

1 Seeing our hand or a tool during visually-guided actions: different
2 effects on the somatosensory and visual cortices

3

4 Benjamin Mathieu^{a*}, Antonin Abillama^{a*}, Simon Moré^a, Catherine Mercier^{b,c}, Martin
5 Simoneau^{b,c}, Jérémy Danna^a, Laurence Mouchnino^{a,d}, Jean Blouin^a

6

7 ^aLaboratoire de Neurosciences Cognitives (LNC), Aix-Marseille Université/ CNRS.
8 Marseille, France

9 ^bCentre interdisciplinaire de recherche en réadaptation et intégration sociale (CIRRIS) du
10 CIUSSS de la Capitale-Nationale, Québec, Québec, Canada

11 ^cFaculté de médecine, Université Laval, Québec, Canada

12 ^dInstitut Universitaire de France (IUF), Paris, France

13

14

15 * Co-first authors

16

17

18

19

20

21 Correspondance :

22 Benjamin Mathieu, Laboratoire de Neurosciences Cognitives, Aix-Marseille Université, 3
23 place Victor Hugo, 13003 Marseille, France

24 benjamin.mathieu@univ-amu.fr

25

26

27

28

29 Abstract

30 The processing of proprioceptive information in the context of a conflict between visual
31 and somatosensory feedbacks deteriorates motor performance. Previous studies have shown
32 that seeing one's hand increases the weighting assigned to arm somatosensory inputs. In
33 this light, we hypothesized that the sensory conflict, when tracing the contour of a shape
34 with mirror-reversed vision, will be greater for participants who trace with a stylus seen in
35 their hand (Hand group, n=17) than for participants who trace with the tip of rod without
36 seen their hand (Tool group, n=15). Based on this hypothesis, we predicted that the tracing
37 performance with mirror vision will be more deteriorated for the Hand group than for the
38 Tool group, and we predicted a greater gating of somatosensory information for the Hand
39 group to reduce the sensory conflict. The participants of both groups followed the outline of
40 a shape in two visual conditions. Direct vision: the participants saw the hand or portion of a
41 light 40 cm rod directly. Mirror Vision: the hand or the rod was seen through a mirror. We
42 measured tracing performance using a digitizing tablet and the cortical activity with
43 electroencephalography. Behavioral analyses revealed that the tracing performance of both
44 groups was similarly impaired by mirror vision. However, contrasting the spectral content
45 of the cortical oscillatory activity between the Mirror and Direct conditions, we observed
46 that tracing with mirror vision resulted in significantly larger alpha (8-12 Hz) and beta (15-
47 25 Hz) powers in the somatosensory cortex for participants of the Hand group. The
48 somatosensory alpha and beta powers did not significantly differ between Mirror and Direct
49 vision conditions for the Tool group. For both groups, tracing with mirror vision altered the
50 activity of the visual cortex: decreased alpha power for the Hand group, decreased alpha
51 and beta power for the Tool group. Overall, these results suggest that seeing the hand
52 enhanced the sensory conflict when tracing with mirror vision and that the increase of alpha
53 and beta powers in the somatosensory cortex served to reduce the weight assigned to
54 somatosensory information. The increased activity of the visual cortex observed for both
55 groups in the mirror vision condition suggests greater visual processing with increased task
56 difficulty. Finally, the fact that the participants of the Tool group did not show better
57 tracing performance than those of the Hand group suggests that tracing deterioration
58 resulted from a sensorimotor conflict (as opposed to a visuo-proprioceptive conflict).

59 Keywords : Electroencephalography, Proprioception, Sensory conflict, Vision, Sensory
60 gating, Body representation

61

62 **1. Introduction**

63 Hands and fingers can be moved with extraordinary precision, notably when interacting with
64 the external world. To successfully control movements with high spatial constraints, the brain
65 uses two main sources of feedback: visual and somatosensory. Although these feedbacks first
66 reach highly sensory-specific areas of the brain (e.g., the primary visual and somatosensory
67 areas), they rapidly converge at common integrative areas (e.g., posterior parietal cortex; see
68 Murray & Wallace, 2012 for a review). Importantly, the great adaptability of the sensorimotor
69 system enables visual and somatosensory information to be spatially (and temporally)
70 congruent. In other words, we see our hand where we feel it, and we feel our hand where we
71 see it. This sensory congruence is a keystone of our fine hand motor skills.

72 There are instances, however, where the congruence between hand visual and
73 somatosensory feedbacks is altered, such as when using a microscope or magnifying lenses.
74 In this context, motor performance is disrupted, most probably because the sensorimotor
75 system is fed with conflicting visual and proprioceptive information (Starch, 1910). An
76 interesting support for this hypothesis was provided by Balslev et al. (2004) who showed that
77 a reduction of hand proprioception induced by repetitive transcranial magnetic stimulations
78 (rTMS) of the somatosensory cortex, decreased the detrimental effect of incongruent visual
79 feedback on movement performance. In this novel visuomotor environment, the suppression
80 of somatosensory information would help reduce the sensory conflict, thereby improving
81 motor performance. Note that the results reported by Balslev et al. (2004) are also in line with
82 studies showing that mirror-reversed vision has little impact on the motor performance of
83 patients suffering from a loss of proprioception who trace the contour of a shape (Lajoie et al.,
84 1992; Miall & Cole, 2007).

85 Previous studies therefore provide clear evidence that processing proprioceptive
86 information is pernicious for controlling movements in the context of a conflict between
87 visual and proprioceptive feedbacks. The question nevertheless remains as to whether the
88 intensity of this conflict is modulated by the possibility/impossibility of seeing the effector
89 from which the conflicting proprioceptive inputs arise. For instance, because the hand
90 muscles are endowed with proprioceptive receptors, the sensory conflict could be enhanced
91 when our hand is visible compared to when we can only see a manipulated tool (e.g., a rod).
92 Indeed, with the sight of the hand, the brain receives visual and somatosensory hand afferents

93 that can be (more or less) directly compared. This context could facilitate detection, and
94 increase the strength, of the sensory mismatch. In this light, it is worth noting that seeing
95 one's body part has been shown to increase the weight assigned to the somatosensory inputs
96 (Kennett et al., 2001; Longo et al., 2011; Taylor-Clarke et al., 2002, 2004; Zhou & Fuster,
97 2000). Accordingly, we might expect a greater sensory conflict when tracing the contour of a
98 shape with a hand-held stylus than with a rod, which is devoid of somatosensory attributes.

99 Here, we tested this prediction by comparing the precision with which healthy human
100 participants traced the contour of a shape with either a stylus (Hand group) or with the tip of a
101 rod (Tool group) in two visual conditions: direct and mirror-reversed vision (i.e., Direct and
102 Mirror conditions, respectively). Based on the hypothesis of a greater sensory conflict when
103 seeing the hand, the tracing performance should be greater for the Tool group than for the
104 Hand group in the Mirror condition. Predictions can also be made regarding the activity of the
105 somatosensory cortex for the Hand and Tool groups when tracing with incongruent visual
106 feedback. Indeed, Bernier et al. (2009) have observed that participants tracing a shape with
107 incongruent visual feedback exhibited a suppression of somatosensory inputs compared to
108 when they were tracing with normal vision. In their study, the somatosensory suppression was
109 evidenced by the decreased evoked potentials within the somatosensory cortex following the
110 electric stimulations of the median nerve at the wrist. Functionally, this suppression of
111 somatosensory information would reduce the sensory conflict (as for the rTMS over the
112 somatosensory cortex, Balslev et al., 2004). Supporting the hypothesis that the sight of the
113 hand increases the visuo-proprioceptive conflict, a gating of somatosensory inputs was not
114 observed by Lebar et al. (2017) when the incongruent hand visual feedback was provided
115 through a digitized dot image (i.e., devoid of somatosensory attributes). In this visual context,
116 Lebar et al. (2017) found a decreased power of beta oscillations (15-25 Hz) in the
117 somatosensory cortex which, on the contrary, reflected greater cortical activity (see Kilavik et
118 al. (2013) for a review on cortical beta oscillations).

119 Because alpha and beta band powers are respectively considered as being inversely
120 related to the levels of excitability (alpha) and processing (beta) of the somatosensory and
121 visual cortices (Anderson & Ding, 2011; Cheyne et al., 2003; Pfurtscheller & Lopes da Silva,
122 1999), we predicted that only the Hand group would show greater alpha (8-12 Hz) and beta
123 (15-25 Hz) powers in the somatosensory cortex when tracing with mirror-reversed vision
124 compared to a context with normal vision.

125

126 **2. Method**

127 *2.1. Participants*

128 Thirty-four volunteers participated to the study. They all had normal or corrected-to-normal
129 vision and were right-handed according to Edinburgh Handedness Inventory (mean laterality
130 score: 77.15 ± 15.4). Informed written consent was obtained before running the experiment.
131 The protocols and procedures were in accordance with the 1964 Declaration of Helsinki and
132 were approved by the CERSTAPS ethic committee. The experiment lasted ~2 hours.

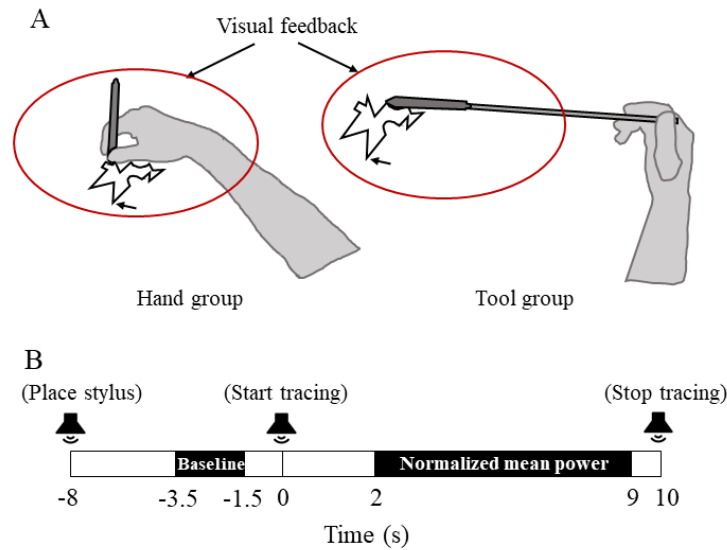
133

134 *2.2. Procedure*

135 The participants were seated in a darkened room in front of an irregular small shape (see Fig.
136 1) laid on a digitizing tablet. The shape was printed in white on a black background, and was
137 lit by small LEDs directly above the tablet. It was made of 16 thin (0.5 mm) straight lines and
138 1 curved line whose lengths varied between 8 and 36 mm (total perimeter 36.7 cm). We
139 deliberately chose a complex template (i.e., with many corners) as it has been shown to
140 increase the complexity of the mirror-drawing task (Miall & Cole, 2007). The task consisted
141 of tracing the outline of this shape as precisely as possible with a digitizing stylus (weight 18
142 grams). The participants of the Hand group ($n = 17$; 8 women; mean age: 23.7 ± 3.7 years)
143 held the stylus in their right hand. The participants of the Tool group ($n = 17$) held in their
144 right hand the extremity of a light aluminum rod (40 cm, 17 grams) on the opposite end of
145 which the stylus was firmly fixed. The data of 2 participants had to be discarded because of
146 technical problems. Thus, for the Tool group, the analyses were performed on 15 participants
147 (8 women, mean age: 23.9 ± 2.8 years).

148 Participants of both groups followed the shape in two visual conditions. In the Direct
149 condition, the participants of the Hand group could directly see their hand while participants
150 of the Tool group could see only about the most extreme half of the rod (see Fig. 1A). For this
151 latter group, vision of the arm and the hand was occluded with a black shield. In the Mirror
152 condition, a mirror (Comair Cabinet Executive mirror, diameter 28 cm) was located to the
153 front left of the participant with an inclination of 45° relative to the subject's frontal plane. In
154 this condition, only the hand (Hand group) or the extremity of the rod (Tool group) could be
155 seen through the mirror. For both groups, direct vision of the right upper limb was occluded
156 with a black shield.

157



158

159 Figure 1. A. Sketches of the visual feedback available during the tracing for the participants of
160 the Hand (left) and Tool (right) groups. The starting position is indicated by the arrows. B.
161 Temporal organization of the trials. For each frequency band (i.e., alpha, beta), the signal
162 computed between 2 s and 9 s after the imperative go signal (i.e., at 0 s) was expressed as a
163 change of power (dB) with respect to a 2-s mean window baseline recorded before the start
164 tracing signal.

165

166

167 Participants of each group performed 40 trials of 18 s duration in both the Direct and
168 Mirror conditions. The temporal organization of every trial is depicted in Fig. 1b. At the
169 beginning of each trial, due to software-related constraints, the tip of the stylus had to be held
170 ~5 cm above the digitizing tablet. For the first trial, all participants held the stylus above the
171 position on the shape indicated by an arrow in Fig. 1a. For the subsequent trials, the
172 participants held the stylus above the position reached at the end of the previous trial. For
173 each trial, with the stylus at these starting positions, the participants sent the verbal message
174 “ready” to the experimenter. Then, on hearing a beep, the participants had to lower the tip of
175 the stylus onto the tablet and to hold the hand and stylus at this position (even if inadvertently
176 the stylus was not on the intended point on the shape). A second beep issued 8 s after the first
177 one served as an imperative signal to start tracing the contour of the shape. A final beep
178 occurring 10 s after the second indicated the end of the trial. All trials were thus composed of
179 a 8 s static phase and of a 10 s dynamic phase. The small size of the shape allowed
180 participants of both groups to perform the tracing using only finger and wrist movements. The

181 participants were instructed that whenever the stylus (or tip of the rod) left the outline of the
182 shape, they should bring it back to the point where it left the shape before continuing the
183 tracing. Participants were required to hold the stylus (Hand group) or the rod (Tool group)
184 with a minimal force and to perform very slow movements. An experimenter demonstrated
185 suitable tracing speeds prior to the experiment and corrective instructions were provided
186 between trials when necessary. Slow movements reduced the muscular activation and the
187 speed of the ocular pursuit which can both contaminate EEG recordings. Offline analyses
188 showed that the mean tracing velocities for the Hand group were 0.54 ± 0.21 cm/s (Direct
189 vision) and 0.47 ± 0.12 cm/s (Mirror vision), and for the Tool group, 0.50 ± 0.11 cm/s (Direct
190 vision) and 0.49 ± 0.11 cm/s (Mirror vision). A 2 x 2 ANOVA did not reveal neither a
191 significant effect of Vision ($F_{1,31} = 2.77$; $p > 0.05$) and of Group ($F_{1,31} = 0.03$; $p > 0.05$), nor a
192 significant Vision x Group interaction ($F_{1,31} = 1.72$; $p > 0.05$).

193 Our goal was to investigate the effect of seeing one's hand on the processing of
194 somatosensory information in the context of incongruence between visual and somatosensory
195 feedbacks. Therefore, several elements of the experimental protocol aimed to limit adaptation
196 to the sensory incongruence. The shape had a complex geometry, and the participants had to
197 start their tracing from the position reached in the previous trial in order to avoid an overly
198 repetitive pattern of the layout. The exposure duration to the sensory conflict was only of
199 6'40'' (i.e., 40 (trials) x 10 s (dynamic phase duration)). Moreover, after every 5 trials,
200 participants were asked to directly watch their hand moving freely. For reasons of
201 homogeneity between the conditions, this procedure was also followed in the Direct
202 condition.

203 Participants of both groups were first tested in the Direct condition. Note that contrary
204 to protocols specifically designed to investigate the modification of the internal representation
205 of the body when using tools (e.g., lengthening of the represented arm length, Martel et al.,
206 2016), the present protocol incorporated features to minimize such modifications in the Tool
207 group (e.g., shape positioned in the proximal space, view of the hand moving without the tool
208 every 5 trials).

209

210 2.3. *Data acquisition and processing*

211 2.3.1. *Behavior*

212 The X and Y coordinates of the tip of the digitizing stylus were recorded using a Wacom
213 Intuos 4L tablet (spatial resolution of <1mm, 100 Hz recording frequency). The tracing

214 performance was assessed by computing a distance/segment index (referred to as distance
215 ratio) which corresponded to the ratio between the total distance covered by the tip of the
216 stylus and the total length of all drawn segments. The closer this ratio was to 1, the more
217 accurate was the tracing. We also computed the number of reversals in direction when the
218 participants traced the contour of the shape. This was done by calculating and then averaging
219 the number of zero-line crossing in the X and Y velocity of the tracing. The smaller the
220 number of zero-line crossing, the smoother the tracing.

221 As it can be seen in Fig. 2, both assessments of the tracing performance showed
222 substantial performance deterioration in the Mirror condition for both the Hand and Tool
223 groups. However, performance improved across the first 20 trials before reaching a plateau.
224 In this light, all analyses (i.e., performance, EMG, EEG) were performed using the first 20
225 EEG artifact-free trials (see below). This series of trial is more likely to better characterize
226 cross-modal conflict between visual and sensorimotor inputs.

227

228 2.3.2. *Electromyography (EMG)*

229 The activity of the muscles acting on the wrist and fingers of the right arm was recorded to
230 control for potential large differences of EMG activities between groups and vision
231 conditions. This verification is particularly relevant in the context of the present study
232 because the decrease of proprioception, which is normally observed during movements
233 (Rushton et al., 1981; Seki & Fetz, 2012) is heightened during strong muscle contractions
234 (Staines et al., 1997).

235 EMG activity was recorded using a Bortec AMT-8 system (Bortec Biomedical, Calgary,
236 Canada; 250 Hz sampling frequency). We recorded the activity of the flexor of the thumb
237 (flexor pollicis brevis) and the first dorsal interosseous muscles, which are both involved in
238 the precision grip. These activities were recorded bipolarly with Ag-AgCl electrodes placed 2
239 cm apart after cleaning the skin with alcohol. Activity of the flexor and extensor muscles of
240 the wrist was recorded with electrodes placed over the wrist extensor bundle (top of the arm)
241 and over the flexor bundle (bottom of the arm). With this wide configuration, both flexion and
242 extension of the wrist can be recorded with a single pair of electrodes (see Criswell & Cram,
243 2011, p. 311). An electrode placed above the right epicondyle was used to reference all EMG
244 recordings.

245 As expected, due to the slow speed of the tracing, the EMG recordings showed tonic
246 activities without clear burst pattern. To compare the EMG activity across groups and

247 conditions, we rectified and integrated the 3 sets of EMG data over both the static phase (-3.5
248 s to -1.5 s) and the dynamic phase (2 s-9 s) for each valid trial (i.e., without EEG artifact). The
249 integrals (i.e., iEMG) obtained in the dynamic phase were expressed as a percentage of the
250 iEMG obtained in the static phase. Then, we computed the mean % iEMG of the 3 set of
251 EMG data for each group (Hand, Tool) and vision condition (Direct, Mirror).

252

253 2.3.3. *Electroencephalography (EEG)*

254 EEG activity was recorded continuously using a cap of 64 Ag/AgCl electrodes at a 1024 Hz
255 sampling frequency (ActiveTwo system, Biosemi, Amsterdam, The Netherlands). The
256 activities recorded by electrodes placed near each external canthus, and electrodes placed
257 below and above the left eye were used to detect blinks and saccades. The EEG data were
258 pre-processed using BrainVision Analyzer2 software (Brain Products, Gilching, Germany).
259 EEG signals were referenced against the average of the activities recorded by all electrodes.
260 The effect of ocular artifacts on the EEG recordings, related to blink and saccades, was
261 reduced using the method of Gratton et al. (1983).

262 For each vision condition, the EEG data were segmented and synchronized with respect
263 to the occurrence of the beep which indicated the beginning of the dynamic phase. Note that
264 due to very slow tracing movements, this segmentation could not be made using kinematic or
265 EMG data within a reasonable temporal margin of error. The recordings were visually
266 inspected and epochs still presenting artifacts were rejected. These trials were replaced by
267 those occurring between the 20th and 27th trials, so that 20 epochs were analyzed for each
268 participant.

269 We used Brainstorm software to estimate the cortical sources of the EEG signals (Tadel
270 et al., 2011). The inverse problem was resolved using the minimum-norm technique and
271 unconstrained dipole orientations. A boundary element method (symmetric BEM, Gramfort et
272 al., 2010) was used to compute the forward models on the anatomical MRI Colin 27 brain
273 template (15,000 vertices) from the Institut Neurologique de Montréal. We opted for a model
274 with three realistic layers (scalp, inner skull, and outer skull) which yields more accurate
275 solutions compared to a simple three concentric spheres model (Sohrabpour et al., 2015).

276 Single-trial EEG data were transformed in the time-frequency domain using the Hilbert-
277 filter method. This method is particularly suited for long times-series such as those analyzed
278 in the present study (Cohen, 2014). The analyses of the time frequency distribution were
279 performed in the source space. We extracted the amplitude envelope (i.e., power) of alpha

280 (mean 8-12 Hz, steps of 0.5 Hz) and beta (mean 15-25 Hz, steps of 1 Hz) bands over both the
281 static and dynamic phases of the trials. For each frequency band, the power computed during
282 the dynamic phase was normalized with respect to the static baseline period (-3.5 to -1.5 s)
283 and then averaged, for each group and condition, between all trials over the 2-9 period after
284 the imperative go (“beep”) signal (see Fig. 4). The selected baseline time window was
285 deliberately chosen away from the beep indicating the onset of the static phase, at which time
286 the participants had to lower the stylus on the digitizing tablet (event that was most likely
287 followed by the cognitive appraisal of the stylus landing position). We indistinctly considered
288 increases of alpha and beta band power as a neurophysiological signature of a gating of
289 somatosensory and visual inputs. Decreases of these low and medium frequency bands rather
290 reflecting a facilitation of these sensory inputs. The analyses were limited to the left
291 hemisphere, which was contralateral to the moving (right) hand.

292 Specific analyses were performed to get insight into the dynamics of the visual
293 feedback-related changes of alpha and beta band powers in the somatosensory and visual
294 cortices. This was done by first identifying from the BEM mesh, and for each participant, the
295 vertex within the somatosensory or visual cortex that exhibited the strongest significant effect
296 (i.e., smallest negative t value or greatest positive t value, see fig. 4) when contrasting the
297 sources of the baseline-normalized alpha and beta band powers estimated in the Direct and
298 Mirror conditions (group analyses, see statistical analyses below). Then, the alpha and beta
299 band powers computed at this vertex in the Mirror condition were extracted from -3.5 s to 9 s,
300 where 0 s indicates the imperative signal to start the tracing movement. Two ways were used
301 to express the time courses of alpha and beta band changes. We computed the mean baseline-
302 normalized power between participants and computed, for each participant, the cumulative
303 integral of the baseline-normalized power. Monotonic increasing or decreasing of the
304 cumulative integral indicates that the increase or decrease of power is preserved throughout
305 the tracing. This computation provides smoother data than the baseline-normalized power and
306 is particularly relevant for appraising the between-participants variability.

307 The EEG data recorded in the electrode space was also transformed in the time-
308 frequency domain using the Hilbert-filter method. This transformation was performed after
309 applying a spatial filter (surface Laplacian, Perrin et al., 1989; order term of the Legendre
310 polynomial=10, smoothing=1e-5, m=4) thereby increasing the topographical selectivity by
311 filtering out volume-conducted potentials (Law et al., 1993; Nunez & Srinivasan, 2006).
312 Analyzing the spectral content of the EEG signals recorded at C3 and C5 electrodes allowed
313 to directly compare, between the Hand and Tool groups, the effect of tracing with mirror-

314 reversed vision on the alpha and beta band powers over the somatosensory cortex (i.e. the key
315 region for testing the effect vision of the hand on somatosensory processes). Indeed, as shown
316 in Fig. 4, electrodes C3 and C5 respectively overlay the left primary (SI) and secondary (SII,
317 upper bank of the Sylvian fissure) somatosensory cortices.

318 2.4. *Statistical analyses*

319 For each Group and Vision conditions, the evolution of the tracing-related variables (i.e.,
320 distance/segment index, number of zero speed crossing, iEMG) over the first valid 20 trials
321 was assessed by computing their mean values over 4 bins of 5 consecutive trials. These
322 variables were submitted to separate 2 (Group: Hand, Tool) x 2 (Vision: Direct, Mirror) x 4
323 (Bin: Bin₁₋₅, Bin₆₋₁₀, Bin₁₁₋₁₅, Bin₁₆₋₂₀) analyses of variance (ANOVA), with repeated
324 measurements on the Vision and Bin factors. Significant effects were further analyzed using
325 Newman-Keuls post-hoc tests. The alpha level was set at 0.05 for all statistical contrasts.

326 For each group, we assessed the effect of the sensory incongruence on the topography
327 and amplitude of the normalized alpha and beta band power by contrasting the sources of
328 alpha and beta band powers estimated in the Direct and Mirror conditions using t-tests
329 (significance threshold $p < 0.05$, uncorrected).

330 Finally, to directly compare the effect of the sensory incongruence on somatosensory
331 alpha and beta band powers between the Hand and Tool groups, we subtracted for both the C3
332 and C5 electrodes and for all participants of each group, the normalized power computed in
333 the Mirror condition from the normalized power computed in the Direct condition. The
334 differences (hereafter referred to as Δ Mirror-Direct) were submitted to independent T-tests
335 (significance threshold $p < 0.05$).

336

337

338 **3. Results**

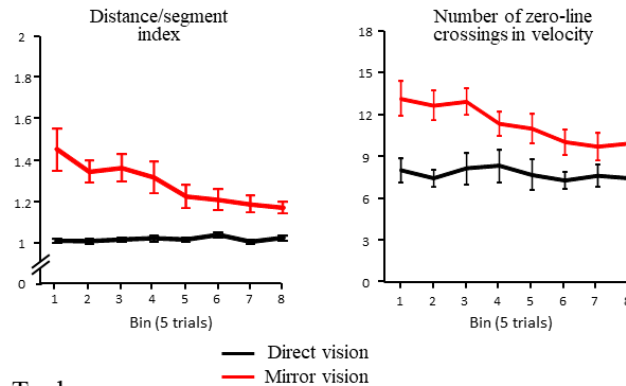
339 3.1. *Tracing performance*

340 The evolution of the distance/segment index and of the number of zero speed crossing
341 throughout the 40 trials are shown in Fig. 2 for both the Hand and Tool groups. Overall, the
342 participants of both groups accurately traced the shape with Direct vision but substantially
343 decreased their tracing accuracy with mirror-reversed vision. Figure 2 shows improvement in
344 tracing performance over the first 20 trials before reaching a relative stable plateau,
345 suggesting that the sensory conflict was perceived greater in the first half of the trials.
346 Because our main goal was to compare the response of the somatosensory cortex when

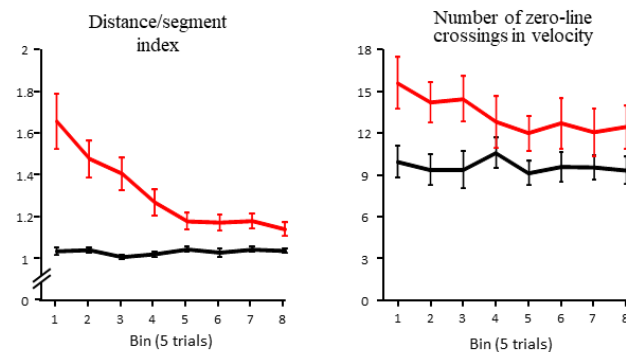
347 tracing a shape in the context of a visuo-proprioceptive conflict, all behavioral and
348 electrophysiological analyses presented below pertained to the first 20 trials (see methods for
349 exceptions).

350

A. Hand group



B. Tool group



351

352 Figure 2. Mean tracing performance over the course of the 40 trials for the Hand group (A)
353 and the Tool group (B). The trials are pooled into 8 bins of 5 consecutive trials. Left panels:
354 The tracing performance is expressed as the average total distance covered by the pen per
355 segment completed in every trial (distance/segment index). Right panels: Number of reversals
356 in direction of the stylus as expressed by the average number of zero-line crossings on the
357 velocity profiles per trial. Error bars: standard error of the mean.

358

359 The distance/segment index was significantly greater in the Mirror (mean: 1.41 ± 0.48)
360 than in the Direct (mean: 1.02 ± 0.04) conditions (main effect of Vision: $F_{1,31} = 63.65$; $p <$
361 0.001 ; $\eta^2 = 0.68$). For this variable, the ANOVA did not reveal a significant effect of Group
362 ($F_{1,31} = 0.78$; $p > 0.05$), but revealed a significant Vision x Bin interaction ($F_{1,31} = 6.89$; $p <$
363 0.001 ; $\eta^2 = 0.19$). Post-hoc analyses confirmed the decrease of the distance ratio over the

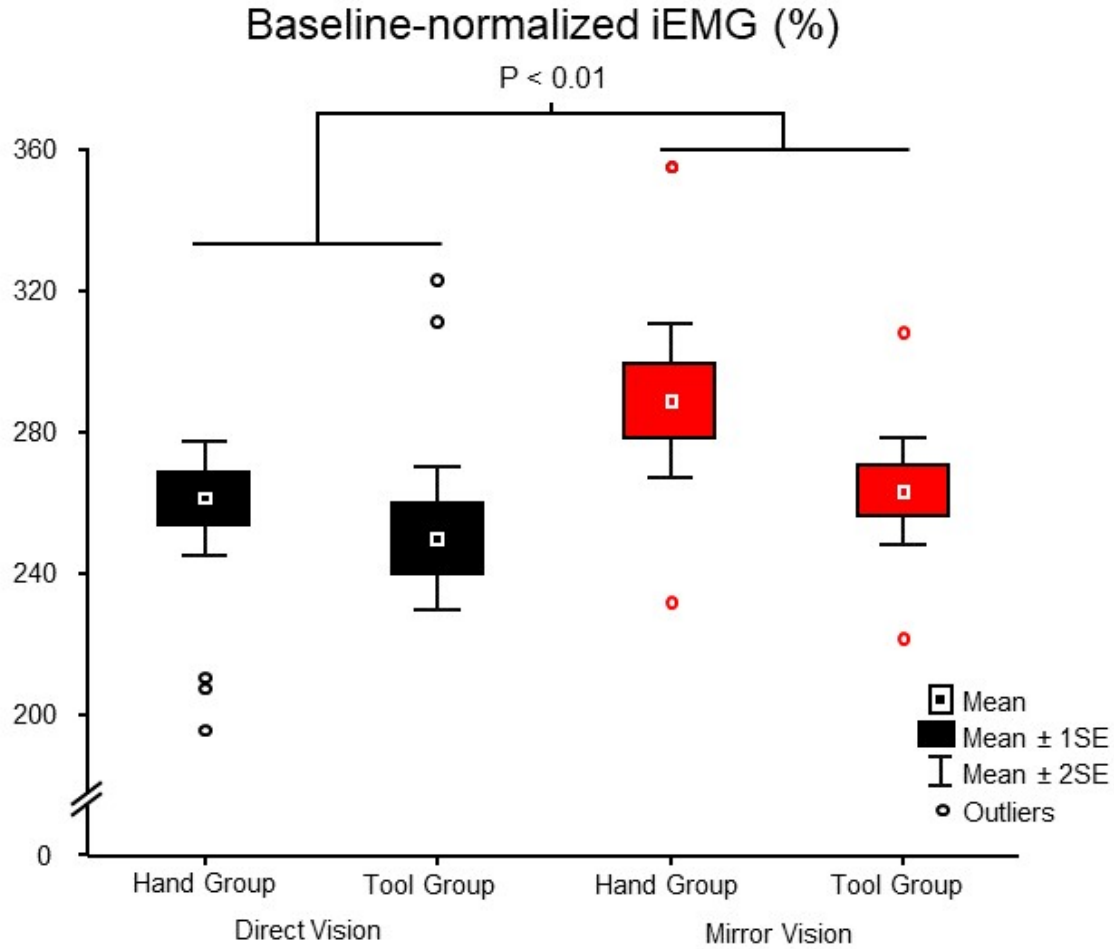
364 trials with mirror-reversed vision, but more importantly, they showed that the distance ratio
365 computed in the last series of 5 trials (i.e., bin no. 4) was still significantly greater than the
366 distance ratio computed in all bins of the Direct condition (all p s < 0.05).

367 The number of zero speed crossing was also significantly greater in the Mirror (mean:
368 13.44 ± 5.04) than in the Direct (8.92 ± 3.68) conditions (main effect of Vision: $F_{1,31} = 44.04$;
369 $p < 0.001$). For this variable, the ANOVA did not reveal neither a significant effect Group
370 ($F_{1,31} = 1.51$; $p > 0.05$), nor a significant Vision x Bin interaction ($F_{1,31} = 2.38$; $p > 0.05$).

371

372 3.2. *EMG recordings*

373 Figure 3 shows the iEMG, computed from the recordings of the forearm and hand muscles
374 during the tracing, normalized to the iEMG computed before starting the tracings. The figure
375 shows that the iEMG was ~200-300% greater during the tracing compared the static period.
376 The ANOVA revealed that the normalized iEMG was significantly greater in the Mirror
377 condition (mean: $278\% \pm 40$) than in the Direct condition (mean: $257\% \pm 34$) ($F_{1,31} = 11.05$; p
378 < 0.005 ; $\eta^2 = 0.29$). However, the effect of Group ($F_{1,31} = 2.26$; $p > 0.05$), the interaction
379 between Vision and Group ($F_{1,31} = 1.31$; $p > 0.05$) and the interaction between Vision and Bin
380 ($F_{1,31} = 0.12$; $p > 0.05$) were not significant. Therefore, if different spectral contents of cortical
381 neural oscillations were to be found between the Hand and Tool groups, they would unlikely
382 result from different muscular activities (see Staines et al., 1997 for the effect motor
383 contractions amplitude on the gating of somatosensory inputs). The increased hand muscle
384 activities observed with mirror-reversed vision could be due to the greater number of
385 reversals in direction when tracing the contour of the shape with incongruent vision (Fig. 3).



386

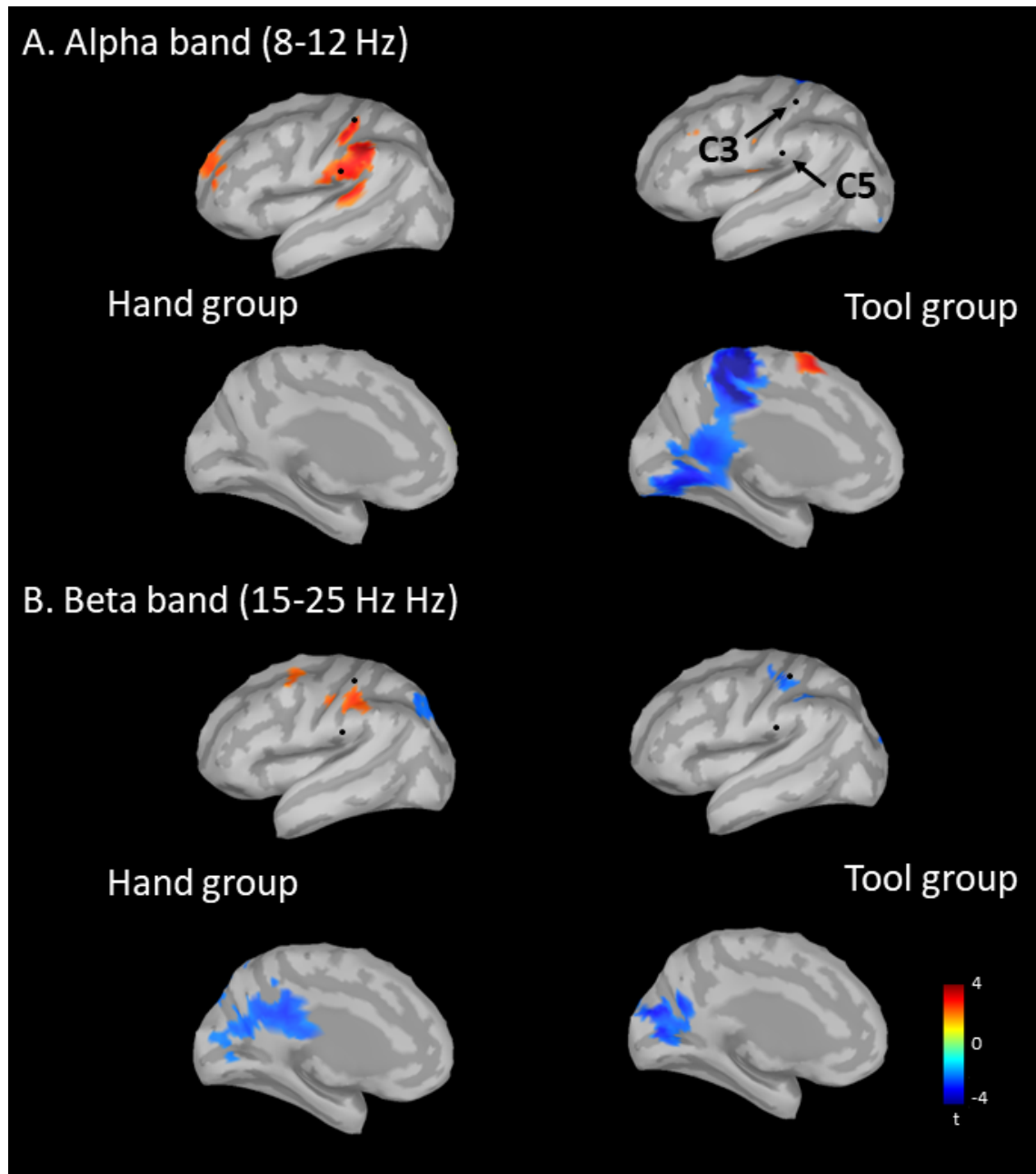
387 Figure 3. Baseline-normalized iEMG for the Hand and Tool groups computed in the Direct
388 and Mirror conditions.

389

390 3.3. EEG data

391 Figure 4 shows the statistical maps of alpha and beta band power resulting from the contrast
392 Mirror vs Direct conditions for both the Hand and Tool groups. Warm colors indicate that
393 alpha and beta band powers were significantly greater in the Mirror condition than in the
394 Direct condition. If observed in sensory areas, warm colors would therefore reflect a relative
395 decrease in weight assigned to the inputs pertaining to these areas when tracing with mirror-
396 reversed vision. Cold colors indicate the opposite pattern. Remarkably, the significant
397 differences resulting from the contrasts Mirror vs Direct conditions were largely
398 circumscribed to the somatosensory and visual areas for the Hand group, and to visual areas
399 for the Tool group.

400



401

402 Figure 4. Statistical maps (source space, left hemisphere) of alpha (A) and beta (B) powers
403 resulting from the contrast Mirror vs Normal conditions for both the Hand (left panels) and
404 Tool (right panels) groups. The position of the C3 and C5 electrodes are shown on the side
405 views. These electrodes overlay the left somatosensory cortex (i.e., contralateral to the tracing
406 hand). The signals recorded at these electrodes were used to compare the effect of the visual
407 conditions (i.e., Direct, Mirror) between the Hand and Tool groups (see Fig. 5).

408

409

410 3.3.1. *EEG data: Somatosensory cortex*

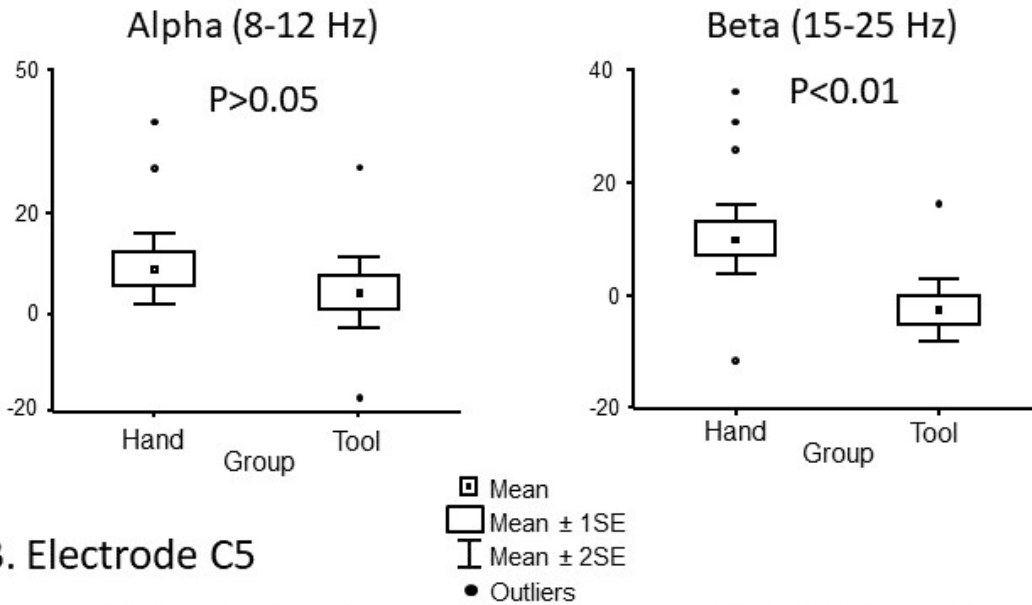
411 For the Hand group, alpha band power was significantly greater when tracing with mirror-
412 reversed vision in areas identified by the source analyses as the primary (SI) and the
413 secondary (SII, i.e. upper bank of the Sylvian fissure) somatosensory cortices (Fig. 4a). Beta
414 band power was also significantly greater with incongruent visual feedback in SI (Fig. 4b).
415 For the Tool group, alpha and beta band powers computed in the somatosensory cortex were
416 strikingly alike between the Mirror and Direct conditions. The statistical map only revealed a
417 significantly smaller alpha band power in a small area of SI (Fig. 4a).

418 Alpha and beta band powers recorded at C3 and C5 electrodes were also compared
419 between Groups and Vision conditions over the same time windows as the analyses in the
420 source space. These electrodes overlay the left postcentral region (Koessler et al., 2009, see
421 also Fig. 4) which was contralateral to the tracing hand. T-tests revealed that the Δ Mirror-
422 Direct beta ($t(30) = 3.01$; $p < 0.01$; $d = 0.95$) and the Δ Mirror-Direct alpha ($t(30) = 2.50$; $p <$
423 0.01 ; $d = 0.83$) significantly differed between groups at electrode C3 and C5, respectively
424 (Fig. 5). Importantly, for the Hand group, the Δ Mirror-Direct beta value (electrode C3) was
425 positive (mean = 9.87 ± 12.77) and was significantly different from 0 (comparison to a
426 standard (i.e., 0); $p < 0.01$). Likewise, for the Hand group, the Δ Mirror-Direct alpha value
427 (electrode C5) was positive (mean = 9.70 ± 18.79) and also significantly differed from 0 ($p <$
428 0.05). However, the Δ Mirror-Direct alpha (C3) and the Δ Mirror-Direct beta (C5) did not
429 significantly differ between groups ($t(30) = 0.93$; $p > 0.05$ and $t(30) = 1.23$; $p > 0.05$, for C3
430 and C5, respectively). For the Tool group, the Δ Mirror-Direct alpha and beta bands computed
431 at electrodes C3 and C5 did not significantly differ from zero ($p > 0.05$).

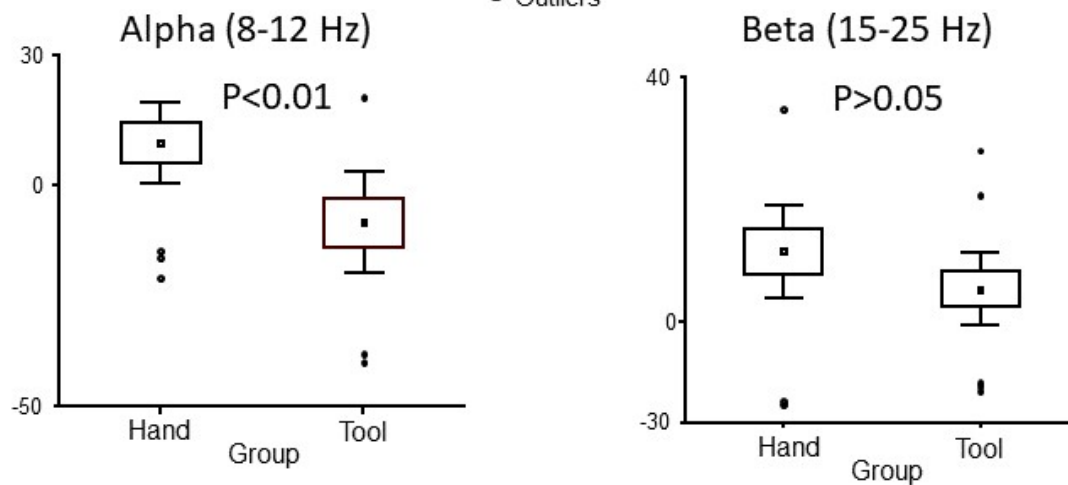
432

433

A. Electrode C3



B. Electrode C5



434

435 *Figure 5. Comparison between the Δ Mirror-Normal (alpha and beta, expressed in signal*
436 *units²/Hz) computed at electrode C3 (A) and electrode C5 (B) for the Hand and Tool groups.*
437 *These electrodes overlay the left sensorimotor cortex (see Fig. 4). The significant effect of*
438 *Group was preserved at electrode C3 ($t(25) = 3.25$; $p < 0.005$) and at electrode C5 ($t(24) =$*
439 *3.18; $p < 0.005$) when performing the tests after removing the outliers.*

440

441 3.3.2. EEG data: Visual cortex

442 The power within alpha and beta bands computed in the medial visual cortex was also altered
443 when tracing with mirror vision. In contrast to what was observed in the somatosensory

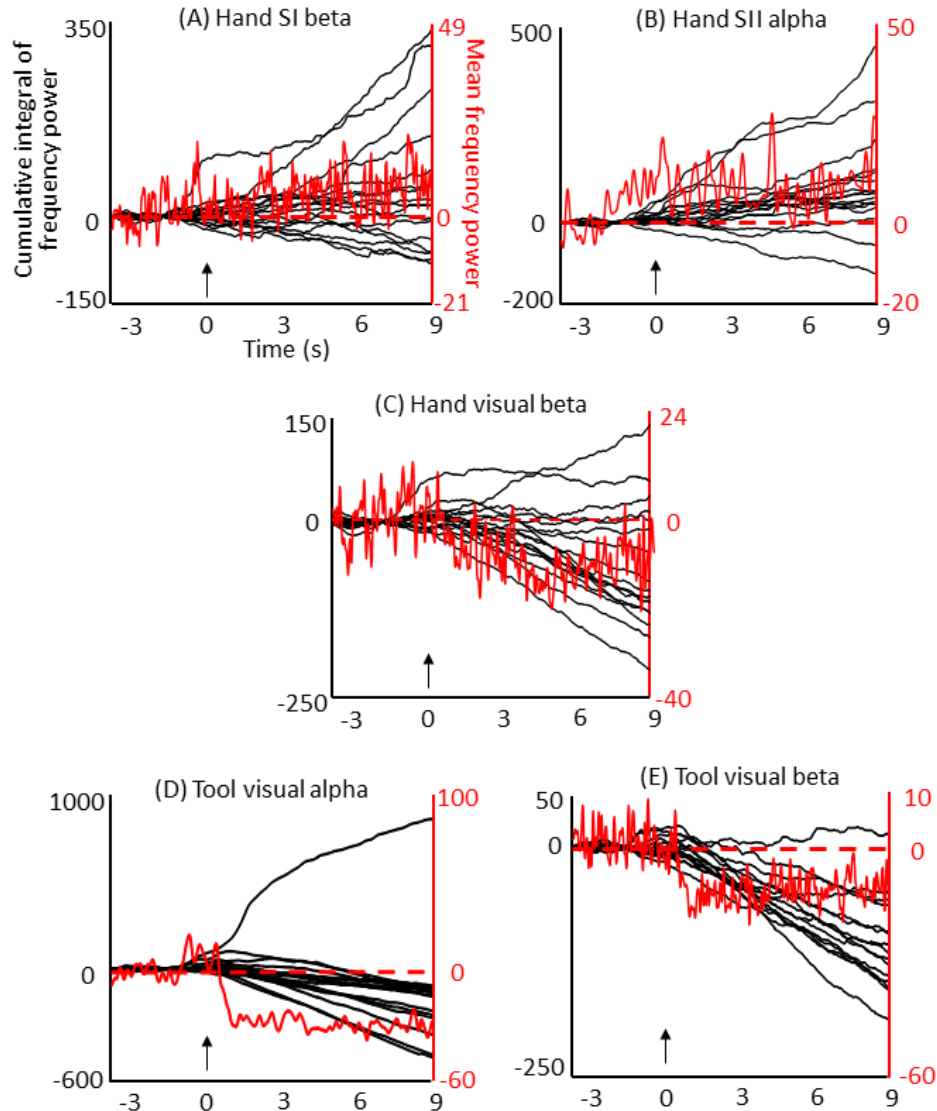
444 cortex, the bias in the visual feedback led to decreases in alpha and beta band powers in visual
445 areas (Fig. 4). This suggests a facilitation of visual feedback with mirror-reversed vision.
446 However, the effect of the incongruent visual feedback on the neural oscillations appeared
447 more pronounced for the Tool group than for the Hand group. Indeed, the statistical maps
448 showed significant smaller power in the Mirror condition in regions estimated by sources
449 analyses as the lingual gyrus (alpha), the medial parietal cortices (alpha) and the cuneus
450 (beta). For the Hand group, the statistical maps only revealed significantly smaller beta band
451 power in the cuneus (Fig. 4). Note that because the effects of mirror-reversed vision occurred
452 in the medial visual cortex, the Δ Mirror-Direct alpha and beta band powers could not be
453 computed in the electrode space.

454 The contrast Mirror vs Direct also revealed smaller alpha band power in the Mirror
455 condition for the Tool group in a region identified as the anterior precuneus cortex.

456

457 3.4. *EEG data: dynamics of the changes of alpha and beta band powers*

458 Figure 6 provides an estimate of the dynamics of the increased in alpha and beta band powers
459 when the participants of the Hand and Tool groups traced the shape with mirror-reversed
460 feedback. Band powers were extracted from vertices within areas showing significant
461 contrasts between the Mirror and Direct conditions (i.e., SI, SII, cuneus, lingual gyrus, see
462 Fig. 4). The figure shows that the increased in power observed in the somatosensory cortex
463 (results obtained only for the Hand group) was more consistent in SII (alpha) than in SI (beta).
464 Indeed, 14 out of 17 participants showed an increase of alpha band power in SII when they
465 traced the shape in the Mirror condition while 10 participants showed an increased beta in SI.



466

467 Figure 6. Time course of the baseline-normalized alpha and beta powers. For each
468 participant, the powers (signal units²/Hz) were extracted from vertices within areas
469 showing, for either the Hand or the Tool groups, significant contrasts between the Mirror
470 and Normal conditions (see Fig. 4). The red traces represent the between-participants
471 mean powers. The black traces represent the cumulative integral of the baseline-
472 normalized power computed for each participant. The arrows indicate the start tracing
473 signal.

474

475

476 On the other hand, the decrease in alpha and beta band powers observed in the
477 visual cortex, when tracing with mirror-reversed vision, was more robust in the Tool

478 group compared to the Hand group; the power decreased in all participants except one.
479 Remarkably, the participant in the Tool group showing a larger increase in alpha band
480 power during mirror vision, also had the greatest number of zero-line crossings in tracing
481 velocity (i.e., worst tracing performer).

482 Together, these results are consistent with those issued from the statistical maps
483 (Fig. 4) that showed i) for the Hand group, a greater cluster exhibiting significant
484 increase in alpha band power sources localized in SII, and ii) for the Tool group, greater
485 clusters exhibiting significant decreases of alpha and beta band powers in the visual
486 cortex.

487

488

489 **4. Discussion**

490

491 We tested the hypothesis that the conflict between visual and arm proprioceptive inputs,
492 when tracing the contour of a shape with mirror-reversed vision, is greater when participants
493 see their hand during tracing. Contrasting the spectral content of the cortical oscillatory
494 activity in conditions with and without incongruent visual feedback (respectively Mirror and
495 Direct conditions), we observed increases of alpha and beta band powers in the
496 somatosensory cortex when participants had vision of their hand when tracing with mirror
497 vision (Hand group). In contrast, for participants tracing with the tip of a rod (i.e., without
498 hand visual feedback, Tool group), alpha and beta band powers in the somatosensory cortex
499 did not significantly differ between the Direct and Mirror conditions. There is a consensus
500 that increases in alpha and beta band powers respectively correspond to a decrease in cortical
501 excitability and processing (Anderson & Ding, 2011; Cheyne et al., 2003; Kilavik et al., 2013;
502 Pfurtscheller & Lopes da Silva, 1999). In this light, the changes of alpha and beta band
503 powers observed in the somatosensory cortex imply a suppression of arm somatosensory
504 information. The fact that only the participants of the Hand group showed a gating of arm
505 somatosensory inputs with mirror vision suggests that seeing the hand enhanced the visuo-
506 proprioceptive conflict. Altered visual feedback, however, deteriorated tracing performance
507 similarly in both the Hand and Tool groups. The results showed by the participants of the
508 Tool group suggest that their altered performance with mirror vision essentially stemmed
509 from a sensory-motor conflict (rather than from a visuo-proprioceptive conflict, see below).

510 Moving our arm or an object when seen through a mirror creates a mismatch between
511 the movement-related information carried by the visual and proprioceptive systems.

512 Conceptually, this mismatch prevailed in the present experiment when the participants of both
513 the Hand and Tool groups traced the shape with mirror vision. However, only the participants
514 of the Hand group showed a suppression of somatosensory information (i.e., greater alpha and
515 beta band powers in the Mirror condition). Functionally, the dynamic suppression of
516 somatosensory information when performing goal-directed movement under incongruent
517 visual inputs is thought to reduce the sensory conflict (Bernier et al., 2009; Goldenkoff et al.,
518 2021). Within this framework, our results are then compatible with two non-mutually
519 exclusive scenarios. One in which vision of the hand would enhance arm somatosensory
520 information, thereby increasing the sensory conflict. This would be consistent with
521 psychophysical studies showing enhanced processing of somatosensory information (from
522 extraocular, neck and arm muscles) with visual feedback (Becker & Saglam, 2001; Blouin et
523 al., 2002; Kennett et al., 2001; Longo et al., 2011; Taylor-Clarke et al., 2002, 2004; Zhou &
524 Fuster, 2000). It would also be compatible with the greater sensitivity of the somatosensory
525 cortex to peripheral somatosensory inputs reported in previous studies when the stimulated
526 body area can be seen (Forster & Eimer, 2005; Sambo et al., 2009; Taylor-Clarke et al.,
527 2002). Another possibility is that the inter-sensory conflict increased for the Hand group
528 because the source of the conflicting somatosensory inputs (i.e., the hand) could be seen,
529 contrary to the Tool group. According to this hypothesis, the view of the hand would allow a
530 more direct comparison between the visual and somatosensory mapping of the hand, and
531 therefore a better detection of a sensory mismatch when controlling movements with
532 incongruent visual feedback.

533 Our results point to an automatic covert processing of arm proprioceptive inputs
534 induced by vision of the hand. In normal visual condition, this covert processing might
535 contribute to the high quality of our broad manual motor repertoire. In conditions with
536 incongruent visual feedback, it would impair movement performance, thereby prompting the
537 brain to decrease the weight of proprioception during the visual and somatosensory feedbacks
538 integration. The fact that the participants of the Tool group did not show significant
539 modulation of somatosensory alpha and beta powers when tracing with mirror vision suggests
540 that vision of a self-moved tool does not enable such covert processing of proprioceptive
541 information. In the present study, we did not control for change of the internal representation
542 of the body when using tools (e.g., lengthening of the represented arm length, Cardinali et al.,
543 2009; Sposito et al., 2012; see Martel et al., 2016 for a review). However, our experiment was
544 designed to minimize such modifications (e.g., participants viewed their hand moving without
545 the tool every 5 trials). Further studies are needed to determine whether the view of the tool

546 also leads to down-weighting of proprioception in the somatosensory cortex when the tool is
547 incorporated into body representations.

548 The present results revealed that the dynamic control exerted by the brain over arm
549 somatosensory information mainly occurred in SII, which is an important hub for processing
550 somatosensory information (Steinmetz et al., 2000). Our findings are then consistent with
551 studies showing greater attention-related processes in SII than in SI (Chapman & Meftah,
552 2005; Nelson et al., 2004). Importantly, SII is thought to contribute to the integration of
553 proprioceptive inputs for the online motor control (Eickhoff et al., 2010; Hinkley et al., 2007).
554 The sensory gating observed in SII areas then likely decreased the weight assigned to arm
555 proprioceptive inputs when controlling movements with incongruent visual and
556 proprioceptive feedbacks.

557 Although occurring outside our pre-defined region of interest (i.e., somatosensory area),
558 we found significant decreases of alpha and beta powers in the occipital cortex when
559 participants traced the shape with mirror-reversed vision. The effect of the incongruent visual
560 feedback on the activity of the occipital cortex was therefore opposed to the effect observed in
561 the somatosensory cortex for the Hand group (i.e., increased alpha and beta powers). The
562 decrease in occipital alpha and beta band powers is consistent with a facilitation of visual
563 inputs when performing movement under visuo-proprioceptive incongruence. This change in
564 occipital alpha and beta powers corroborates brain imaging studies (e.g., EEG, fMRI)
565 reporting increased activity in the occipital lobe when performing movements under
566 discrepant visual feedback (Lebar et al., 2015; Limanowski et al., 2017, 2020).

567 The changes in alpha and beta band powers observed in the occipital were more robust
568 for the Tool than for the Hand groups. This observation suggests that seeing a self-moved tool
569 under incongruent visual feedback is a favorable context to create a visual attentional set,
570 which increases visual brain activity (see Limanowski & Friston, 2019; Limanowski, 2022).
571 On the other hand, for the Tool group, the shift of attention away from arm proprioception
572 (and perhaps away from hand working space), and the absence of covert processing of arm
573 proprioceptive inputs in the absence of hand visual feedback, might have reduced the weight
574 of arm proprioceptive inputs when tracing the shape with normal visual feedback. Viewed
575 from this perspective, there would be no functional necessity to further downregulate arm
576 somatosensory inputs when tracing with incongruent visual feedback. This could explain why,
577 contrary to the Hand group, the Tool group showed similar somatosensory alpha and beta
578 band powers between the Mirror and Direct conditions. Therefore, the present results could
579 reconcile the apparent discrepancy between the suppression of somatosensory inputs reported

580 by Bernier et al. (2009) when participants traced the contour of a shape while seeing their
581 hand through an inclined mirror (as in the present study) and the reduction of somatosensory
582 beta band power (i.e., increased processing) reported by Lebar et al. (2017) when the
583 incongruent hand visual feedback was provided using a digitized dot image.

584 Our source analyses estimated the cuneus (for the Hand and Tool groups) and the
585 lingual gyrus (for the Tool group) as the origin of the occipital decrease of alpha and beta
586 band powers in the Mirror condition. These medial visual areas are known to encode space in
587 an allocentric frame of reference (Chen et al., 2014; Committeri et al., 2004; Ruotolo et al.,
588 2019). In this frame of reference, the body (including the hand) and the objects of the
589 environment would be encoded relative to each other within a retinal map (i.e., object-based
590 coding of space) (Burgess et al., 2004; Galati et al., 2000; Paillard, 1987). Such visual
591 representation of space would be largely independent of somatosensory inputs (Ambrosini et
592 al., 2012; Blouin et al., 1993; Medendorp et al., 2008). Accordingly, our results suggest that
593 controlling the motion of the hand or of a tool with incongruent visual feedback enables the
594 use of an allocentric reference frame. The fact that the Tool group showed stronger between-
595 subjects consistency regarding the decreased alpha and beta band powers in the medial visual
596 cortex implies that the manipulated tool was selectively encoded with an object-based frame
597 of reference. The observation that the only participant of the Tool group who showed a strong
598 increase in alpha band power in the Mirror condition was the worst tracing performer
599 provides evidence that this frame of reference was more relevant for controlling arm
600 movements in this novel visuomotor environment than somatosensory-based egocentric
601 reference frames. Moreover, the finding of both increase and decrease of visual beta band
602 power when the participants of the Hand group traced with mirror vision supports the
603 suggestion that the selection of the frames of reference is subject and context dependent
604 (Bernier & Grafton, 2010; Bridgeman, 1991; Byrne & Henriques, 2013). The enhanced
605 object-based coding of space for the Tool group in the Mirror condition is also supported by
606 the decreased alpha band power observed in the anterior precuneus with mirror vision. Indeed,
607 this medial area of the parietal cortex has been shown to selectively encode the motor goal in
608 visual coordinates (Bernier & Grafton, 2010).

609 We reasoned that because the tool is devoid of somatosensory attributes, the visuo-
610 proprioceptive conflict should be less perceived for the Tool group. Accordingly, we
611 predicted better performance for the Tool than for the Hand groups in conditions with
612 incongruent visual feedback. Behavioral analyses rather revealed that the tracing performance
613 of both groups was similarly impaired with mirror vision. A likely explanation is that the

614 performance degradation showed by the Tool group mainly resulted from a sensorimotor
615 conflict (rather than from a visuo-proprioceptive conflict). During visually-guided
616 movements, this conflict would result from the incongruence between the actual visual
617 feedback and the predicted visual feedback issued from the motor commands (Brun et al.,
618 2020; Miall & Cole, 2007; Shadmehr et al., 2010). Similar conflict could have emerged
619 between the predicted and the actual somatosensory feedbacks. In our study, the hand motor
620 commands when manipulating the tool might have enabled these sensory predictions. Most
621 likely, the visuomotor conflict also degraded the tracing performance of the Hand group.
622 However, the fact that for the Tool group, the incongruence between visual and
623 somatosensory feedbacks had no significant impact on the somatosensory alpha and beta band
624 powers suggests that the visuomotor conflict had only negligible effect on the activity of the
625 somatosensory cortex.

626

627

628 **5. Conclusion**

629

630 We found that the control of tracing movement under incongruent visual and somatosensory
631 information was associated with an increased alpha (8-12 Hz) and beta (15-25 Hz) band
632 powers in the somatosensory cortex if participants had visual feedback of their hand. This
633 modulation of alpha and beta activities, which suggested reduced proprioception, was not
634 found if participants traced the shape with the tip of a rod without seeing their hand. Taken
635 together, our findings are in line with a covert processing of arm somatosensory information
636 induced by vision of the hand. This covert processing would have a detrimental effect on
637 movements that are controlled under incongruent visual and proprioceptive feedbacks, and
638 would prompt the brain to exert a control over somatosensory information. Our results
639 suggest that the processing of arm somatosensory inputs during the control of goal-directed
640 hand movements differs largely between conditions where hand visual feedback is available
641 and conditions where the hand cannot be seen. This could explain results from previous
642 studies (e.g., Clower & Boussaoud, 2000; Norris et al., 2001) showing that the sensorimotor
643 adaptation to prismatic displacement is greater when the participants can see their hand than
644 when the participants see their hand in a more abstract form (e.g., digitized dot, video).

645

646 Acknowledgments

647 The authors thank Marie Fabre, Aurélie Grandjean and Chloé Sutter for their help at
648 various stages of this research project.

649

650 Declarations of interest: none

651 Funding: this research did not receive any specific grant from funding agencies in the public,
652 commercial, or not-for-profit sectors.

653

654 **6. References**

655 Ambrosini, E., Ciavarro, M., Pelle, G., Perrucci, M. G., Galati, G., Fattori, P., Galletti,
656 C., & Committeri, G. (2012). Behavioral investigation on the frames of reference
657 involved in visuomotor transformations during peripheral arm reaching. *PLoS*
658 *ONE*, 7(12), e51856. <https://doi.org/10.1371/journal.pone.0051856>

659 Anderson, K. L., & Ding, M. (2011). Attentional modulation of the somatosensory mu
660 rhythm. *Neuroscience*, 180, 165–180.
661 <https://doi.org/10.1016/j.neuroscience.2011.02.004>

662 Balslev, D., Christensen, L. O., Lee, J. H., Law, I., Paulson, O. B., & Miall, R. C. (2004).
663 Enhanced accuracy in novel mirror drawing after repetitive transcranial magnetic
664 stimulation-induced proprioceptive deafferentation. *Journal of Neuroscience*,
665 24(43), 9698-9702. <https://doi.org/10.1523/JNEUROSCI.1738-04.2004>

666 Becker, W., & Saglam, H. (2001). Perception of angular head position during attempted
667 alignment with eccentric visual objects. *Experimental Brain Research*, 138(2), 185–
668 192. <https://doi.org/10.1007/s002210100703>

669 Bernier, P.-M., Burle, B., Vidal, F., Hasbroucq, T., & Blouin, J. (2009). Direct evidence
670 for cortical suppression of somatosensory afferents during visuomotor
671 adaptation. *Cerebral Cortex*, 19(9), 2106–
672 2113. <https://doi.org/10.1093/cercor/bhn233>

673 Bernier, P.-M., & Grafton, S. T. (2010). Human posterior parietal cortex flexibly
674 determines reference frames for reaching based on sensory context. *Neuron*, 68(4),
675 776–788. <https://doi.org/10.1016/j.neuron.2010.11.002>

676 Blouin, J., Amade, N., Vercher, J.-L., Teasdale, N., & Gauthier, G. M. (2002). Visual
677 signals contribute to the coding of gaze direction. *Experimental Brain*
678 *Research*, 144(3), 281–292. <https://doi.org/10.1007/s00221-002-1029-5>

- 679 Blouin, J., Bard, C., Teasdale, N., Paillard, J., Fleury, M., Forget, R., & Lamarre, Y.
680 (1993). Reference systems for coding spatial information in normal subjects and a
681 deafferented patient. *Experimental Brain*
682 *Research*, 93(2). <https://doi.org/10.1007/BF00228401>
- 683 Bridgeman, B. (1991). Complementary Cognitive and Motor Image Processing. In G.
684 Obrecht & L. W. Stark (Eds.), *Presbyopia Research* (pp. 189–198). Springer
685 US. https://doi.org/10.1007/978-1-4757-2131-7_19
- 686 Brun, C., McCabe, C. S., & Mercier, C. (2020). The contribution of motor commands to
687 the perturbations induced by sensorimotor conflicts in
688 fibromyalgia. *Neuroscience*, 434, 55–
689 65. <https://doi.org/10.1016/j.neuroscience.2020.03.017>
- 690 Burgess, N., Spiers, H., & Paleologou, E. (2004). Orientational manoeuvres in the dark:
691 dissociating allocentric and egocentric influences on spatial
692 memory. *Cognition*, 94(2), 149–166. <https://doi.org/10.1016/j.cognition.2004.01.001>
- 693 Byrne, P. A., & Henriques, D. Y. P. (2013). When more is less: increasing allocentric
694 visual information can switch visual–proprioceptive combination from an optimal to
695 sub-optimal process. *Neuropsychologia*, 51(1), 26–
696 37. <https://doi.org/10.1016/j.neuropsychologia.2012.10.008>
- 697 Cardinali, L., Frassinetti, F., Brozzoli, C., Urquizar, C., Roy, A. C., & Farnè, A. (2009).
698 Tool-use induces morphological updating of the body schema. *Current*
699 *Biology*, 19(12), R478–R479. <https://doi.org/10.1016/j.cub.2009.05.009>
- 700 Chapman, C. E., & Meftah, E.-M. (2005). Independent controls of attentional influences
701 in primary and secondary somatosensory cortex. *Journal of Neurophysiology*, 94(6),
702 4094–4107. <https://doi.org/10.1152/jn.00303.2005>
- 703 Chen, Y., Monaco, S., Byrne, P., Yan, X., Henriques, D. Y. P., & Crawford, J. D. (2014).
704 Allocentric versus egocentric representation of remembered reach targets in human
705 cortex. *Journal of Neuroscience*, 34(37), 12515–
706 12526. <https://doi.org/10.1523/JNEUROSCI.1445-14.2014>
- 707 Cheyne, D., Gaetz, W., Garnero, L., Lachaux, J.-P., Ducorps, A., Schwartz, D., &
708 Varela, F. J. (2003). Neuromagnetic imaging of cortical oscillations accompanying
709 tactile stimulation. *Cognitive Brain Research*, 17(3), 599–
710 611. [https://doi.org/10.1016/S0926-6410\(03\)00173-3](https://doi.org/10.1016/S0926-6410(03)00173-3)

- 711 Clower, D. M., & Boussaoud, D. (2000). Selective use of perceptual recalibration versus
712 visuomotor skill acquisition. *Journal of Neurophysiology*, 84(5), 2703–
713 2708. <https://doi.org/10.1152/jn.2000.84.5.2703>
- 714 Cohen, M. X. (2014). *Analyzing neural time series data: Theory and practice*. The MIT
715 Press.
- 716 Committeri, G., Galati, G., Paradis, A.-L., Pizzamiglio, L., Berthoz, A., & LeBihan, D.
717 (2004). Reference frames for spatial cognition: different brain areas are involved in
718 viewer-, object-, and landmark-centered judgments about object location. *Journal of*
719 *Cognitive Neuroscience*, 16(9), 1517–
720 1535. <https://doi.org/10.1162/0898929042568550>
- 721 Criswell, E., & Cram, J. R. (Eds.). (2011). *Cram's introduction to surface*
722 *electromyography* (2nd ed). Jones and Bartlett.
- 723 Eickhoff, S. B., Jbabdi, S., Caspers, S., Laird, A. R., Fox, P. T., Zilles, K., & Behrens, T.
724 E. J. (2010). Anatomical and functional connectivity of cytoarchitectonic areas
725 within the human parietal operculum. *Journal of Neuroscience*, 30(18), 6409–
726 6421. <https://doi.org/10.1523/JNEUROSCI.5664-09.2010>
- 727 Forster, B., & Eimer, M. (2005). Vision and gaze direction modulate tactile processing in
728 somatosensory cortex: Evidence from event-related brain potentials. *Experimental*
729 *Brain Research*, 165(1), 8–18. <https://doi.org/10.1007/s00221-005-2274-1>
- 730 Galati, G., Lobel, E., Vallar, G., Berthoz, A., Pizzamiglio, L., & Le Bihan, D. (2000).
731 The neural basis of egocentric and allocentric coding of space in humans: A
732 functional magnetic resonance study. *Experimental Brain Research*, 133(2), 156–
733 164. <https://doi.org/10.1007/s002210000375>
- 734 Goldenkoff, E. R., McGregor, H. R., Mergos, J., Gholizadeh, P., Bridenstine, J., Brown,
735 M. J., & Vesia, M. (2021). Reversal of visual feedback modulates somatosensory
736 plasticity. *Neuroscience*, 452, 335-344.
737 <https://doi.org/10.1016/j.neuroscience.2020.10.033>
- 738 Gramfort, A., Papadopoulos, T., Olivi, E., & Clerc, M. (2010). OpenMEEG: opensource
739 software for quasistatic bioelectromagnetics. *BioMedical Engineering OnLine*, 9(1),
740 45. <https://doi.org/10.1186/1475-925X-9-45>
- 741 Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off-line removal
742 of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, 55(4),
743 468–484. [https://doi.org/10.1016/0013-4694\(83\)90135-9](https://doi.org/10.1016/0013-4694(83)90135-9)

- 744 Hinkley, L. B., Krubitzer, L. A., Nagarajan, S. S., & Disbrow, E. A. (2007).
745 Sensorimotor integration in S2, PV, and parietal rostroventral areas of the human
746 Sylvian fissure. *Journal of Neurophysiology*, *97*(2), 1288–
747 1297. <https://doi.org/10.1152/jn.00733.2006>
- 748 Kennett, S., Taylor-Clarke, M., & Haggard, P. (2001). Noninformative vision improves
749 the spatial resolution of touch in humans. *Current Biology*, *11*(15), 1188–
750 1191. [https://doi.org/10.1016/S0960-9822\(01\)00327-X](https://doi.org/10.1016/S0960-9822(01)00327-X)
- 751 Kilavik, B. E., Zaepffel, M., Brovelli, A., MacKay, W. A., & Riehle, A. (2013). The ups
752 and downs of beta oscillations in sensorimotor cortex. *Experimental Neurology*, *245*,
753 15–26. <https://doi.org/10.1016/j.expneurol.2012.09.014>
- 754 Koessler, L., Maillard, L., Benhadid, A., Vignal, J. P., Felblinger, J., Vespignani, H., &
755 Braun, M. (2009). Automated cortical projection of EEG sensors: anatomical
756 correlation via the international 10–10 system. *NeuroImage*, *46*(1), 64–
757 72. <https://doi.org/10.1016/j.neuroimage.2009.02.006>
- 758 Lajoie, Y., Paillard, J., Teasdale, N., Bard, C., Fleury, M., Forget, R., & Lamarre, Y.
759 (1992). Mirror drawing in a deafferented patient and normal subjects:
760 Visuoproprioceptive conflict. *Neurology*, *42*(5), 1104–
761 1104. <https://doi.org/10.1212/WNL.42.5.1104>
- 762 Law, S. K., Rohrbaugh, J. W., Adams, C. M., & Eckardt, M. J. (1993). Improving spatial
763 and temporal resolution in evoked EEG responses using surface
764 Laplacians. *Electroencephalography and Clinical Neurophysiology/Evoked
765 Potentials Section*, *88*(4), 309–322. [https://doi.org/10.1016/0168-5597\(93\)90055-T](https://doi.org/10.1016/0168-5597(93)90055-T)
- 766 Lebar, N., Bernier, P.-M., Guillaume, A., Mouchnino, L., & Blouin, J. (2015). Neural
767 correlates for task-relevant facilitation of visual inputs during visually-guided hand
768 movements. *NeuroImage*, *121*, 39–
769 50. <https://doi.org/10.1016/j.neuroimage.2015.07.033>
- 770 Lebar, N., Danna, J., Moré, S., Mouchnino, L., & Blouin, J. (2017). On the neural basis
771 of sensory weighting: alpha, beta and gamma modulations during complex
772 movements. *NeuroImage*, *150*, 200–
773 212. <https://doi.org/10.1016/j.neuroimage.2017.02.043>
- 774 Limanowski, J., & Friston, K. (2019). Active inference under visuo-proprioceptive
775 conflict: Simulation and empirical results. *Scientific Reports*, *10*(1), 1–
776 14. <https://doi.org/10.1038/s41598-020-61097-w>

- 777 Limanowski, J. (2022). Precision control for a flexible body
778 representation. *Neuroscience & Biobehavioral Reviews*, *134*,
779 104401. <https://doi.org/10.1016/j.neubiorev.2021.10.023>
- 780 Limanowski, J., Kirilina, E., & Blankenburg, F. (2017). Neuronal correlates of
781 continuous manual tracking under varying visual movement feedback in a virtual
782 reality environment. *NeuroImage*, *146*, 81–
783 89. <https://doi.org/10.1016/j.neuroimage.2016.11.009>
- 784 Limanowski, J., Litvak, V., & Friston, K. (2020). Cortical beta oscillations reflect the
785 contextual gating of visual action feedback. *NeuroImage*, *222*,
786 117267. <https://doi.org/10.1016/j.neuroimage.2020.117267>
- 787 Longo, M. R., Pernigo, S., & Haggard, P. (2011). Vision of the body modulates
788 processing in primary somatosensory cortex. *Neuroscience Letters*, *489*(3), 159–
789 163. <https://doi.org/10.1016/j.neulet.2010.12.007>
- 790 Martel, M., Cardinali, L., Roy, A. C., & Farnè, A. (2016). Tool-use: An open window
791 into body representation and its plasticity. *Cognitive Neuropsychology*, *33*(1–2), 82–
792 101. <https://doi.org/10.1080/02643294.2016.1167678>
- 793 Medendorp, W. P., Beurze, S. M., Van Pelt, S., & Van Der Werf, J. (2008). Behavioral
794 and cortical mechanisms for spatial coding and action planning. *Cortex*, *44*(5), 587–
795 597. <https://doi.org/10.1016/j.cortex.2007.06.001>
- 796 Miall, R. C., & Cole, J. (2007). Evidence for stronger visuo-motor than visuo-
797 proprioceptive conflict during mirror drawing performed by a deafferented subject
798 and control subjects. *Experimental Brain Research*, *176*(3), 432–
799 439. <https://doi.org/10.1007/s00221-006-0626-0>
- 800 Murray, M. M., & Wallace, M. T. (2012). *The neural bases of multisensory processes*.
801 CRC Press.
- 802 Nelson, A. J., Staines, W. R., Graham, S. J., & McIlroy, W. E. (2004). Activation in SI
803 and SII; the influence of vibrotactile amplitude during passive and task-relevant
804 stimulation. *Cognitive Brain Research*, *19*(2), 174–
805 184. <https://doi.org/10.1016/j.cogbrainres.2003.11.013>
- 806 Norris, S. A., Greger, B. E., Martin, T. A., & Thach, W. T. (2001). Prism adaptation of
807 reaching is dependent on the type of visual feedback of hand and target
808 position. *Brain Research*, *905*(1–2), 207–219. [https://doi.org/10.1016/S0006-
809 8993\(01\)02552-5](https://doi.org/10.1016/S0006-8993(01)02552-5)

- 810 Nunez, P. L., & Srinivasan, R. (2006). *Electric Fields of the Brain*. Oxford University
811 Press. <https://doi.org/10.1093/acprof:oso/9780195050387.001.0001>
- 812 Paillard, J. (1987). Cognitive versus sensorimotor encoding of spatial information. In P.
813 Ellen & C. Thinus-Blanc (Eds.), *Cognitive Processes and Spatial Orientation in*
814 *Animal and Man* (pp. 43–77). Springer Netherlands. [https://doi.org/10.1007/978-94-](https://doi.org/10.1007/978-94-009-3533-4_5)
815 [009-3533-4_5](https://doi.org/10.1007/978-94-009-3533-4_5)
- 816 Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp
817 potential and current density mapping. *Electroencephalography and Clinical*
818 *Neurophysiology*, 72(2), 184–187. [https://doi.org/10.1016/0013-4694\(89\)90180-6](https://doi.org/10.1016/0013-4694(89)90180-6)
- 819 Pfurtscheller, G., & Lopes da Silva, F. H. (1999). Event-related EEG/MEG
820 synchronization and desynchronization: basic principles. *Clinical*
821 *Neurophysiology*, 110(11), 1842–1857. [https://doi.org/10.1016/S1388-](https://doi.org/10.1016/S1388-2457(99)00141-8)
822 [2457\(99\)00141-8](https://doi.org/10.1016/S1388-2457(99)00141-8)
- 823 Ruotolo, F., Ruggiero, G., Raemaekers, M., Iachini, T., van der Ham, I. J. M., Fracasso,
824 A., & Postma, A. (2019). Neural correlates of egocentric and allocentric frames of
825 reference combined with metric and non-metric spatial relations. *Neuroscience*, 409,
826 235–252. <https://doi.org/10.1016/j.neuroscience.2019.04.021>
- 827 Rushton, D. N., Roghwell, J. C., & Craggs, M. D. (1981). Gating of somatosensory
828 evoked potentials during different kinds of movement in Man. *Brain*, 104(3), 465–
829 491. <https://doi.org/10.1093/brain/104.3.465>
- 830 Sambo, C. F., Gillmeister, H., & Forster, B. (2009). Viewing the body modulates neural
831 mechanisms underlying sustained spatial attention in touch. *European Journal of*
832 *Neuroscience*, 30(1), 143–150. <https://doi.org/10.1111/j.1460-9568.2009.06791.x>
- 833 Seki, K., & Fetz, E. E. (2012). Gating of sensory input at spinal and cortical levels during
834 preparation and execution of voluntary movement. *Journal of Neuroscience*, 32(3),
835 890–902. <https://doi.org/10.1523/JNEUROSCI.4958-11.2012>
- 836 Shadmehr, R., Smith, M. A., & Krakauer, J. W. (2010). Error correction, sensory
837 prediction, and adaptation in motor control. *Annual Review of Neuroscience*, 33(1),
838 89–108. <https://doi.org/10.1146/annurev-neuro-060909-153135>
- 839 Sohrabpour, A., Lu, Y., Kankirawatana, P., Blount, J., Kim, H., & He, B. (2015). Effect
840 of EEG electrode number on epileptic source localization in pediatric
841 patients. *Clinical Neurophysiology*, 126(3), 472–
842 480. <https://doi.org/10.1016/j.clinph.2014.05.038>

- 843 Sposito, A., Bolognini, N., Vallar, G., & Maravita, A. (2012). Extension of perceived
844 arm length following tool-use: Clues to plasticity of body
845 metrics. *Neuropsychologia*, *50*(9), 2187–
846 2194. <https://doi.org/10.1016/j.neuropsychologia.2012.05.022>
- 847 Staines, W. R., Brooke, J. D., Cheng, J., Misiaszek, J. E., & MacKay, W. A. (1997).
848 Movement-induced gain modulation of somatosensory potentials and soleus H-
849 reflexes evoked from the leg I. Kinaesthetic task demands: I. Kinaesthetic task
850 demands. *Experimental Brain Research*, *115*(1), 147–
851 155. <https://doi.org/10.1007/PL00005674>
- 852 Starch, D. (1910). A demonstration of the trial and error method of
853 learning. *Psychological Bulletin*, *7*(1), 20–23. <https://doi.org/10.1037/h0063796>
- 854 Steinmetz, P. N., Roy, A., Fitzgerald, P. J., Hsiao, S. S., Johnson, K. O., & Niebur, E.
855 (2000). Attention modulates synchronized neuronal firing in primate somatosensory
856 cortex. *Nature*, *404*(6774), 187–190. <https://doi.org/10.1038/35004588>
- 857 Tadel, F., Baillet, S., Mosher, J. C., Pantazis, D., & Leahy, R. M. (2011). Brainstorm: a
858 user-friendly application for MEG/EEG Analysis. *Computational Intelligence and*
859 *Neuroscience*, *2011*, 1–13. <https://doi.org/10.1155/2011/879716>
- 860 Taylor-Clarke, M., Kennett, S., & Haggard, P. (2002). Vision modulates somatosensory
861 cortical processing. *Current Biology*, *12*(3), 233–236. [https://doi.org/10.1016/S0960-9822\(01\)00681-9](https://doi.org/10.1016/S0960-9822(01)00681-9)
- 862
- 863 Taylor-Clarke, M., Kennett, S., & Haggard, P. (2004). Persistence of visual–tactile
864 enhancement in humans. *Neuroscience Letters*, *354*(1), 22–
865 25. <https://doi.org/10.1016/j.neulet.2003.09.068>
- 866 Zhou, Y.-D., & Fuster, J. M. (2000). Visuo-tactile cross-modal associations in cortical
867 somatosensory cells. *Proceedings of the National Academy of Sciences*, *97*(17),
868 9777–9782. <https://doi.org/10.1073/pnas.97.17.9777>

869

870 **Credit Authorship Contribution Statement**

871 Benjamin Mathieu: Conceptualization, Methodology, Investigating, Data analyses,
872 Writing, Reviewing & Editing. Antonin Abillama: Conceptualization, Methodology,
873 Investigating, Data analyses. Simon Moré: Software. Catherine Mercier:
874 Conceptualization, Reviewing & Editing. Martin Simoneau: Conceptualization,
875 Reviewing & Editing. Jérémy Danna: Software, Reviewing & Editing. Laurence
876 Mouchnino: Conceptualization, Methodology, Reviewing & Editing. Jean Blouin:

877 Conceptualization, Methodology, Investigating, Data analyses, Writing, reviewing &
878 editing.