation. Note that the mere presence of some transfer provides
609 another piece of evidence for our interpretation that adaptive processes largely dominated potential
610 strategies in the decrease of tactile saccade gain observed during exposure. This strong asymmetry of
611 adaptation transfers between visual-to-tactile versus tactile-to-visual suggests multiple adaptation
612 functional loci for tactile saccades, with at least one located upstream from the adaptation locus of
613 visual saccades and from of the oculomotor commands common to all saccade's modalities.

614 Vision is known to be the dominant sensory modality that we rely on to localize in our
615 environment the targets of our motor responses, including saccades (4, 8). When auditory and visual or
616 tactile and visual targets are presented simultaneously at relatively close locations, the perception of
617 auditory and tactile targets is biased toward the visual ones if the latter provides clear information
618 about its location, a phenomenon known as the ventriloquist effect (34). Furthermore, the dominance of
619 vision and its important role in shaping the perception from other senses can be seen in the deficits in

620 auditory localization in children with visual impairment compared to normal-sighted children (35). The
621 separation of functional adaptation loci that we suggest based on the asymmetrical cross-modal transfer
622 can be also thought as a higher weight given by the adaptation processes to visual information in
623 comparison to other sensory modalities, leading to a generalization of saccadic adaptation induced by a
624 visual error to saccades performed toward tactile or auditory targets but only partially in the other way
625 around. According to this hypothesis, the adaptation of auditory saccades, if possible, should also
626 transfer asymmetrically to visual saccades. Further studies will test this prediction and should first
627 determine whether auditory saccades can be adapted at all.

628 The second main finding of our study is that RS toward tactile targets can be adapted, even
629 though its prevalence appears reduced as compared to visual RS adaptation (several individual
630 participants failed to demonstrate a significant after-effect). To our knowledge, this is the first
631 demonstration that the gain of non-visual saccades can be reduced with a modified version of the
632 double step target paradigm. Tactile saccades (like other non-visual saccades) differ from visual saccades
633 by their longer latency, their reduced speed and, critically in the context of saccade adaptation, their
634 gain is much more variable and lower on average. Also, the modified double step paradigm used here to
635 adapt tactile saccades may differ from the double step paradigm originally designed to adapt visual
636 saccades by the way that the change of stimulated finger during the ongoing saccade is interpreted by
637 participants' central nervous system. In particular, since this double tactile stimulation was consciously
638 detected by all except one participant (as confirmed by report at debriefing), as opposed to the intra-
639 saccadic target step of the visual saccade adaptation procedure, which is frequently masked by saccadic
640 suppression, one may wonder whether it can truly yield an adequate error signal for adaptation
641 mechanisms. These peculiarities lead us to consider whether the decrease in tactile saccades gain seen
642 in the adaptation exposure of Experiment 2 is related to genuine adaptation mechanisms and to discuss
643 potential alternative explanations. The first alternative cause is strategy, that our participants could
644 have used during exposure as they consciously detected the change in location of tactile stimulation
645 during their saccades. However, the gain of tactile saccades 1) progressively decreased (see
646 supplemental figures) during the adaptation exposure phase and 2) remained low in the post-exposure
647 phase (after-effect) despite the fact that the tactile target no longer 'jumped'. These observations differ
648 i) from the sudden drop of saccade gain which can be expected at the beginning of the exposure phase if
649 participants only used a conscious strategy, and ii) from the immediate recovery of saccade gain which
650 can be expected at the beginning of the post-exposure phase when target no longer jumps, and the
651 potentially associated strategy, are discontinued. As explained in the method sections the order of the
652 visual and tactile saccades block was counterbalanced between participants. Therefore, in experiment 2
653 half of our participants performed the visual POST-exposure block directly after the exposure phase and
654 only then, the tactile POST-exposure block, making highly unlikely the possibility that they maintained a
655 strategy across a complete block of visual saccades. In addition, if such strategy was used by the
656 remaining participants who performed the tactile POST-exposure block immediately after exposure, we
657 should have seen an effect of 'block order' when tested as a between subjects factor in the ANOVA of
658 gain change ratio, which was not the case. In previous saccadic adaptation studies, including when the
659 intra-saccadic visual target step is consciously detected (36–38), both the slow gain change during
660 exposure and the post-exposure after-effect are considered as hallmarks of true (or implicit) adaptation.
661 Furthermore, a recent study by Heins and Lappe (38) showed that saccadic adaptation takes place even
662 when the error was attributed to external sources i.e. to error in machine decoding. In their experiment,
663 participants were presented with a fixation point around which multiple objects were placed in a

664 circular array. They were instructed to choose a certain object while fixating and then to communicate
665 this object to the computer by performing a saccade toward it once the fixation point disappeared. At
666 the end of the saccade, a feedback about the decoded chosen target was presented to the participants.
667 Participants were warned that some bias could be erroneously added to the saccade endpoint
668 information used to decode which target they chose, and that in such case they have to take into
669 account these mistakes to keep trying enabling the machine to correctly decode the chosen targets. The
670 results of this experiment show that changes in saccades trajectory occurred progressively during
671 exposure and were preserved in post exposure indicating a genuine adaptive learning even though
672 participants applied some strategies in order to reach a better machine decoding performance. In
673 addition, another study performed by the same team (37) showed that backward saccadic adaptation
674 occurs when participants were aware of the intrasaccadic step irrespective of whether they were told to
675 follow the target step at the end of the primary saccade, or to ignore this second step and maintain
676 fixation on the first target location. Also, in the tactile modality, it is well-established that healthy people
677 make frequent errors in determining the identity of touched fingers (39, 40). Therefore, in Experiment 2
678 even if participants can clearly feel that 2 fingers were touched, it cannot be taken for granted that they
679 know which ones, nor which exactly was the last one, therefore making the use of a strategy less likely.
680 Despite all these considerations, and according to a reviewer's suggestion, the hypothesis that changes
681 in tactile saccade gain in Experiment 2 are due to strategic responses of participants to the double-finger
682 stimulation during exposure cannot be ruled out in full. For this, further experiments will be necessary ,
683 for example by testing whether these changes of tactile saccade gain do transfer to other spatial
684 locations/body parts.

685 The second alternative is fatigue, which would also account for the decrease of the amplitude
686 of the tactile saccades in Experiment 1. Yet, our control sessions of both Experiments 1 and 2 argue
687 against this possibility. Indeed, we have seen no significant changes in tactile or visual saccades gain
688 either during the exposure phase or between the PRE- and the POST-exposure phases of the control
689 sessions. Thus, the gain changes observed during the exposure of adaptation sessions were specific,
690 ruling out any explanation based on fatigue.

691 A third alternative explanation of the tactile saccades gain decrease seen in the adaptation
692 sessions of this study is the proprioceptive drift. In the dark, the perception of our hands placed in an
693 eccentric position tends to drift toward our midline progressively over time, as shown by Wann and
694 Ibrahim (30) and we still don't know why it occurs. In this study we showed that our participants'
695 perception of their right hand's middle finger did drift toward their midline, with a higher drift rate
696 reached in the POST- vs PRE- proprioceptive assessment blocks. Importantly however, this drift did not
697 differ between the adaptation and the control sessions, which provided evidence that the
698 proprioceptive drift was not responsible for the decrease in tactile saccades gain seen both in
699 Experiment 1 and in Experiment 2.

700 Thus, altogether and in addition to the partial tactile-to-visual transfer demonstrated, these
701 observations led us to propose that saccades toward tactile targets can both be modified via transfer of
702 visual saccade adaptation (Experiment 1) and can themselves be directly adapted (Experiment 2).

703 An interesting issue raised by the present findings concerns the nature of error signals driving
704 saccadic adaptation. Four main candidates have been considered in the literature: corrective saccades,
705 post-saccadic retinal error, prediction error and postdiction error. Although corrective saccades and
706 post-saccadic retinal error are the simplest motor or sensory signals the brain can use to monitor the
707 accuracy of primary saccades, experimental evidence soon argued in favor of the prediction error (18,

708 41–43). This prediction error hypothesis (44, 45) states that the error signal is the result of a
709 comparison between the predicted error (target location relative to the saccade landing position
710 predicted from the efference copy) and the actual error (post-saccadic target retinal image relative to
711 the fovea). In their recent modeling study, Masselink and Lappe (46) proposed the postdictive error
712 hypothesis, according to which error signals driving saccadic adaptation mechanisms result from a
713 comparison between the motor command of the saccade and the post-saccadic visual error postdicted
714 back to pre-saccadic space based on the efferent copy. Note that in all these four different accounts,
715 saccadic adaptation always relies on visual information of post-saccadic target location either directly
716 (post-saccadic retinal error hypothesis) or indirectly through the generation of a corrective saccade, or
717 through the computation of the prediction error or of the postdiction error. In sharp contrast, the
718 present Experiment 2 suggests that saccades toward tactile targets, thus executed in absence of any
719 visual feedback, could still be adapted. Therefore, our study highlights that the saccadic error feedback
720 involved in saccadic adaptation is not necessarily visual but can be extracted from tactile information
721 about the target location on the body. Further studies are required to determine how this non-visual
722 information is transformed from its native anatomical frame of reference into an eye-centered frame of
723 reference suitable for the saccadic adaptation mechanisms.

724 In conclusion, we showed that the adaptation of visual RS transfers strongly to tactile RS, in
725 favor of a motor functional locus of RS adaptation. We also revealed for the first-time evidence for a
726 possible induction of backward adaptation of tactile RS via a tactile double step target paradigm and
727 that this adaptation transfers very partially to visual RS, suggesting that an adaptation locus specific of
728 tactile RS is upstream the locus of visual RS adaptation.

729 **DATA AVAILABILITY**

730 Source data for this study are openly available at
731 https://osf.io/ehjd2/?view_only=8fe4eda5446847be84ee6dc0968cd057

732 **SUPPLEMENTAL MATERIAL**

733 Supplementary analysis can be found at
734 https://osf.io/ehjd2/?view_only=8fe4eda5446847be84ee6dc0968cd057

735 **ACKNOWLEDGMENTS**

736 We are grateful to Sonia Alouche, Jean-Louis Borach, and Frederic Volland from IMPACT team at Lyon
737 Neuroscience Research Center for their administrative and technical help during this study. We are also
738 grateful to the constructive remarks and suggestions provided by all the reviewers .

739 **GRANTS**

740 This study was supported by the ANR grant DEC-SPACE (ANR-21-CE28-0001) to A.F. and has been
741 performed within the framework of the LABEX CORTEX (ANR-11-LABX-0042).

742 **DISCLOSURES**

743 The authors declare that they have no competing interests.

744 **AUTHOR CONTRIBUTIONS**

745 Conception and design of the study: A.B., V.G., M.T.N.P., A.F., and D.P; Setup preparation and Software:
746 A.B., V.G., E.K., and R.S.; Data collection: A.B. and V.G.; Data analysis: A.B.; Data interpretation: A.B., A.F.
747 and D.P; Original draft: A.B.; Critical revisions: A.F. and D.P; All the authors approved the final
748 manuscript for submission.

749 **REFERENCES**

- 750 1. **Gaymard B, Ploner CJ, Rivaud S, Vermersch AI, Pierrot-Deseilligny C.** Cortical control of saccades.
751 *Exp Brain Res* 123: 159–163, 1998. doi: 10.1007/s002210050557.
- 752 2. **Jay MF, Sparks DL.** Sensorimotor integration in the primate superior colliculus. I. Motor
753 convergence. *J Neurophysiol* 57: 22–34, 1987. doi: 10.1152/jn.1987.57.1.22.
- 754 3. **Blanke O, Grüsser O-J.** Saccades guided by somatosensory stimuli. *Vision Res* 41: 2407–2412,
755 2001. doi: 10.1016/S0042-6989(01)00125-0.
- 756 4. **Sullivan A, Fitzmaurice K, Abel LA.** Latency and accuracy of saccades to somatosensory targets.
757 *Exp Brain Res* 154: 407–410, 2004. doi: 10.1007/s00221-003-1749-1.
- 758 5. **Groh JM, Sparks DL.** Saccades to somatosensory targets. I. behavioral characteristics. *J*
759 *Neurophysiol* 75: 412–427, 1996. doi: 10.1152/jn.1996.75.1.412.
- 760 6. **Overvliet KE, Azañón E, Soto-Faraco S.** Somatosensory saccades reveal the timing of tactile spatial
761 remapping. *Neuropsychologia* 49: 3046–3052, 2011. doi: 10.1016/j.neuropsychologia.2011.07.005.
- 762 7. **Amlôt R, Walker R.** Are somatosensory saccades voluntary or reflexive? *Exp Brain Res* 168: 557–
763 565, 2006. doi: 10.1007/s00221-005-0116-9.
- 764 8. **Neggers SF, Bekkering H.** Integration of visual and somatosensory target information in goal-
765 directed eye and arm movements. *Exp Brain Res* 125: 97–107, 1999. doi: 10.1007/s002210050663.
- 766 9. **Heed T, Azañón E.** Using time to investigate space: a review of tactile temporal order judgments as
767 a window onto spatial processing in touch. *Front Psychol* 5: 76, 2014. doi:
768 10.3389/fpsyg.2014.00076.
- 769 10. **Groh JM, Sparks DL.** Saccades to somatosensory targets. II. motor convergence in primate superior
770 colliculus. *J Neurophysiol* 75: 428–438, 1996. doi: 10.1152/jn.1996.75.1.428.
- 771 11. **Groh JM, Sparks DL.** Saccades to somatosensory targets. III. eye-position-dependent
772 somatosensory activity in primate superior colliculus. *J Neurophysiol* 75: 439–453, 1996. doi:
773 10.1152/jn.1996.75.1.439.
- 774 12. **McLaughlin SC.** Parametric adjustment in saccadic eye movements. *Percept Psychophys* 2: 359–
775 362, 1967. doi: 10.3758/BF03210071.
- 776 13. **Péllisson D, Alahyane N, Panouillères M, Tilikete C.** Sensorimotor adaptation of saccadic eye
777 movements. *Neurosci Biobehav Rev* 34: 1103–1120, 2010. doi: 10.1016/j.neubiorev.2009.12.010.

- 778 14. **Hopp JJ, Fuchs AF.** The characteristics and neuronal substrate of saccadic eye movement plasticity.
779 *Prog Neurobiol* 72: 27–53, 2004. doi: 10.1016/j.pneurobio.2003.12.002.
- 780 15. **Iwamoto Y, Kaku Y.** Saccade adaptation as a model of learning in voluntary movements. *Exp Brain*
781 *Res* 204: 145–162, 2010. doi: 10.1007/s00221-010-2314-3.
- 782 16. **Blurton SP, Raabe M, Greenlee MW.** Differential cortical activation during saccadic adaptation. *J*
783 *Neurophysiol* 107: 1738–1747, 2012. doi: 10.1152/jn.00682.2011.
- 784 17. **Métais C, Nicolas J, Diarra M, Cheviet A, Koun E, Pélisson D.** Neural substrates of saccadic
785 adaptation: Plastic changes versus error processing and forward versus backward learning.
786 *NeuroImage* 262: 119556, 2022. doi: 10.1016/j.neuroimage.2022.119556.
- 787 18. **Guillaume A, Fuller JR, Srimal R, Curtis CE.** Cortico-cerebellar network involved in saccade
788 adaptation. *J Neurophysiol* 120: 2583–2594, 2018. doi: 10.1152/jn.00392.2018.
- 789 19. **Gerardin P, Miquée A, Urquizar C, Pélisson D.** Functional activation of the cerebral cortex related
790 to sensorimotor adaptation of reactive and voluntary saccades. *NeuroImage* 61: 1100–1112, 2012.
791 doi: 10.1016/j.neuroimage.2012.03.037.
- 792 20. **Liem EIML, Frens MA, Smits M, van der Geest JN.** Cerebellar activation related to saccadic
793 inaccuracies. *Cerebellum Lond Engl* 12: 224–235, 2013. doi: 10.1007/s12311-012-0417-z.
- 794 21. **Alahyane N, Salemme R, Urquizar C, Cotti J, Guillaume A, Vercher J-L, Pélisson D.** Oculomotor
795 plasticity: Are mechanisms of adaptation for reactive and voluntary saccades separate? *Brain Res*
796 1135: 107–121, 2007. doi: 10.1016/j.brainres.2006.11.077.
- 797 22. **Collins T, Doré-Mazars K.** Eye movement signals influence perception: evidence from the
798 adaptation of reactive and volitional saccades. *Vision Res* 46: 3659–3673, 2006. doi:
799 10.1016/j.visres.2006.04.004.
- 800 23. **Cotti J, Guillaume A, Alahyane N, Pelisson D, Vercher J-L.** Adaptation of voluntary saccades, but
801 not of reactive saccades, transfers to hand pointing movements. *J Neurophysiol* 98: 602–612,
802 2007. doi: 10.1152/jn.00293.2007.
- 803 24. **Cotti J, Panouillères M, Munoz DP, Vercher J-L, Pélisson D, Guillaume A.** Adaptation of reactive
804 and voluntary saccades: different patterns of adaptation revealed in the antisaccade task. *J Physiol*
805 587: 127–138, 2009. doi: 10.1113/jphysiol.2008.159459.
- 806 25. **Panouillères M, Weiss T, Urquizar C, Salemme R, Munoz DP, Pélisson D.** Behavioral evidence of
807 separate adaptation mechanisms controlling saccade amplitude lengthening and shortening. *J*
808 *Neurophysiol* 101: 1550–1559, 2009. doi: 10.1152/jn.90988.2008.
- 809 26. **Ethier V, Zee DS, Shadmehr R.** Changes in control of saccades during gain adaptation. *J Neurosci*
810 *Off J Soc Neurosci* 28: 13929–13937, 2008. doi: 10.1523/JNEUROSCI.3470-08.2008.
- 811 27. **Frens MA, van Opstal AJ.** Transfer of short-term adaptation in human saccadic eye movements.
812 *Exp Brain Res* 100: 293–306, 1994. doi: 10.1007/BF00227199.

- 813 28. **Collins T, Heed T, Röder B.** Eye-movement-driven changes in the perception of auditory space.
814 *Atten Percept Psychophys* 72: 736–746, 2010. doi: 10.3758/APP.72.3.736.
- 815 29. **Terry Bahill A, McDonald JD.** Smooth pursuit eye movements in response to predictable target
816 motions. *Vision Res* 23: 1573–1583, 1983. doi: 10.1016/0042-6989(83)90171-2.
- 817 30. **Wann JP, Ibrahim SF.** Does limb proprioception drift? *Exp Brain Res* 91: 162–166, 1992. doi:
818 10.1007/BF00230024.
- 819 31. **Tsakiris M, Haggard P.** The rubber hand illusion revisited: visuotactile integration and self-
820 attribution. *J Exp Psychol Hum Percept Perform* 31: 80–91, 2005. doi: 10.1037/0096-1523.31.1.80.
- 821 32. **Alahyane N, Pélisson D.** Long-lasting modifications of saccadic eye movements following
822 adaptation induced in the double-step target paradigm. *Learn Mem Cold Spring Harb N* 12: 433–
823 443, 2005. doi: 10.1101/lm.96405.
- 824 33. **Collins T, Doré-Mazars K, Lappe M.** Motor space structures perceptual space: Evidence from
825 human saccadic adaptation. *Brain Res* 1172: 32–39, 2007. doi: 10.1016/j.brainres.2007.07.040.
- 826 34. **Alais D, Newell FN, Mamassian P.** Multisensory processing in review: from physiology to
827 behaviour. *Seeing Perceiving* 23: 3–38, 2010. doi: 10.1163/187847510X488603.
- 828 35. **Cappagli G, Gori M.** Auditory spatial localization: Developmental delay in children with visual
829 impairments. *Res Dev Disabil* 53–54: 391–398, 2016. doi: 10.1016/j.ridd.2016.02.019.
- 830 36. **Fujita M, Amagai A, Minakawa F, Aoki M.** Selective and delay adaptation of human saccades.
831 *Brain Res Cogn Brain Res* 13: 41–52, 2002. doi: 10.1016/s0926-6410(01)00088-x.
- 832 37. **Heins F, Meermeier A, Lappe M.** Volitional control of saccadic adaptation. *PLoS One* 14: e0210020,
833 2019. doi: 10.1371/journal.pone.0210020.
- 834 38. **Heins F, Lappe M.** Oculomotor behavior can be adjusted on the basis of artificial feedback signals
835 indicating externally caused errors. *PLoS One* 19: e0302872, 2024. doi:
836 10.1371/journal.pone.0302872.
- 837 39. **Tamè L, Dransfield E, Quettier T, Longo MR.** Finger posture modulates structural body
838 representations. *Sci Rep* 7: 43019, 2017. doi: 10.1038/srep43019.
- 839 40. **Rusconi E, Gonzaga M, Adriani M, Braun C, Haggard P.** Know thyself: behavioral evidence for a
840 structural representation of the human body. *PLoS One* 4: e5418, 2009. doi:
841 10.1371/journal.pone.0005418.
- 842 41. **Bahcall DO, Kowler E.** The control of saccadic adaptation: implications for the scanning of natural
843 visual scenes. *Vision Res* 40: 2779–2796, 2000. doi: 10.1016/s0042-6989(00)00117-6.
- 844 42. **Herman JP, Cloud CP, Wallman J.** End-point variability is not noise in saccade adaptation. *PLoS One*
845 8: e59731, 2013. doi: 10.1371/journal.pone.0059731.

- 846 43. **Wallman J, Fuchs AF.** Saccadic Gain Modification: Visual Error Drives Motor Adaptation. *J*
847 *Neurophysiol* 80: 2405–2416, 1998. doi: 10.1152/jn.1998.80.5.2405.
- 848 44. **Collins T, Wallman J.** The relative importance of retinal error and prediction in saccadic
849 adaptation. *J Neurophysiol* 107: 3342–3348, 2012. doi: 10.1152/jn.00746.2011.
- 850 45. **Wong AL, Shelhamer M.** Sensorimotor adaptation error signals are derived from realistic
851 predictions of movement outcomes. *J Neurophysiol* 105: 1130–1140, 2011. doi:
852 10.1152/jn.00394.2010.
- 853 46. **Masselink J, Lappe M.** Visuomotor learning from postdictive motor error. *eLife* 10: e64278, 2021.
854 doi: 10.7554/eLife.64278.

855

856 **FIGURE LEGENDS**

857 Figure 1: Experiment 1 setup and procedure. (A) A vertical board was placed in the frontal plane at 30
858 cm from the participants' eyes. The right hand was immobilized in a supine position on the board
859 through rings located on the 5 fingers. The rings, separated from each other by five degrees, contained a
860 red LED that served as visual target, and a pair of electrodes placed on each finger allowed to generate
861 an electrocutaneous stimulation which served as tactile target. Another red LED serving as fixation point
862 was placed on the board five degrees to the left of the participant's midline. At the top of the board, a
863 ruler was made visible to participants during the proprioceptive location assessment. At any other time,
864 the environment was completely dark and invisible (except a single lit LED in visual saccade trials), as the
865 whole set-up was painted black, the participants' hand was covered by a black tissue glove and when lit,
866 the LEDs' intensity was low. (B) Participants gazed at the FP which disappeared simultaneously with the
867 presentation of a peripheral stimulus on one of their fingers in the visual or tactile modality, according
868 to counterbalanced blocks of trials; once the saccade onset detected, the stimulus either stepped
869 backward in the exposure phase of the ADAPT session (I), remained stationary until the end of the trial
870 in the exposure phase of the CTRL session (II), or turned off in the PRE- and POST-exposure phases (III).

871 Figure 2: Experiment 1 individual data (participant 15, ADAPTATION session): the gain of tactile (blue)
872 and visual (orange) saccades toward the middle and the index fingers in the PRE- and the POST-exposure
873 phases (black lines represent the mean gain value) as well as the variation of gain across trials in the
874 Exposure phase (slope value and statistical significance of the linear regression are presented in the
875 central panel).

876 Figure 3: Experiment 1 adaptation results (all participants). Panel A: mean saccadic gain change in the
877 exposure phase (slope of the linear regression between saccadic gain and trial number) in the
878 ADAPTATION and CONTROL sessions. Panel B: mean saccadic gain change ratio between the PRE- and
879 the POST-exposure phases in the ADAPTATION and CONTROL sessions. In both graphs, only visual
880 saccades toward the index and the middle fingers were considered. Error bars represent standard
881 deviations. *** : t-tests ($p < .001$).

882 Figure 4: Experiment 1 generalization and transfer results (only adapted participants). Mean saccadic
883 gain change ratio in the ADAPTATION and the CONTROL sessions, plotted as a function of the target
884 location separately for visual (Panel A) and tactile (Panel B) saccades, as well as the grand mean (MEAN)

885 of gain change ratio across all locations plotted in each panel. Only non-adapted locations are plotted in
886 this figure. Error bars represent standard deviations. *** : t-test ($p < .001$).

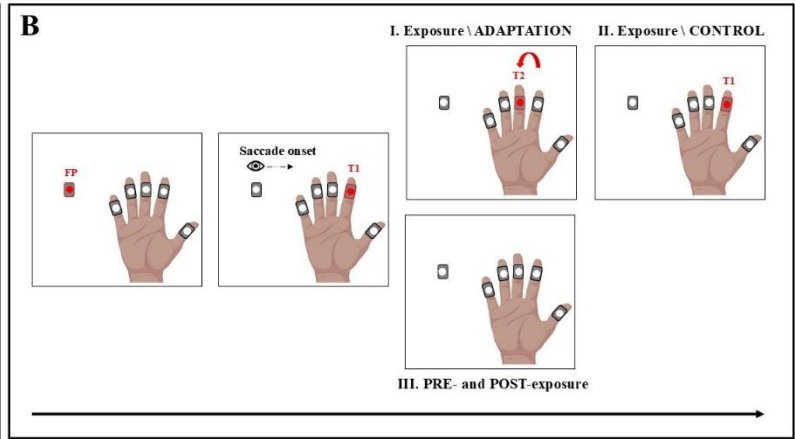
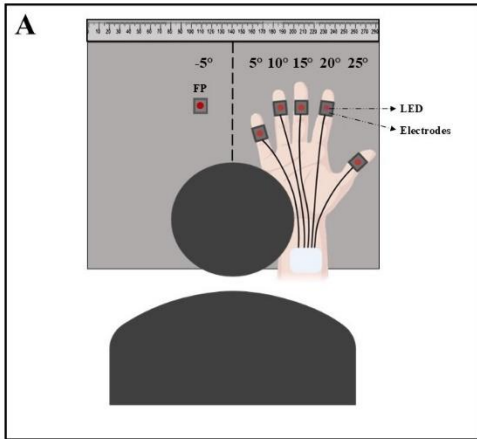
887 Figure 5: Experiment 1 proprioceptive drift results (all participants). Mean estimated position of the
888 middle finger location in the PRE- and POST- proprioceptive location assessment phases of the
889 ADAPTATION and CONTROL sessions are plotted separately (Panel A) and as a grand mean pooled over
890 both sessions (Panel B). The dotted line represents the actual middle finger location. Error bars
891 represent the standard deviation. ns : t-test ($p > .05$), *** : t-test ($p < .001$).

892 Figure 6: Experiment 2 individual data (participant 16, ADAPTATION session): the gain of tactile (blue)
893 and visual (orange) saccades toward the middle and the index fingers in the PRE- and the POST-exposure
894 phases (black lines represent the mean gain value) as well as the variation of gain across trials in the
895 Exposure phase (slope value and statistical significance of the linear regression are presented in the
896 central panel).

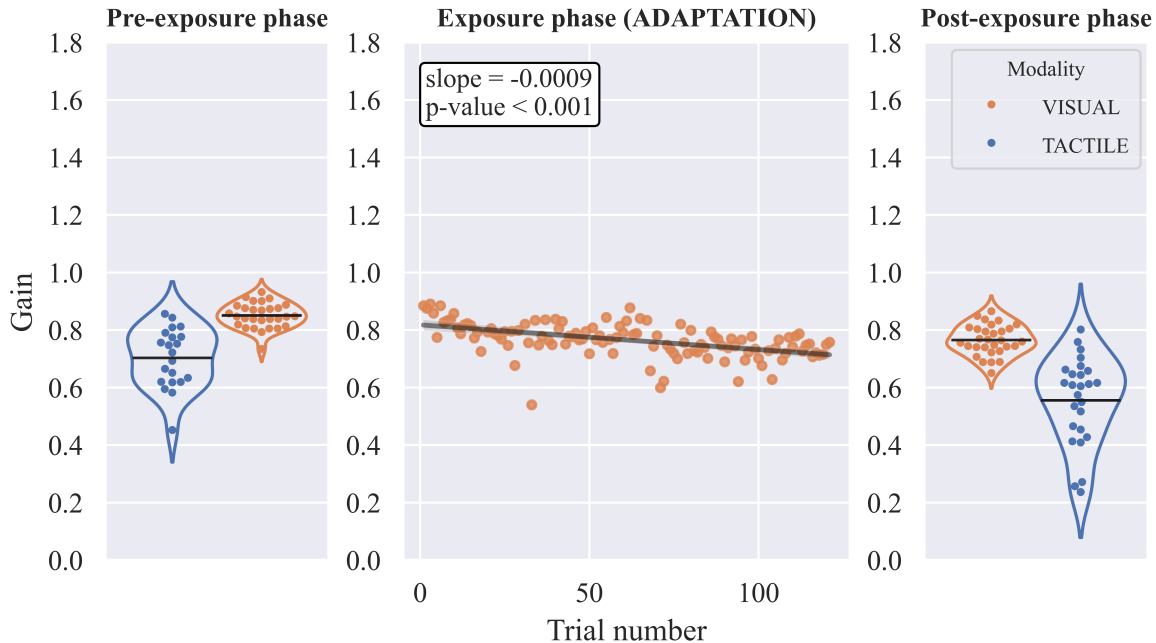
897 Figure 7: Experiment 2 adaptation results (all participants). Panel A: mean saccadic gain change in the
898 exposure phase (slope of the linear regression between saccadic gain and trial number) in the
899 ADAPTATION and CONTROL sessions. Panel B: mean saccadic gain change ratio between the PRE- and
900 the POST-exposure phases in the ADAPTATION and CONTROL sessions. In both graphs only tactile
901 saccades toward the index and the middle fingers were considered. Error bars represent standard
902 deviations. * : t-test ($p < .05$), ** : t-test ($p < .01$).

903 Figure 8: Experiment 2 generalization and transfer results (only adapted participants). Mean saccadic
904 gain change ratio in the ADAPTATION and the CONTROL sessions, plotted as a function of the target
905 location separately for tactile (Panel A) and visual (Panel B) saccades, as well as the grand mean (MEAN)
906 of gain change ratio across all locations for visual saccades. Only non-adapted locations are plotted in
907 this figure. Error bars represent standard deviations. t-tests : * ($p < .05$), ** ($p < .01$).

908 Figure 9: Experiment 2 proprioceptive drift results (all participants). Mean estimated position of the
909 middle finger location in the PRE- and POST- proprioceptive location assessment phases of the
910 ADAPTATION and CONTROL sessions plotted separately (Panel A) and as a grand mean pooled over both
911 sessions (Panel B). The dotted line represents the actual middle finger real location. Error bars represent
912 the standard deviation. ns : t-test ($p > .05$), *** : t-test ($p < .001$).

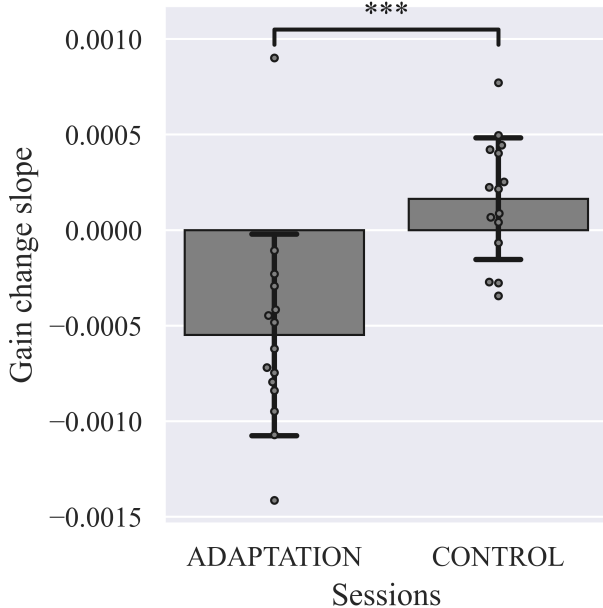


Saccadic gain (Participant 15, Experiment 1)

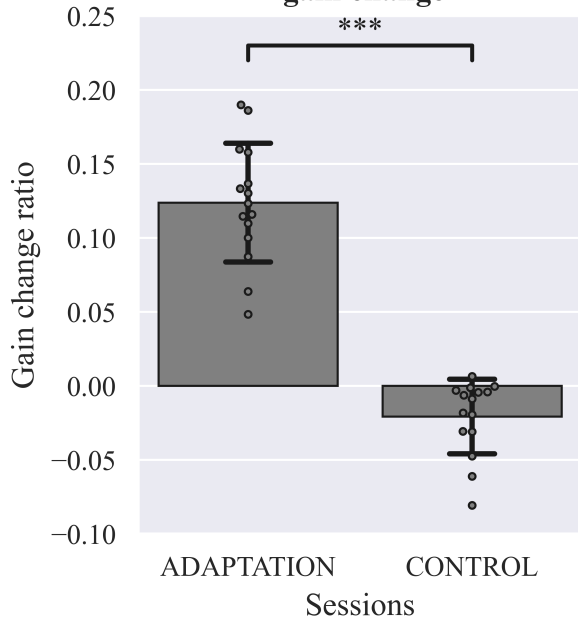


Visual saccades (N=15)

A. Gain change in the Exposure phase



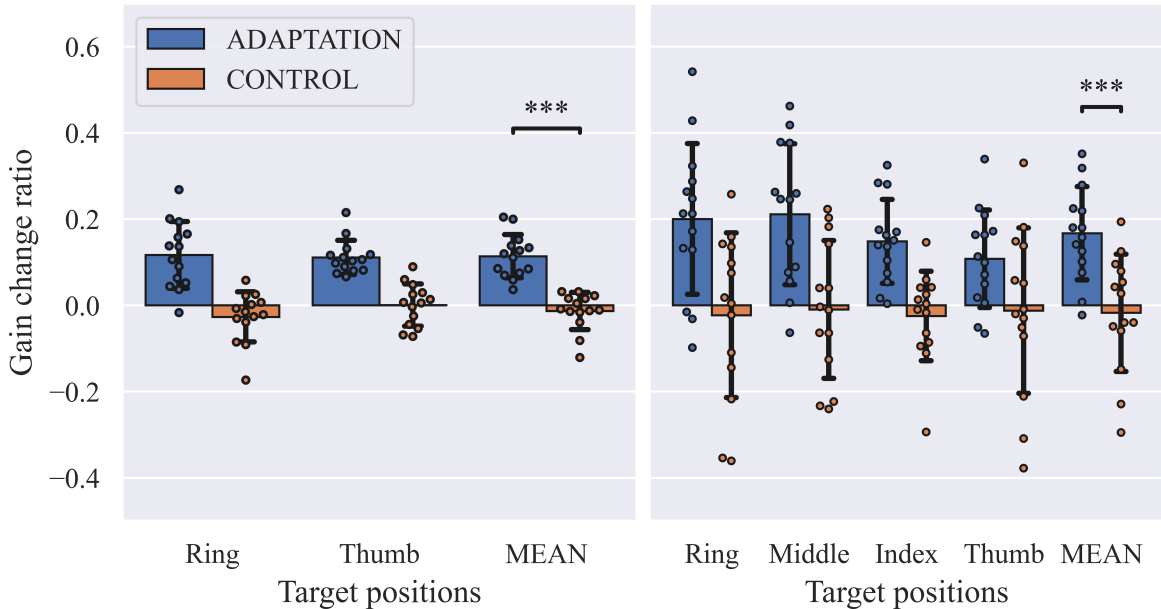
B. Pre- vs Post- exposure gain change



Gain change ratio (N=14 adapted participants)

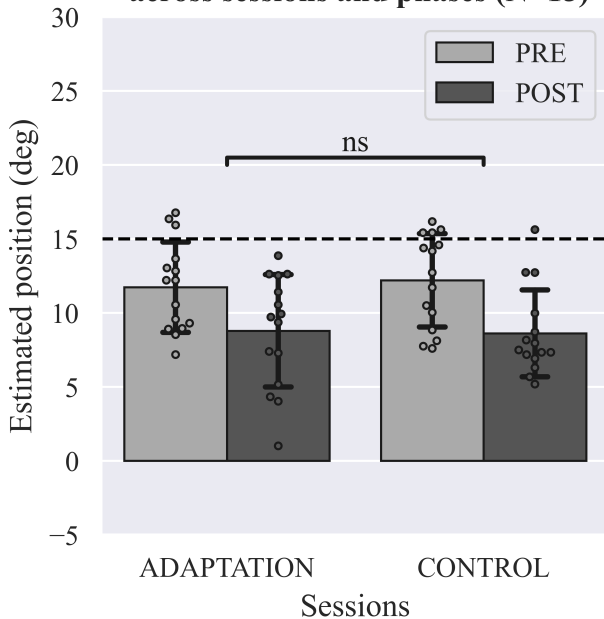
A. Visual saccades

B. Tactile saccades

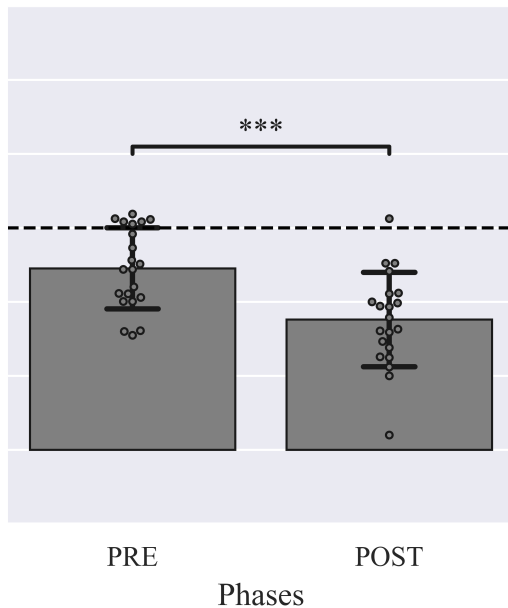


Proprioceptive drift

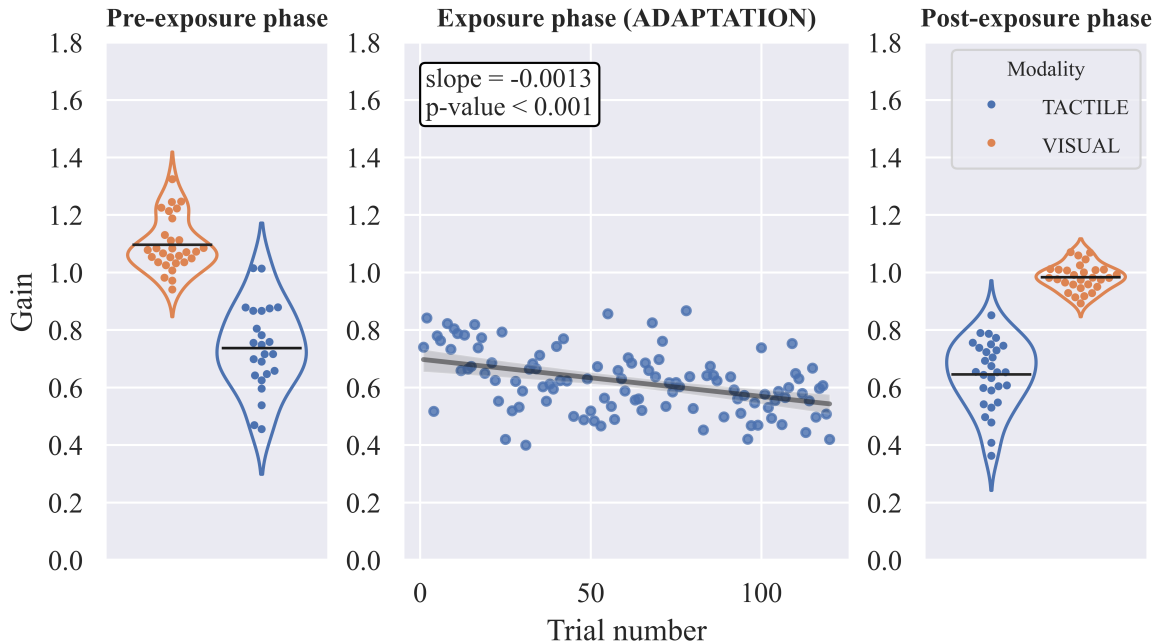
A. Middle finger estimated position across sessions and phases (N=15)



B. Middle finger estimated position across phases (N=21)

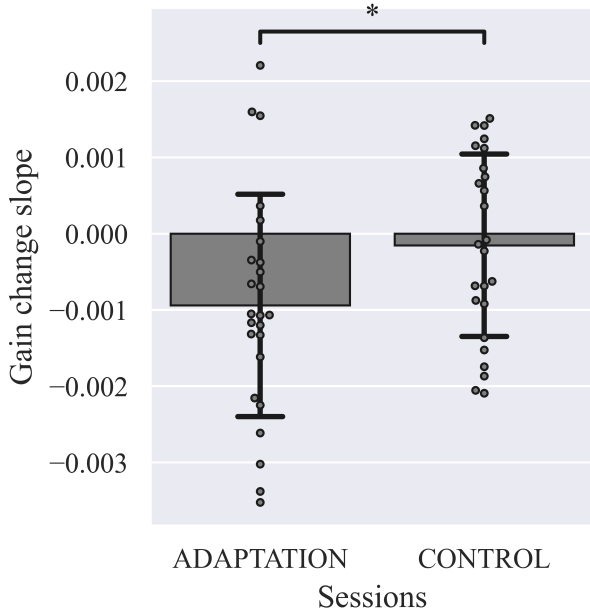


Saccadic gain (Participant 16, Experiment 2)

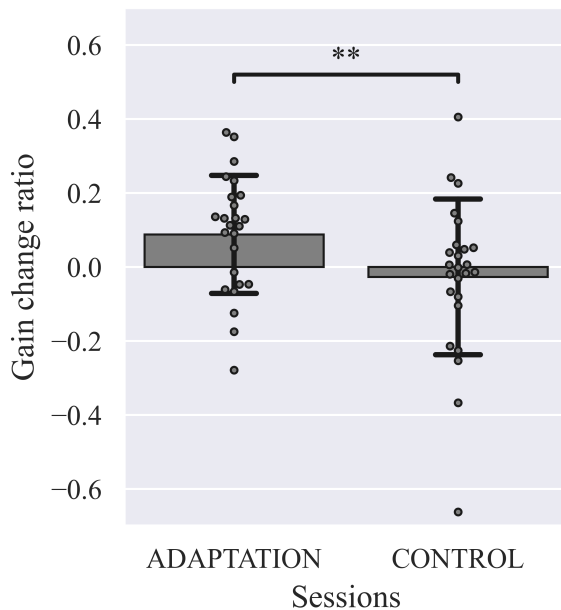


Tactile saccades (N=25)

A. Gain change in the Exposure phase



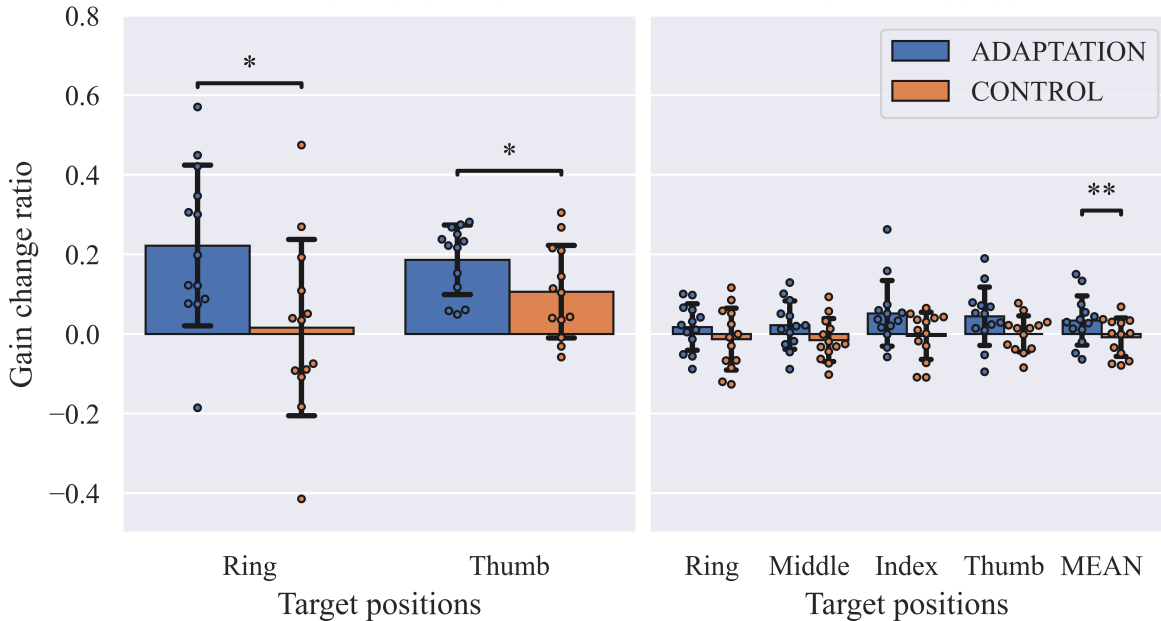
B. Pre- vs Post- exposure gain change



Gain change ratio (N=13 adapted participants)

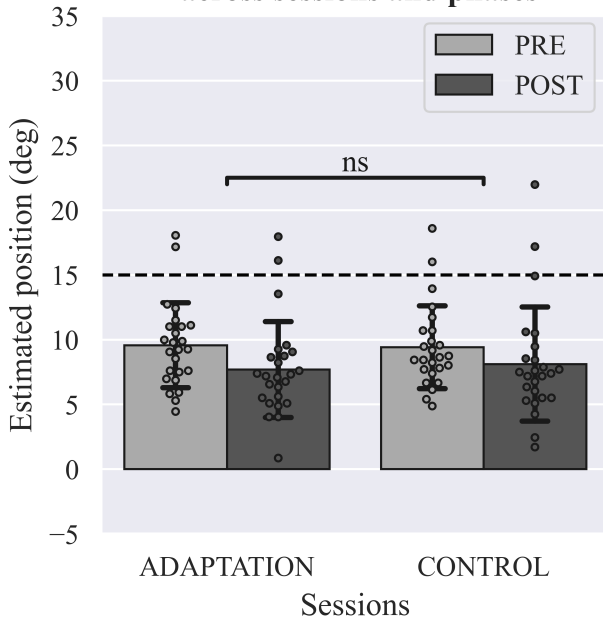
A. Tactile saccades

B. Visual saccades

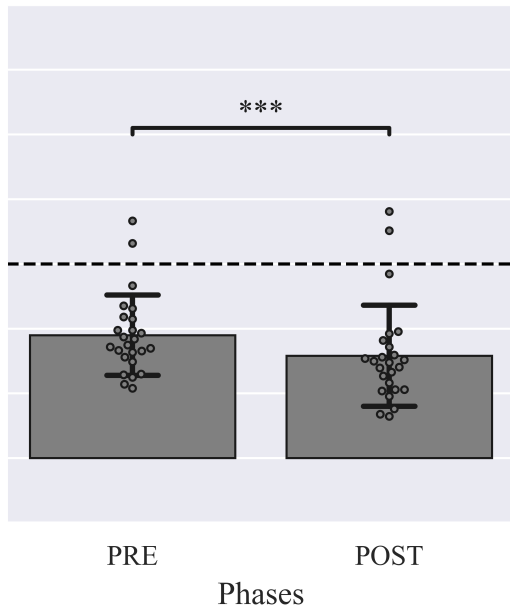


Proprioceptive drift (N=25)

A. Middle finger estimated position across sessions and phases

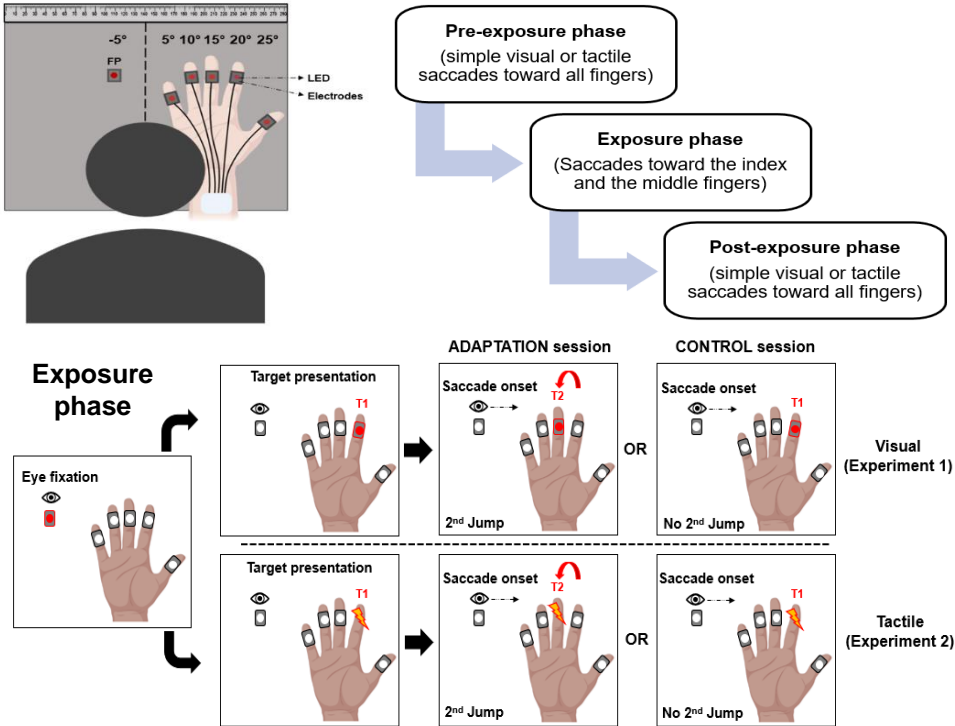


B. Middle finger estimated position across phases

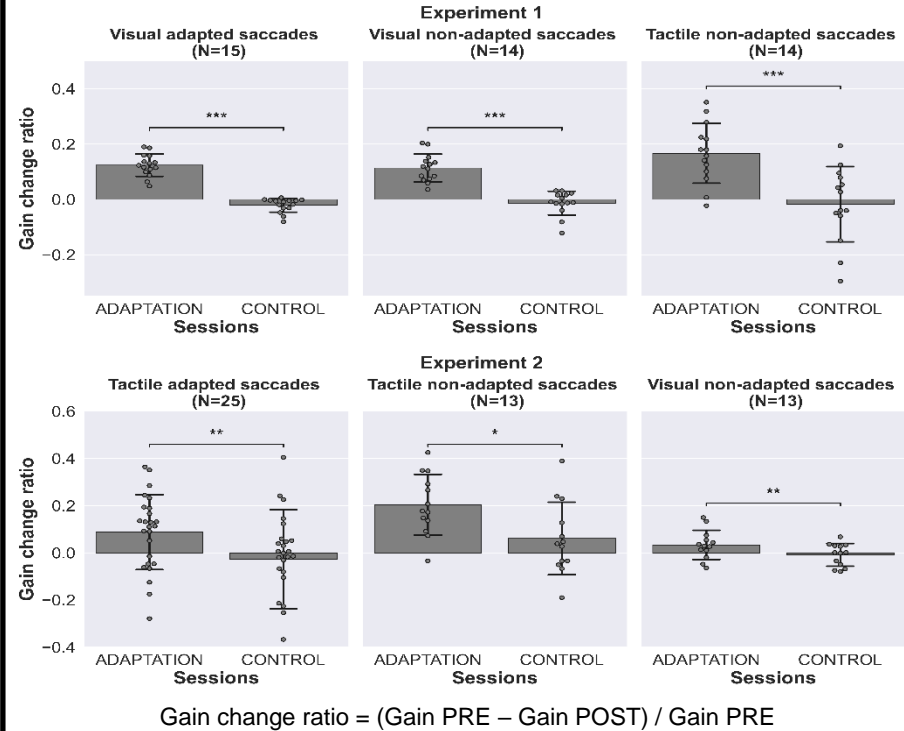


Saccades to both vision and touch are modified following adaptation but cross-modal transfers are asymmetrical.

METHODS



OUTCOME



CONCLUSION

- *Visual saccade adaptation transfers to tactile saccades.*
- *Tactile saccades show adaptive changes using the double-step target paradigm.*
- *Tactile saccade adaptation : 1. generalizes to nearby non-adapted locations, 2. transfers partly to visual saccades.*