



HAL
open science

The visual encoding of purely proprioceptive intermanual tasks is due to the need of transforming joint signals, not to their interhemispheric transfer

Léo Arnoux, Sebastien Fromentin, Dario Farotto, Mathieu Beraneck, Joseph Mcintyre, Michele Tagliabue

► **To cite this version:**

Léo Arnoux, Sebastien Fromentin, Dario Farotto, Mathieu Beraneck, Joseph Mcintyre, et al.. The visual encoding of purely proprioceptive intermanual tasks is due to the need of transforming joint signals, not to their interhemispheric transfer. *Journal of Neurophysiology*, 2017, 118 (3), pp.1598-1608. 10.1152/jn.00140.2017. hal-02111090

HAL Id: hal-02111090

<https://hal.science/hal-02111090v1>

Submitted on 16 May 2019

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.

1 **The visual encoding of purely proprioceptive intermanual tasks is**
2 **due to the need of transforming joint signals, not to their inter-**
3 **hemispheric transfer**

4
5 Léo Arnoux¹, Sebastien Fromentin¹, Dario Farotto¹, Mathieu Beraneck¹, Joseph
6 McIntyre^{1,2,3}, Michele Tagliabue¹

7 ¹ Center for Neurophysics, Physiology, Pathology, UMR 8119, CNRS Université Paris
8 Descartes, Sorbonne Paris Cité, Paris, France

9 ² Ikerbasque Science Foundation, Bilbao, Spain

10 ³ Tecnalia Research & Development, Health Division, San Sebastian, Spain

11
12 **Running Head:**

13 Visual encoding of purely proprioceptive intermanual tasks

14
15 **Keywords:**

16 Sensory encoding; bimanual movements; goal-oriented hand movements; kinesthesia;
17 sensory transformations.

18
19 **Corresponding Author:**

20 Michele Tagliabue

21 Center for Neurophysics, Physiology, Pathology,

22 UMR 8119, CNRS - Université Paris Descartes,

23 45 rue des St-Pères 75270, Paris, France.

24 E-mail: michele.tagliabue@parisdescartes.fr

25
26 **Authors Contributions:**

27 MT Conceived and designed research;

28 LA, SF, DF, MT Performed experiments;

29 LA, SF, DF, MT Analyzed data

30 MB, JM, MT Interpreted results of experiments

31 MT Prepared figures

32 MT Drafted manuscript

33 MB, JM, MT Edited and revised manuscript

34 LA, SF, DF, MB, JM, MT Approved final version of manuscript

35 **Abstract**

36 To perform goal-oriented hand movement humans combine multiple sensory signals
37 (e.g. vision and proprioception) that can be encoded in various reference frames (body-
38 centered and/or exo-centered). In a previous study we showed that when aligning a
39 hand to a remembered target orientation the brain encodes both target and response in
40 visual space when the target is sensed by one hand and the response is performed by
41 the other, even though both are sensed only through proprioception. Here we ask
42 whether such visual encoding is due i) to the necessity of transferring sensory
43 information across the brain hemispheres or ii) to the necessity, due to the arms'
44 anatomical mirror symmetry, of transforming the joint signals of one limb into the
45 reference frame of the other. To answer this question we asked subjects to perform
46 purely proprioceptive tasks in different conditions: *Intra* – the same arm sensing the
47 target and performing the movement; *Inter/Parallel* – one arm sensing the target and
48 the other reproducing its orientation; and *Inter/Mirror* – one arm sensing the target and
49 the other mirroring its orientation. Performance was very similar between *Intra* and
50 *Inter/Mirror* (conditions not requiring joint-signal transformations) while both differed
51 from *Inter/Parallel*. Manipulation of the visual scene in a virtual-reality paradigm
52 showed visual encoding of proprioceptive information only in the latter condition. These
53 results suggest that the visual encoding of purely proprioceptive tasks is not due to
54 inter-hemispheric transfer of the proprioceptive information *per se*, but to the necessity
55 of transforming joint signals between mirror-symmetric limbs.

56 **New & Noteworthy**

57 Why does the brain encode goal-oriented, inter-manual tasks in a visual space, even in
58 the absence of visual feedback about the target and the hand? We show that the visual

59 encoding is not due to the transfer of proprioceptive signals between brain hemispheres
60 *per se*, but to the need, due to the mirror symmetry of the two limbs, of transforming
61 joint angle signals of one arm in different joint signals of the other.

62 **Introduction**

63 To plan and control movements the brain can potentially use multiple sources of
64 sensory information. For instance, visual signals inform the brain about the
65 environment and the body's relative position in space, while proprioception, i.e. the
66 ensemble of skin, muscle and joint signals, provide information about the position,
67 movement and exerted efforts of the body segments (Proske and Gandevia 2012).
68 Several studies have shown that when performing goal oriented hand movements the
69 brain uses such sources of information in a statistically optimal fashion (Van Beers et al.
70 1996,1999, Ghahramani et al. 1997, Kording and Wolpert 2004, Bays and Wolpert 2007,
71 Faisal and Wolpert 2009, Sabes 2011, Fetsch et al. 2012, Rohe and Noppeney 2016). For
72 instance, it has been demonstrated experimentally and theoretically that to control hand
73 movements the brain privileges direct comparisons between the information concerning
74 the moving hand and the target position/orientation (Sober and Sabes 2005, Sarlegna
75 and Sainburg 2007, Tagliabue McIntyre 2011, Blouin et al. 2014). As a consequence, if
76 the hand and target position can be sensed through the same sensory modality, the
77 brain would tend to avoid using other signals requiring sensory transformations. Thus,
78 if reaching to a visual target with the hand in view, the task will be represented in visual
79 coordinates, while blindly moving the hand to a remembered position (e.g. reaching for
80 your car's stick shift while keeping your eyes on the road) would be carried out in
81 proprioceptive reference frame. Other studies, however, have shown evidence for the
82 use of visual encoding of reaching task even when both target and hand position could

83 be sensed only through proprioception (Pouget et al. 2002, Sober and Sabes 2005,
84 Sarlegna and Sainburg 2007, McGuire and Sabes 2009, Jones et al. 2010). How to
85 reconcile these different observations remains an open question.

86 We tackled this apparent contradiction in a specific experiment in which the subjects
87 had to sense a hand orientation, remember it, and later reproduce that same orientation
88 without visual feedback of the hand (Tagliabue and McIntyre 2013). The subjects
89 performed the task in two different conditions. In the first condition, a replica of a
90 previous task in which we observed a purely proprioceptive encoding (Tagliabue and
91 McIntyre 2011), the subject used the same hand to sense and then reproduce the
92 orientation. In the second condition subjects had to reproduce with one hand the
93 remembered orientation that was sensed with the other. This latter task is typical of
94 other paradigms for which a visual encoding has previously been observed (Pouget et al.
95 2002, Sober and Sabes 2005, Sarlegna and Sainburg 2007, McGuire and Sabes 2009,
96 Jones et al. 2010). Our result showed that the apparently contradicting results found in
97 the literature could be reconciled by the asserting that it is the use of two different
98 hands to sense and reach the target that induces a visual encoding of the available
99 proprioceptive information. Supported by the results of a statistical optimization model,
100 we concluded that the necessity of performing inter-limb transformations induces a
101 visual representation of otherwise purely proprioceptive tasks, ostensibly because this
102 improves movement precision. The rationale for this conclusion stems from the fact that
103 sensorimotor transformations add variability to the intrinsic noise of the visual or
104 proprioceptive sensors. According to principles of maximum likelihood, when multiple
105 channels of noisy information are combined in an optimal fashion, the resulting signal is
106 less noisy than any of the component channels, provided that the noise in the different

107 channels are statistically independent from each other. Thus, if there exists multiple,
108 parallel pathways that allow one to compare target to hand, it makes sense to use all of
109 them so that the effects of noise introduced by each individual pathway can be reduced.
110 On the other hand, comparing the posture of the hand to the remembered posture of the
111 same hand does not, *a priori*, require any transformations to compare target with
112 response. In this case, the central nervous system (CNS) achieves the theoretical
113 optimum by avoiding sensorimotor transformations altogether, carrying out the task
114 entirely in the intrinsic frame of the proprioceptive sensors themselves (Tagliabue and
115 McIntyre 2013).

116 The necessity, or not, of performing transformations appears, therefore, to be a key
117 factor in determining when the CNS will carry out sensorimotor tasks in one set of
118 coordinate frames or another. This theoretical framework adequately predicts the
119 empirical results from our previous comparison of an inter- versus intra-manual task
120 described above, because the former required transformations while the latter did not.
121 But this reasoning does not provide the full story. In our previous inter-manual task,
122 subjects not only had to transfer the proprioceptive signals between brain hemispheres,
123 they also had to map joint angles of one arm into different joint angles of the other arm.
124 For instance, a target inclination, sensed through a left hand supination had to be
125 transformed into a right hand pronation to align the two hands in space, i.e. to make
126 them parallel as required by the task instructions. Therefore, to reproduce with one
127 hand the orientation of a target sensed with the other, subjects could not just reproduce
128 the intrinsic wrist, elbow and shoulder angles, as this would have let to a mirror
129 symmetric (i.e. non-parallel) hand orientation with respect to the subject's sagittal
130 plane. Thus, our previous inter-manual orientation task differed from the intra-manual

131 task in two fundamentally different ways: inter-hemispheric transfer of information and
132 inter-limb transformation of joint configurations. Further experiments were therefore
133 needed to disentangle these confounding factors.

134 Here we introduce a new task to our series of studies to address this open question.
135 Instead of matching the absolute orientation of the hands, as in both our previous intra-
136 manual task (which we will hereafter refer to as our *Intra* task) and our previous inter-
137 manual task (designated *Inter/Parallel* in the following), the new task consists of
138 mirroring with one hand the orientation of the target sensed with the other hand
139 (referred to as *Inter/Mirror* in the following). In terms used within the literature on
140 proprioceptive sense (c.f. Goble 2010), our *Intra* task corresponds to an “ipsilateral
141 matching task”, while our *Inter/Mirror* task involves “contralateral remembered
142 matching”. The latter requires inter-hemisphere transfer of proprioceptive information,
143 but still allows for direct comparison of joint-related proprioceptive signals. Our third
144 condition, i.e. *Inter/Parallel*, is distinct from the other two because direct comparison of
145 joint positions cannot be used to achieve the task, for the reasons described above, and
146 as such does not constitute a “joint position matching task” at all, although it certainly
147 does qualify as a proprioceptive matching task. All three tasks include a memory
148 interval, raising the possibility that factors arising from the internal storage of
149 proprioceptive information might come into play (Goble, 2010; McIntyre et al. 1998;
150 Carrozzo et al. 2002). They differ, therefore, primarily in the need for inter-hemispheric
151 transfer (*Inter/Parallel* and *Inter/Mirror*) or not (*Intra*) and the ability to directly
152 compare joint angles (*Inter/Mirror* and *Intra*), or not (*Inter/Parallel*), as summarized in
153 Figure 1. Comparison of the three conditions (*Intra*, *Inter/Mirror* and *Inter/Parallel*)
154 allows us to discriminate whether the visual encoding of purely proprioceptive tasks is

155 induced by the inter-hemispheric sensory transfer *per se*, or by the necessity of
156 transforming intrinsic joint signals to another representation or reference frame to
157 achieve the task.

158 To test these alternative hypotheses we therefore performed two experiments using a
159 virtual reality setup. In a first experiment the subjects performed a purely
160 proprioceptive task consisting of reproducing a target orientation felt by a hidden hand
161 in the three different conditions described above: *Intra*, *Inter/Mirror* and *Inter/Parallel*
162 (see Figure 1A). In this experiment we also probed for the use of visual encoding by
163 simply observing the effect of adding or removing visual scene information (Figure 1B),
164 the rationale being that the presence of environmental visual information should
165 improve accuracy and precision in the conditions in which the brain uses a visual
166 encoding of the task, as shown in previous studies on reaching movements (Diedrichsen
167 et al. 2004, Obhi and Goodale 2005). A second experiment was performed to specifically
168 quantify the visual encoding of the proprioceptive information. To this end, we
169 compared the amplitude of the deviation of the subjects' motor responses due to an
170 artificially imposed tilt of the visual scene in the *Inter/Mirror* and *Inter/Parallel*
171 conditions. Here, the tilt of the visual information should affect more the subject motor
172 responses in the task where the sensory weighing of the visual information is greater
173 (Whitney et al. 2003, Sober and Sabes 2005, Sarlegna and Sainburg 2007, Tagliabue and
174 McIntyre 2011).

175 (Figure 1 about here)

176 **Methods**

177 **Ethics Statement**

178 The experimental protocol was approved by the Internal Review Board of University
179 Paris Descartes (Comité de Personnes Ile-de-France II, IRB registration number
180 00001073, protocol number 20121300001072) and all participants gave written
181 informed consent in line with the Declaration of Helsinki.

182 **Experimental Setup**

183 For the present experiments we used the same experimental setup employed in our
184 previous work investigating the differences between intra-manual and inter-manual
185 proprioceptive tasks (Tagliabue and McIntyre 2013). The system consisted of several
186 components: an active-marker motion-analysis system (CODAmotion; Charnwood
187 Dynamics) used for real-time recording of the three-dimensional position of 27 infrared
188 LEDs (sub-millimeter accuracy, 200Hz sampling frequency). Eight markers were
189 distributed ~10 cm apart on the surface of stereo virtual-reality goggles (nVisor sx60,
190 NVIS) worn by the subjects, eight on the surface of tools (350 g, isotropic inertial
191 moment around the roll axis) that were attached to each of the subjects' hands and three
192 attached to a fixed reference frame placed in the laboratory.

193 The 3D position of the infrared markers was used to estimate in real-time the position
194 and the orientation of the subject's viewpoint and hands and thus to update accordingly
195 the images shown to him/her in the virtual reality goggles. The virtual environment
196 shown to the subjects through the goggles consisted of a cylindrical horizontal tunnel
197 (Figure 1B). Longitudinal marks parallel to the tunnel axis could be added on the walls
198 to help the subjects to perceive their own spatial orientation in the virtual world. The fact

199 that the marks went from white in the ceiling to black on the floor facilitated the
200 identification of the visual vertical.

201 **Experiment 1 (Intra – Inter/Mirror – Inter/Parallel)**

202 *Experimental procedure*

203 The subject was seated comfortably in a chair with the head upright and the arms
204 resting alongside the body. At the beginning of each trial, the main phases of which are
205 depicted in Figure 2A, an auditory command asked the subject to raise a hand (the left
206 for the intermanual tasks and the right for the intramanual one) and the color of virtual
207 environment changed depending on the hand pronosupination angle. The color
208 changed from red to green as the hand approached the orientation that had to be
209 memorized (target). After 2.5 sec during which he/she actively explored the desired
210 orientation (memorization time), the color of the virtual environment became no longer
211 sensitive to the hand orientation and the subject was instructed to lower the hand along
212 his/her body. After a 5-sec delay, an audio instruction was given to the subject to raise
213 the right hand and align it to the target orientation. Once the subject was satisfied with
214 his/her motor response, he/she validated the trial by pressing a foot-pedal. Since the
215 orientation of the hand was never rendered in the virtual reality goggles, subjects could
216 use only proprioceptive information for both target memorization and to control the
217 hand movement. For this reason the task is defined as purely proprioceptive.

218 (Figure 2 about here)

219 The three experimental conditions (*Intra*, *Inter/Mirror* and *Inter/Parallel*) represented
220 in Figure 1 were tested in distinct blocks of trials. All three conditions were also tested
221 in two different visual environments with the aim of detecting the effects of external

222 visual references in each condition. In one condition *no visual landmarks* were provided,
223 whilst in the other *visual landmarks* were shown to the subject (see Figure 1B).

224 For each experimental condition and visual environment the subjects performed 21
225 trials: three for each of the seven target orientations (-45°, -30°, -15°, 0°, +15°, +30°,
226 +45°), for a total of 126 trials.

227 *Participants*

228 Twenty-four volunteers (12 males, 12 females) participated in this experiment, age
229 27 ± 8 (mean \pm standard deviation). All subjects performed the task in all three
230 experimental conditions, with and without visual landmarks. We compensated for
231 possible order effects for task condition and visual environment by randomizing among
232 subjects the order of the 3 experimental conditions (6 possible combinations) and of the
233 2 visual environments.

234 *Data Analysis*

235 Figure 3 shows simulated data of typical responses provided by a subject in one
236 condition, to illustrate the analysis methods. Responses to each target are plotted
237 against the target's orientation and the dashed line shows the best-fit linear regression
238 through the ensemble of individual responses. Responses were analyzed in terms of
239 global bias, accuracy, precision and contraction of the responses around the vertical
240 (McIntyre and Liptshits, 2008, Tagliabue and McIntyre, 2011), as detailed below.

241 *Bias* quantifies whether the subject' responses were, on average, globally rotated
242 clockwise or counterclockwise and it is computed as it follows. First, as shown in Figure
243 3A, for each of the seven targets (Θ_i) the mean ($\bar{\theta}_i$), of the three corresponding

244 responses, $\theta_{t,i}$, was computed, as well as the corresponding mean response error $\overline{\Delta\theta}_t$,
245 often referred to as the *signed constant error*.

$$\bar{\theta}_t = \frac{\sum_{i=1}^3 \theta_{t,i}}{3}$$

$$\overline{\Delta\theta}_t = \bar{\theta}_t - \Theta_t$$

246 (Figure 3 about here)

247 Then the average global *Bias* was computed as the algebraic mean across targets of
248 signed constant errors:

$$249 \quad Bias = \frac{\sum_{t=1}^7 \overline{\Delta\theta}_t}{7}.$$

250 In Figure 3, one can see that the mean response errors for positive and negative targets
251 tended to compensate each other in this example, resulting in a small global *Bias* of the
252 responses.

253 We characterized the overall accuracy (*Accu*) by computing the average magnitude of
254 the constant error $\overline{\Delta\theta}_t$ across the seven targets:

$$Accu = \frac{\sum_{t=1}^7 |\overline{\Delta\theta}_t|}{7}$$

255 In the example reported in Figure 3A, although the global rotational *Bias* across all
256 targets is small, the amplitude of target-specific errors is significant.

257 Orientation reproduction tasks are typically affected by responses' attraction to, or
258 repulsion from specific axes (McIntyre and Lipshits 2008, Tagliabue and McIntyre
259 2011), notably the vertical axis. This phenomenon can be characterized by the term
260 "local distortion" (McIntyre et al. 1998; McIntyre and Lipshits 2008), which is a measure
261 of whether responses to nearby targets are spaced closer together (contraction) or

262 farther apart (expansion) compared to the distance between the targets themselves. In
 263 the specific case here, contraction around the vertical axis can also be measured by how
 264 much responses to targets on either side of zero orientation were deviated towards
 265 zero, i.e. in the positive direction for negative targets and vice versa. Thus, to quantify
 266 the local distortion around zero, we computed the response contraction (*Contr*), as we
 267 did in our previous publications (Tagliabue and McIntyre 2011):

$$Contr = -\frac{\sum_{t=1}^7 (\overline{\Delta\theta}_t \cdot sign(\Theta_t))}{7}$$

268 where $sign(\Theta_t) = 1$, for $\Theta_t > 0$; $sign(\Theta_t) = -1$, for $\Theta_t < 0$; and $sign(\Theta_t) = 0$, for $\Theta_t = 0$.
 269 In the example of Figure 3 the responses are characterized by an attraction toward the
 270 vertical and thus a positive value of *Contr*.

271 To quantify the responses' precision (*Prec*), for each subject we computed the root mean
 272 square of the residuals (*res*) around the best-fit regression line passing through the
 273 points (see Fig. 3):

$$Prec = \sqrt{\frac{\sum_{t=1}^7 \sum_{i=1}^3 res_{t,i}^2}{21}}$$

274 This technique allowed for a robust estimation of the variability despite the fact that for
 275 each target orientation the subject provided only three responses. As shown in the
 276 example of Figure 3, this procedure allowed us to obtain an estimation of precision that
 277 is independent of the global bias and the contraction/expansion of the responses,
 278 because those two characteristics are captured by the regression line, yet uses all 21
 279 data points. Note that systematic patterns of errors that vary non-linearly with target
 280 orientation could potentially affect this quantification of precision, because they would
 281 not be captured by the linear regression. In order to show that *Prec* was not affected by

282 such patterns of errors, we verified the lack of significant effects of the target orientation
283 on the residuals (*res*) from the regression.

284 **Statistical Analyses**

285 An ANOVA for repeated measures was performed on the four parameters (*Bias, Accu,*
286 *Contr, Prec*). The ANOVA model used the task type (*Intra, Inter/Mirror* or *Inter/Parallel*)
287 and visual scene condition (*no visual landmarks, visual landmarks*) as independent
288 within-subject factors. Newman-Keuls post-hoc tests were performed to assess
289 differences between two specific conditions whenever the ANOVA showed significant
290 effects or interactions between independent factors'.

291 **Experiment 2 (Sensory Weighting quantification – *Inter/Mirror* vs *Inter/Parallel*)**

292 ***Experimental procedure***

293 To quantify the importance given to environmental visual information as a function of
294 task, we performed an additional experiment to compare the reliance on the visual field
295 in the *Inter/Mirror* versus *Inter/Parallel* conditions.

296 Procedurally, the only difference for the subject with respect to Experiment 1 was that
297 during the 5-s delay period after memorization he or she had to perform a controlled
298 15° lateral head tilt to the right or to the left, depending on the trial (Figure 2B). To
299 guide subjects to the desired inclination of the head, audio feedback was provided: a
300 sound with a left-right balance corresponding to the direction of the desired head
301 inclination decreased in volume as the head approached 15°. If the subject could not
302 extinguish the sound within 5 s, the trial was interrupted and was repeated later on.
303 Once he/she reached the desired head inclination, after the 5 sec delay period (including
304 the head roll movement) an auditory signal was given to the subject to raise the right

305 hand to respond. The *Inter/Parallel* condition replicates the "INTER-manual" condition
306 presented in our previous study (Tagliabue and McIntyre 2013).

307 *Sensory Conflict During Tilting of the Head:*

308 Unbeknownst to the subject, however, these trials also differed from Experiment 1 by
309 the introduction of artificially induced conflict between visual and proprioceptive
310 information about the head tilt. Tracking the virtual-reality goggles was normally used
311 to hold the visual scene stable with respect to the real world during movements of the
312 head. But in 50% of the trials we generated a gradual, imperceptible conflict such that
313 when the head rotates, the subject received visual information corresponding to a larger
314 tilt. The amplitude of the angle between the visual vertical and gravity varied
315 proportionally (by a factor of 0.6) with the actual head tilt with respect to gravity, so
316 that when the head was straight there was no conflict, and when the head was tilted to
317 15°, the conflict was 9° (see fig 2B). At the end of the session the experimenter explicitly
318 interviewed the subjects about the conflict perception. None of the subjects in this
319 experiment reported to have noticed the tilt of the visual scene.

320 *Participants*

321 Twenty subjects participated in this study: 10 male and 10 female, age 24±3 years
322 (mean ± standard deviation). All subjects performed both experimental conditions and
323 to compensate for possible order effects, half of them started with the *Inter/Mirror*
324 condition and the other half with the *Inter/Parallel* condition. For each of the two
325 experimental conditions the subjects performed 56 trials: two for each combination of
326 seven target orientations (-45°, -30°, -15°, 0°, +15°, +30°, +45°), two head inclinations
327 (±15°), and two levels of conflict (with and without conflict).

328 *Data Analysis*

329 As in Tagliabue and McIntyre (2013), the recorded subjects' responses, θ , were analyzed
330 in terms of errors (*Err*) made in reproducing the memorized target orientations, Θ . So
331 that for the i^{th} response to a target, t , the error $Err_{t,i} = \theta_{t,i} - \Theta_t$. In order to focus the
332 analyses on the effect of the sensory conflict, we first corrected for any global rotation of
333 responses that might occur due to possible Muller or Aubert effects (for review see
334 Howard 1982), independent from the tilt of the visual scene in the conflict situation. To
335 this end, we subtracted the global response *Bias* after left head tilts without sensory
336 conflict, from all *Err* values for trials performed with the head tilted to the left (with and
337 without conflict) and the same was done for the trials with right head tilts, on a subject-
338 by-subject basis. By subtracting the potential response biases associated to the head
339 tilts, we were able to analyze together the results of the trials with right and left tilt of
340 the head. Then we subtracted the mean of all responses without conflict from each *Err*
341 associated to each specific trial with conflict and we normalized this difference by the
342 actual rotation of the visual scene.

$$\forall t \in \text{trial}_{\text{withconfl}} \quad dev_t = \frac{Err_t - \text{mean}(Err_{\text{withoutconfl}})}{-\text{head_angle}_t \cdot 0.6} \quad (1)$$

343 Next, the mean value of these normalized deviations was computed, for each subject and
344 for each condition.

$$\overline{dev} = \frac{\sum_{t=1}^{28} dev_t}{28} \cdot 100 \quad (2)$$

345 The average deviation \overline{dev} corresponds to the percentage weight given to the visual
346 information versus other sources of information.

347

348 We also evaluated the subjects' precision, *Prec*. To this end, we employed for the trials
349 without conflict of this set of data the same linear regression technique used for
350 Experiment 1, with the only difference being that, before combining the responses
351 following right and left head tilts, we subtracted the respective global *Bias* in order to
352 compensate for possible Muller or Aubert effects induced by head tilts with respect to
353 gravity. For sake of simplicity we have restricted the analyses of this second experiment
354 to the parameters directly comparable with the results previously obtained in Tagliabue
355 and McIntyre (2013), i.e. \overline{dev} and Precision.

356 *Statistical Analyses*

357 A t-test for repeated measures was performed on the average response deviations
358 \overline{dev} and on the response precision, *Prec*. The t-test model used the task type
359 (*Inter/Mirror* or *Inter/Parallel*) as the single independent within-subject factor. To test
360 whether the response deviations due the scene tilt were significantly greater than zero,
361 according to our *a priori* hypothesis, one-tailed Student's t-tests were performed.

362 **Results**

363 **Experiment 1 (*Intra – Inter/Mirror – Inter/Parallel*)**

364 Figure 4 shows the motor responses for individual subjects for each of the three
365 experimental conditions without visual landmarks. Although errors were non-negligible
366 for individual targets, the subject globally succeeded in performing the task.
367 Qualitatively, the *Inter/Parallel* condition seems characterized by larger errors with
368 respect to the other two conditions.

369

(Figure 4 about here)

370 *Accuracy:* As shown in Figure 5A, subjects were most accurate (smaller values of Accu)
371 in the *Intra*-manual condition, less so in the *Inter/Mirror* condition and significantly
372 worse in the *Inter/Parallel* condition. *Accu* was indeed clearly affected by the
373 experimental condition ($F_{(2,46)}=27.74$, $p<10^{-5}$), with a level of accuracy significantly
374 different between each conditions. The effect sizes for each condition are reported in
375 Table 1. The presence of visual landmarks did not seem to affect the absolute error
376 made by the subjects ($F_{(1,23)}=0.12$, $p=0.73$) and no statistically significant interaction
377 between the effect of the experimental condition and the visual landmarks was observed
378 ($F_{(2,46)}=1.02$, $p=0.37$).

379 (Figure 5 about here)

380 (Table 1 about here)

381 *Bias:* In Figure 5B the global deviation of the subjects' responses appears very similar in
382 the *Intra* and *Inter/Mirror* conditions and larger, and in the opposite direction, in the
383 *Inter/Parallel* condition. This latter difference, however, was not statistically significant,
384 because no clear effect of the experimental condition resulted from the ANOVA test
385 ($F_{(2,46)}=2.76$, $p=0.07$). As for the Accuracy, no significant effect of the visual landmarks
386 on *Bias* was detected ($F_{(1,23)}=1.15$, $p=0.29$).

387 *Contraction:* The deviation of the subjects' responses toward or away from the vertical
388 was affected by the experimental condition ($F_{(2,46)}=9.07$, $p<0.001$). Responses in the
389 *Inter/Parallel* condition were attracted toward the vertical (t-test $Contr > 0$: $F_{(23)}=2.42$,
390 $p=0.01$) and this pattern of errors significantly differed from the one seen in both *Intra*
391 and *Inter/Mirror* conditions (post-hoc tests $p<0.001$, effect sizes in Table 1), where the
392 responses tended to be slightly repelled by the vertical instead (t-test $Contr < 0$:
393 $F_{(23)} = -3.24$, $p=0.002$ and $F_{(23)}=-1.74$, $p=0.05$ for *Intra* and *Inter/Mirror* respectively).

394 The visual landmarks appear to have had no significant effect on contraction of
395 responses toward the vertical ($F_{(1,23)}=0.41$, $p=0.53$) and no interaction between the
396 experimental condition and visual landmarks was observed ($F_{(2,46)}=1.28$, $p=0.29$).

397 *Precision*: The residuals around the regression line were not significantly affected by
398 target orientation ($F_{(6,138)}=1.41$, $p=0.21$), thus the *Prec* parameter appears to well
399 represents the within-subject response variability. *Prec* was significantly modulated by
400 the experimental condition ($F_{(2,46)}=41.12$, $p<10^{-5}$), with a significantly larger variable
401 error in the *Inter/Parallel*, than in either the *Intra* and *Inter/Mirror* conditions (post-hoc
402 comparisons : $p<0.001$). Effect sizes of the condition factor are reported in Table 1.
403 Visual landmarks did not appear to affect response precision ($F_{(1,23)}=1.15$, $p=0.29$) nor
404 did they significantly interact with the effect of the experimental condition ($F_{(2,46)}=0.66$,
405 $p=0.52$).

406 Overall, this first experiment allows for an evaluation of the new *Inter/Mirror* procedure
407 compared to the *Intra* and the *Inter/Parallel* conditions. While the *Inter/Mirror*
408 paradigm appears intermediate in term of accuracy, all other parameters (*Bias*; *Contr*;
409 *Prec*) were similar to the *Intra* condition and differed significantly from the
410 *Inter/Parallel* condition.

411

412 Experiment 2 (Sensory Weighting – *Inter/Mirror* vs *Inter/Parallel*)

413 In this experiment, a sensory conflict was used in order to dissociate the visual and the
414 gravitational verticals (see Figure 2 and procedures) and thus estimate the reliance on a
415 visual representation of the task. Because all the methodologies are similar to the one
416 previously used, results of the present *Inter/Mirror* Vs *Inter/Parallel* experiment can be

417 directly compared to the results obtained in our previous *Intra Vs Inter* experiment
418 (Tagliabue and McIntyre 2013).

419 The effect of tilting the visual scene in each of the experimental conditions is
420 qualitatively represented in Figure 6. In the *Inter/Mirror* condition the conflict appears
421 to have had no clear effect on the subjects' responses, as was the case in the *Intra-*
422 *manual* condition from our previous study (Figure 4 and 5A in Tagliabue and McIntyre,
423 2013). On the other hand, in the *Inter/Parallel* condition the hand of the subjects
424 deviated significantly in the direction of the scene rotation, reproducing the same effect
425 that we observed in the "INTER-manual" condition of Tagliabue and McIntyre (2013).

426 (Figure 6 about here)

427 Statistical analyses of the average responses' deviation, \overline{dev} , (see Figure 7A) fully
428 support this qualitative observation. The t-test shows that \overline{dev} , was strongly affected by
429 the experimental condition ($F_{(1,19)}=14.25$, $p=0.001$, effect size: 22%). Figure 7A allows
430 one to appreciate how such modulation between the *Inter/Mirror* and *Inter/Parallel*
431 conditions was very similar to what we previously obtained with a statistically
432 significant effect between the *Intra-* and *Inter-*manual conditions.

433 Modulation of *Precision* shown in figure 7B is consistent with the statistically significant
434 modulation that we observed between the analogous two conditions in the Experiment
435 1 and it is also very similar to the precision modulation between the *Intra-* and *Inter-*
436 *manual* conditions observed in our previously work (Tagliabue and McIntyre 2013). The
437 within-subject variability indeed increased significantly between the *Inter/Mirror* and
438 *Inter/Parallel* condition ($F_{(1,19)}=5.30$, $p=0.03$, effect size: 1.6°).

439 (Figure 7 about here)

440 Overall, these results confirm and extend our previous findings by demonstrating that
441 the increased sensory weighting of the visual scene observed during the *Inter/Parallel*
442 task does not depend on the use of both limbs *per se*. These results are further discussed
443 below.

444

445 Discussion

446 The present experiments aimed at better understanding which factors lead the brain to
447 visually encode goal-oriented motor tasks in which both target and movement are
448 sensed using proprioceptive information only. We recently demonstrated that
449 sensorimotor tasks in which the subjects have to sense the target with one hand and
450 reach/point it with the other hand result in a partial representation of the task in visual
451 frame, based on an observed reliance on the orientation of the visual scene. Conversely,
452 when this inter-limb transfer of information is not required, the brain appears to avoid
453 using visual encoding of the task (Tagliabue and McIntyre 2011, 2013). These
454 experimental observations are consistent with the theoretical predictions that the visual
455 reconstruction of the purely proprioceptive task can statistically improve the
456 sensorimotor precision only when the necessity of transferring the proprioceptive
457 signals between the two limbs prevents direct comparison between the target and hand
458 information. Our previous study, however, did not allow us to disentangle whether the
459 direct comparison between the target and hand information was prevented by the
460 necessity of transferring the proprioceptive information between hemispheres *per se* or
461 by the necessity of transforming the joint angles of one arm into different angles of the
462 other arm so as to match the orientation of the hand. Here we have presented the results
463 of two experiments allowing us to answer to this question.

464

465 *Experiment 1*

466 In the first experiment we directly compared different quantitative assessments of
467 alignment errors (bias, accuracy, contraction and precision) of subjects performing
468 tasks requiring: neither inter-hemispheric transfer nor joint-signal transformations
469 (*Intra*), inter-hemispheric transfer but not joint-signal transformations (*Inter/Mirror*)
470 and both inter-hemispheric transfers and joint-signal transformations (*Inter/Parallel*).
471 Although some differences were observed between the analyzed parameters, the
472 sensorimotor errors in the two conditions not requiring joint-signal transformations
473 (*Intra* and *Inter/Mirror*) tended to be similar, and both appeared smaller than the
474 *Inter/Parallel* condition that requires transformations of the joint angles. These results
475 suggest that sensory signals are processed in a similar way when comparing intrinsic
476 joint configurations, despite the fact that one task is intra-hemispheric and the other is
477 inter-hemispheric. Only in the condition where the proprioceptive joint signals needed
478 to be transformed did the information appear to be processed in a different way. In
479 particular, lower accuracy and precision in the *Inter/Parallel* condition than in the other
480 two conditions is consistent with the hypothesis that a more complex processing of the
481 sensory information is necessary in the *Inter/Parallel* condition. The fact that both the
482 *Intra* and *Inter/Mirror* conditions were characterized by a slight repulsion from the
483 vertical, which was previously shown for a purely proprioceptive task (Tagliabue and
484 McIntyre, 2011), and which differs from the slight attraction toward the vertical
485 observed in the *Inter/Parallel* condition and other multimodal tasks (Tagliabue and
486 McIntyre, 2011), is also consistent with our hypothesis and provides a first clue that

487 both *Intra* and *Inter/Mirror* tasks are encoded in a purely proprioceptive reference
488 frame, whilst the *Inter/Parallel* task entails the integration of other sensory signals.

489 The greater accuracy and precision in the *Inter/Mirror* than in the *Inter/Parallel*
490 condition observed here appears to be highly consistent with the similar findings on
491 bimanual tracking tasks reported by Alaerts et al. (2007) and of Boisgontier et al.
492 (2014). The results of the present study seem, nonetheless, to contrast with the finding
493 of Iandolo et al. (2015), who showed that blindfolded subjects tend to perform better
494 when reproducing the spatial location of the contralateral hand (extrinsic condition)
495 than when mirroring it with respect to their sagittal plane (intrinsic condition). These
496 apparently contradicting results can be reconciled, however, by the fact that an imposed
497 10-cm height difference between the two hands (for hands placed on average at a 6.5cm
498 horizontal distance) actually prevented the mirroring of the hand positions by simply
499 reproducing the same joint angles in the two arms. As a consequence, and in contrast to
500 our experiment, the subjects in that experiment most likely had to perform a sensory
501 transformation in both intrinsic and extrinsic conditions.

502 To understand whether the differences observed here actually correspond to the
503 reconstruction of a visual representation of the task, we investigated whether adding, or
504 removing environmental visual landmarks would affect the motor errors made by the
505 subjects; the rationale being that, the additional visual environmental information
506 should improve the performance mainly in the conditions where a visual encoding is
507 used. The addition of visual landmarks in the virtual environment did not, however,
508 produce clear improvement in the response accuracy and precision. Although, we
509 cannot exclude, of course, the possibility that visual information was not used at all in
510 this first experiment, we believe that the lack of the effect of the landmarks could be due

511 to an insufficient sensitivity of this experimental technique to modulations of the
512 contribution of the visual information. Indeed, we note that all components of the
513 reaching error tended to be reduced, although not significantly, by the presence of the
514 visual landmarks only in the *Inter/Parallel* condition. This qualitative observation
515 appears to support the hypothesis that visual information might have been used in this
516 condition, but that its effect wasn't large enough to be quantified by our experimental
517 paradigm. Experiment 2 was more effective in this regard (see below).

518

519 *Experiment 2*

520 To investigate modulations in the use of a visual representation of our proprioceptive
521 task, we performed a second experiment in which we compared the two Inter-limb
522 conditions (*Inter/Mirror* and *Inter/Parallel*), which differ by the necessity, or not, of
523 transforming intrinsic joint angle signals. In this experiment we measured the deviation
524 of the motor responses generated by an imperceptible deviation of the visual
525 environment in order to quantify the relative weight given by the brain to the visual and
526 proprioceptive representations of the task, respectively. This technique, which we
527 extensively used in the past to show modulations of multisensory weighting (Tagliabue
528 and McIntyre 2011, 2012, 2013, 2014, Tagliabue et al 2013), allowed us to quantify the
529 difference between the *Inter/Mirror* and *Inter/Parallel* conditions in terms of the
530 importance given by the brain to the visual environment. This difference between
531 conditions appears very similar to what we observed between the *Intra* and
532 *Inter/Parallel* conditions in Tagliabue and McIntyre (2013) (see Figure 7). More
533 specifically, in the *Inter/Mirror* condition subjects appeared to neglect the visual scene,
534 as we previously observed in the *Intra* condition, whilst in the *Inter/Parallel* condition

535 the relative weight given to the visual representation rose to nearly 30%. This latter
536 result is fully consistent with what we observed in our previous study (Tagliabue and
537 McIntyre 2013) for the *Inter* condition, of which the present *Inter/Parallel* condition is a
538 replica.

539 The here-observed modulation of the sensory weighting, and its strong similarity with
540 the modulation between intra-manual and inter-manual task shown in Tagliabue and
541 McIntyre (2013), confirms that the reconstruction of the visual representation of purely
542 proprioceptive tasks is not due to the inter-hemispheric transfer of the proprioceptive
543 information *per se*, as the results of our previous work could have suggested. This
544 modulation appears to be related rather to the necessity of transforming the
545 proprioceptive signals relative to the intrinsic joint angles of one arm into different
546 angles for the other arm.

547 If these findings are interpreted in the frame of our modular sensory-integration model
548 (Tagliabue and McIntyre 2011, 2013, 2014), more detailed conclusions can be drawn.
549 Our model predicts that the brain does not reconstruct representations of the movement
550 in additional sensory modalities when a direct, uni-modal comparison between the
551 sensory information related to the target and to the moving hand is possible. It follows
552 that the very similar results observed in the *Intra* and *Inter/Mirror* conditions, both in
553 terms of errors patterns and sensory weighting, would mean that the brain can directly
554 match proprioceptive signals from the two different hemispheres with almost no
555 additional processing, as if they came from the same receptors, provided that they come
556 from homologous sensors (see Figure 8). This conclusion could have a neural correlate
557 in the finding of Diedrichsen and colleagues (2012), showing that, during uni-manual
558 finger movement, patterns of activity identical to those generated by contralateral

559 mirror-symmetric movement can be observed on the ipsilateral hemisphere S1 and M1.
560 One could indeed think that this kind of mirror-symmetric ‘resonance’ between
561 hemispheres could reflect privileged connections between inter-hemispheric
562 homologous hand proprioceptive receptors and actuators.

563 (Figure 8 about here)

564 On the other hand, the clear difference between the *Inter/Parallel* and the *Inter/Mirror*
565 conditions both in terms of errors (Experiment 1) and in terms of visual encoding
566 (Experiment 2) is consistent with the prediction of our model for conditions in which a
567 direct comparison between the target and response sensory signal is not possible. In our
568 previous works (Tagliabue and McIntyre 2013-2014) we have shown that in this
569 situation the statistically optimal solution (*maximum likelihood principle*) consists of
570 transforming the proprioceptive signals to encode them in multiple reference frames,
571 including, in some cases, a visual representation (Tagliabue and McIntyre, 2013). Such
572 use of the sensory signals provides, indeed, partially independent representations of the
573 task, whose combination reduces the task-execution variability compared to what would
574 be obtained by encoding the task in any single reference frame. The less-than-full
575 deviation of the responses due to the tilt of the visual scene observed in the
576 *Inter/Parallel* condition hence reflects the encoding of the proprioceptive signals into a
577 visual reference frame that is combined with the encoding of the same information in
578 other reference frames that are not affected by the tilt of the visual scene. Among these
579 latter reference frames there are probably egocentric (for instance trunk- or head-
580 centered) encodings as well as external encodings using gravitational information
581 (Tagliabue and McIntyre 2012). Such multiple encoding of the information is
582 simplistically represented in Figure 8.

583 The differences reported here between the *Mirror* and *Parallel* inter-manual tasks and
584 our interpretation of this finding in terms of different information processing appear
585 consistent with the results of several other brain imaging studies. Parallel tasks (often
586 referred to as “anti-phase tasks” for repetitive movements) appear to activate additional
587 brain areas (SMA, S1, M1, CMA and PM) with respect to Mirror (in-phase) tasks (Sadato
588 et al 1997, Goerres et al. 1998, Stephan et al. 1999a-b, Immisch et al. 2001). One could
589 speculate that these brain areas could be involved in encoding the task in additional
590 reference frames. However, the activation of any ‘visual’ areas, which would even better
591 match our prediction, has not been detected. This could be due to the fact that no
592 “useful” visual information were provided to the subject and that fast rhythmic
593 movements tested in these previous studies could lend themselves less easily to a visual
594 representation with respect to the slow goal-oriented motor task we tested. Although
595 the encoding of the proprioceptive information in multiple reference frames and their
596 optimal combination correspond to the best sensorimotor performance, this is by
597 definition still noisier than the direct comparison of the proprioceptive signals, such as
598 those used in the *Intra* and *Inter/Mirror* conditions (Tagliabue and McIntyre 2013). This
599 model prediction perfectly matches the observed increase in variability between the
600 *Inter/Parallel* and the other two experimental conditions.

601

602 *Inter-manual coordination*

603 The present findings not only provide a clear answer to our initial question about the
604 visual encoding of purely proprioceptive tasks, but could also contribute to a better
605 understanding of the neural mechanisms underlying the coordination of bimanual cyclic
606 movements (for review see Swinnen 2002, Swinnen and Wenderoth 2004). Specifically,

607 the results from our experiments show that “parallel” matching tasks tend to show
608 higher variability than “mirror” matching tasks. Although one might question whether
609 the quasi-static matching tasks performed here can directly speak to mechanisms of
610 rhythmic movements, the legitimacy of transposing the present findings from discrete to
611 rhythmic movements is supported by the fact that theoretically both movement
612 categories can be generated by the same sensorimotor control mechanisms (Ronsee et
613 al. 2009). Our observations about the noisiness of parallel versus mirror tasks, applied
614 cautiously, gives rise to new perspectives on the phenomena observed in more dynamic
615 tasks, as we describe below.

616 Several studies have shown that in-phase (*Mirror*) rhythmic movements of the hands
617 are significantly more stable than anti-phase (*Parallel*) movements, so that subjects
618 asked to perform rapid anti-phase cyclic movements show sudden abrupt transitions to
619 the in-phase movements; and once this transition occurred they do not go back to the
620 anti-phase mode (Yamanishi et al. 1980, Kelso 1984, Carson 1995, Semjen et al. 1995,
621 Swinnen et al 1997-1998). Interestingly, these phenomena appear to have more
622 sensorial than motor origins (Mechsner et al 2001, Weigelt and Cardoso de Oliveira
623 2003, Ronsse et al. 2009), although the debate is not settled yet (Swinnen et al. 2003).

624 Several studies successfully modeled this phenomenon by describing the system as non-
625 linear oscillators with potential functions as represented in Figure 9A. In these models
626 in-phase movements correspond to a deep global minimum and the anti-phase
627 movements correspond to a smaller local minimum, which disappear at high
628 frequencies (Haken et al. 1985, Schoner et al. 1986, Beek et al. 2002). Abrupt transitions
629 from the anti-phase to the in-phase movement can be described as a ball falling from the
630 local minimum to the global minimum, due to modification of the potential curve profile

631 and to some random noise/perturbation (represented as arrows in Figure 9). Whilst in
632 the original model this noise was considered independent from the phase between the
633 hands, here we have shown that the noise of the sensory system is actually greater in the
634 *Parallel* than in the *Mirror* condition. This suggests that different levels of noise may
635 characterize the in- and anti- phase bimanual movements. If this noise modulation is
636 taken into account, then our results lead to an alternative system representation
637 characterized by a potential curve with two similar minima for the in- and anti-phase
638 movements (Figure 9B). In this case the ball would tend to move from the anti-phase to
639 the in-phase condition, and not vice-versa, because in the former, but not in the latter, a
640 large noise would tend to push it outside the local minimum. Further experiments will
641 be needed to specifically investigate this alternative interpretation of instability
642 phenomena during bi-manual cyclic movements.

643 (Figure 9 about here)

644 **Conclusions**

645 The present findings suggest that the inter-hemispheric transfer of the information
646 necessary in the task of mirroring one hand with the other does not increase
647 sensorimotor errors *per se*. This suggests that the brain can directly compare the
648 sensory signals coming from homologous muscles/receptor in the same way as signals
649 coming from the same receptors. Moreover, we were able to show that, in agreement
650 with the idea of optimal multi-sensory integration, the brain tends to build up multiple
651 representations of a purely proprioceptive sensorimotor task (both target sensing and
652 movement control only through proprioceptive information), including a visual
653 representation, but only when a noisy transformation of the joint signals is necessary,
654 and not simply when an inter-hemispheric transfer is involved in the task execution.

655 Interestingly, the present findings could also contribute to a better understanding of the
656 inter-manual coordination by suggesting an important role of the sensory noise in the
657 instability of anti-phase with respect to in-phase movements.

658 Acknowledgements

659 This work was supported by the French Space Agency (Centre National d'Etudes
660 Spatiales). We gratefully acknowledge the support of the Paris Descartes Platform for
661 Sensorimotor Studies (Université Paris Descartes, CNRS, INSERM, Région Île-de- France)
662 and of Patrice Jegouzo (Université Paris Descartes) for technical support.

663 References

- 664 Alaerts K, Levin O, Swinnen SP. Whether feeling or seeing is more accurate depends on tracking direction
665 within the perception-action cycle. *Behavioural brain research* 178: 229-234, 2007.
- 666 Bays PM, Wolpert DM. Computational principles of sensorimotor control that minimize uncertainty and
667 variability. *J Physiol* 578(Pt 2): 387-396, 2007.
- 668 Beek PJ, Peper CE, Daffertshofer A. Modeling rhythmic interlimb coordination: beyond the Haken-Kelso-
669 Bunz model. *Brain Cogn* 48(1): 149-165, 2002.
- 670 van Beers RJ, Sittig AC, van der Gon JJD. How humans combine simultaneous proprioceptive and visual
671 position information. *Exp Brain Res* 111(2): 253-261, 1996.
- 672 van Beers RJ, Sittig AC, Gon JJD. Integration of proprioceptive and visual position-information: An
673 experimentally supported model. *J Neurophysiol* 81(3): 1355-1364, 1999.
- 674 Blouin J, Saradjian AH, Lebar N, Guillaume A, Mouchnino L. Opposed optimal strategies of weighting
675 somatosensory inputs for planning reaching movements toward visual and proprioceptive targets. *J*
676 *Neurophysiol* 112: 2290-2301, 2014.
- 677 Boisgontier MP, Van Halewyck F, Corporaal SHA, Willacker L, Van Den Bergh V, Beets IAM, Levin O,
678 Swinnen SP. Vision of the active limb impairs bimanual motor tracking in young and older adults. *Frontiers in*
679 *aging neuroscience* 6: 320, 2014.
- 680 Carrozzo M, Stratta F, McIntyre J, Lacquaniti F. Cognitive allocentric representations of visual space shape
681 pointing errors. *Exp Brain Res* 147:426-436, 2002.
- 682 Carson RG. The dynamics of isometric bimanual coordination. *Exp Brain Res* 105(3): 465-476, 1995.
- 683 Diedrichsen J, Werner S, Schmidt T, Trommershäuser J. Immediate spatial distortions of pointing movements
684 induced by visual landmarks. *Perception & psychophysics* 66: 89-103, 2004.
- 685 Diedrichsen J, Wiestler T, Krakauer JW. Two Distinct Ipsilateral Cortical Representations for Individuated
686 Finger Movements. *Cereb Cortex* 23(6): 1362-1377, 2012.
- 687 Faisal AA, Wolpert DM. Near optimal combination of sensory and motor uncertainty in time during a
688 naturalistic perception-action task. *J Neurophysiol* 101(4): 1901-1912, 2009.
- 689 Fetsch CR, Pouget A, DeAngelis GC, Angelaki DE. Neural correlates of reliability-based cue weighting
690 during multisensory integration. *Nat Neurosci* 15(1): 146-154, 2012.
- 691 Ghahramani Z, Wolpert DM, Jordan MI. Computational models of sensorimotor integration, *In: Self-*
692 *organization, Computational Maps, and Motor Control*, Oxford: Elsevier, 1997, p. 117-147.
- 693 Goble DJ. Proprioceptive acuity assessment via joint position matching: from basic science to general
694 practice. *Phys Ther.* 90: 1176 –1184, 2010.
- 695 Goerres GW, Samuel M, Jenkins IH, Brooks DJ. Cerebral control of unimanual and bimanual movements: an
696 H2(15)O PET study. *Neuroreport* 9(16): 3631-3638, 1998.

- 697 Haken H, Kelso JA, Bunz H. A theoretical model of phase transitions in human hand movements. *Biol*
698 *Cybern* 51(5): 347-356, 1985.
- 699 Howard I. *Human visual orientation*, New York: Wiley, 1982.
- 700 Iandolo R, Squeri V, De Santis D, Giannoni P, Morasso P, Casadio M. Proprioceptive bimanual test in
701 intrinsic and extrinsic coordinates. *Front Hum Neurosci* 9: 72, 2015.
- 702 Immisch I, Waldvogel D, van Gelderen P, Hallett M. The role of the medial wall and its anatomical
703 variations for bimanual antiphase and in-phase movements. *Neuroimage* 14(3): 674-684, 2001.
- 704 Jones SAH, Cressman EK, Henriques DYP. Proprioceptive localization of the left and right hands. *Exp Brain*
705 *Res* 204(3): 373-383, 2010.
- 706 Kelso JA. Phase transitions and critical behavior in human bimanual coordination. *Am J Physiol* 246(6 Pt
707 2): R1000-R1004, 1984.
- 708 Körding KP, Wolpert DM. Bayesian integration in sensorimotor learning. *Nature* 427(6971): 244-247,
709 2004.
- 710 McGuire LMM, Sabes PN. Sensory transformations and the use of multiple reference frames for reach
711 planning. *Nat Neurosci* 12(8): 1056-1061, 2009.
- 712 McIntyre J, Lipshits M. Central processes amplify and transform anisotropies of the visual system in a test
713 of visual-haptic coordination. *J Neurosci* 28: 1246-1261, 2008.
- 714 McIntyre J, Stratta F, Lacquaniti F. Short-term memory for reaching to visual targets: psychophysical
715 evidence for body-centered reference frames. *J Neurosci* 18: 8423-8435, 1998.
- 716 Mechsner F, Kerzel D, Knoblich G, Prinz W. Perceptual basis of bimanual coordination. *Nature* 414(6859):
717 69-73, 2001.
- 718 Obhi SS, Goodale MA. The effects of landmarks on the performance of delayed and real-time pointing
719 movements. *Exp Brain Res* 167: 335-344, 2005.
- 720 Pouget A, Deneve S, Duhamel JR. A computational perspective on the neural basis of multisensory spatial
721 representations. *Nat Rev Neurosci* 3(9): 741-747, 2002.
- 722 Proske U, Gandevia SC. The proprioceptive senses: their roles in signaling body shape, body position and
723 movement, and muscle force. *Physiological reviews* 92: 1651-1697, 2012.
- 724 Rohe T, Noppeney U. Distinct Computational Principles Govern Multisensory Integration in Primary
725 Sensory and Association Cortices. *Curr Biol* 26(4): 509-514, 2016.
- 726 Ronsse R, Miall RC, Swinnen SP. Multisensory integration in dynamical behaviors: maximum likelihood
727 estimation across bimanual skill learning. *J Neurosci* 29(26): 8419-8428, 2009.
- 728 Ronsse R, Sternad D, Lefèvre P. A computational model for rhythmic and discrete movements in uni- and
729 bimanual coordination. *Neural Computation* 21: 1335-1370, 2009.
- 730 Sabes PN. Sensory integration for reaching: models of optimality in the context of behavior and the
731 underlying neural circuits. *Prog Brain Res* 191: 195-209, 2011.
- 732 Sadato N, Yonekura Y, Waki A, Yamada H, Ishii Y. Role of the supplementary motor area and the right
733 premotor cortex in the coordination of bimanual finger movements. *J Neurosci* 17(24): 9667-9674, 1997.
- 734 Sarlegna FR, Sainburg RL. The effect of target modality on visual and proprioceptive contributions to the
735 control of movement distance. *Exp Brain Res* 176(2): 267-280, 2007.
- 736 Schöner G, Haken H, Kelso JA. A stochastic theory of phase transitions in human hand movement. *Biol*
737 *Cybern* 53(4): 247-257, 1986.
- 738 Semjen A, Summers JJ, Cattaert D. Hand coordination in bimanual circle drawing. *Journal of Experimental*
739 *Psychology: Human Perception and Performance* 21(5): 1139, 1995.
- 740 Sober SJ, Sabes PN. Flexible strategies for sensory integration during motor planning. *Nat Neurosci* 8(4):
741 490-497, 2005.
- 742 Stephan KM, Binkofski F, Halsband U, Dohle C, Wunderlich G, Schnitzler A, Tass P, Posse S, Herzog H,
743 Sturm V, Zilles K, Seitz RJ, Freund HJ. The role of ventral medial wall motor areas in bimanual co-
744 ordination. A combined lesion and activation study. *Brain* 122(Pt 2): 351-368, 1999.

745 Stephan KM, Binkofski F, Posse S, Seitz RJ, Freund HJ. Cerebral midline structures in bimanual
746 coordination. *Exp Brain Res* 128(1-2): 243-249, 1999.

747 Swinnen SP. Intermanual coordination: from behavioural principles to neural-network interactions. *Nat*
748 *Rev Neurosci* 3(5): 348-359, 2002.

749 Swinnen SP, Jardin K, Meulenbroek R, Dounskaia N, Brandt MHVD. Egocentric and Allocentric Constraints
750 in the Expression of Patterns of Interlimb Coordination. *Journal of Cognitive Neuroscience* 9(3): 348-377,
751 1997.

752 Swinnen SP, Jardin K, Verschueren S, Meulenbroek R, Franz L, Dounskaia N, Walter CB. Exploring
753 interlimb constraints during bimanual graphic performance: effects of muscle grouping and direction.
754 *Behav Brain Res* 90(1): 79-87, 1998.

755 Swinnen SP, Puttemans V, Vangheluwe S, Wenderoth N, Levin O, Dounskaia N. Directional interference
756 during bimanual coordination: is interlimb coupling mediated by afferent or efferent processes. *Behav*
757 *Brain Res* 139(1-2): 177-195, 2003.

758 Swinnen SP, Wenderoth N. Two hands, one brain: cognitive neuroscience of bimanual skill. *Trends Cogn*
759 *Sci* 8(1): 18-25, 2004.

760 Tagliabue M, McIntyre J. A modular theory of multisensory integration for motor control. *Front Comput*
761 *Neurosci* 8: 1, 2014.

762 Tagliabue M, McIntyre J. When Kinesthesia Becomes Visual: A Theoretical Justification for Executing
763 Motor Tasks in Visual Space. *PLoS ONE* 8(7): e68438, 2013.

764 Tagliabue M, McIntyre J. Eye-hand coordination when the body moves: Dynamic egocentric and exocentric
765 sensory encoding. *Neurosci Lett* 513: 78-83, 2012.

766 Tagliabue M, McIntyre J. Necessity is the Mother of Invention: Reconstructing Missing Sensory
767 Information in Multiple, Concurrent Reference Frames for Eye-Hand Coordination. *J Neurosci* 31(4): 1397-
768 1409, 2011.

769 Weigelt C, Cardoso de Oliveira S. Visuomotor transformations affect bimanual coupling. *Exp Brain Res*
770 148(4): 439-450, 2003.

771 Whitney D, Westwood DA, Goodale MA. The influence of visual motion on fast reaching movements to a
772 stationary object. *Nature* 423: 869-873, 2003.

773 Yamanishi J, Kawato M, Suzuki R. Two coupled oscillators as a model for the coordinated finger tapping by
774 both hands. *Biol Cybern* 37(4): 219-225, 1980.

775

776 **TABLES**

Table 1: Size of the condition effects for the response Accuracy (*Acc*), global Bias, Contraction (*Contr*) and Precision (*Prec*) expressed as the average difference between the three experimental conditions.

	<i>Accu</i>	<i>Bias</i>	<i>Contr</i>	<i>Prec</i>
Inter/Mirr.-Intra	1.8°	-0.6°	-0.1°	0.2°
Inter/Parall.-Intra	4.4°	2.7°	2.9°	2.3
Inter/Parall.-Inter/Mirr.	2.7°	3.2°	3.0°	2.1

777

778 **FIGURES**

779 **Figure 1:** Experimental conditions.

780 A) In the *Intra* condition the subject senses with the right hand the target orientation and after a delay
 781 (during which the hand is lowered) he/she reproduces the orientation with the same hand. In the
 782 *Inter/Mirror* condition the subject senses the target orientation with the left hand and after a delay he/she
 783 mirrors the memorized orientation with the right hand.

784 In the *Inter/Parallel* condition the target is sensed with the left hand and its orientation is reproduced
 785 with the right hand.

786 On the right part of the figure a table reports whether each of the experimental conditions requires an
 787 inter-hemispheric transfer of the proprioceptive information and/or the transformation of the joint
 788 signals.

789 B) The visual environment shown to the subject in the head mounted display consisted in a cylindrical
 790 tunnel. During half of the experiment the tunnel walls had no landmarks (left image), whilst in the other
 791 half visual landmarks were added (right image).

792 **Figure 2:** Experimental paradigms for Experiments 1 and 2. For both experiments the condition
 793 *Inter/Parallel* is used as an example. In this graphical representation the images displayed to the subject
 794 through the virtual reality goggles are represented in a square placed in front of the avatar shown in the
 795 figures. Note that for illustrative purpose, the hand was drawn, however the subject's hand was never
 796 rendered in the VR goggles and the head mounted display prevented direct visual observation of the
 797 hand's orientation in space.

798 A) Experiment 1. During the memorization phase the subject rotated his/her hand in front of him/her and
 799 the virtual environment changed color as function of the hand pronosupination. The subject had to
 800 memorize the hand orientation corresponding to the green color. After memorization the subject was
 801 asked to lower the arm and wait for 5 s. After the delay, the subject had to raise his/her hand and
 802 reproduce the memorized orientation.

803 B) Experiment 2. The paradigm was the same as in Experiment 1, but during the 5 s delay after
 804 memorization the subject performed an audio-controlled 15° head rotation and responded while keeping
 805 the head tilted. In 50% of the trials a gradual, imperceptible conflict was applied: the visual scene was
 806 tilted with respect to gravity by an angle equal to -0.6 times the head inclination, so that the visual and
 807 gravitational verticals no longer matched.

808 **Figure 3:** Data analyses. Simulated data showing typical data for a single subject's responses, θ , to
 809 different target orientation, Θ . For each target three responses were provided by the subject. For each
 810 target the mean response, $\bar{\theta}$, is represented (squares). $\bar{\theta}$ was then used to compute the global response
 811 *Bias* (small in this example), the average response accuracy, *Accu*, as well as the response contraction,
 812 *Contr*, toward the vertical. To estimate response precision (variability) the linear regression of all 21
 813 responses is performed (dashed line), then for each response the residual, *res*, from the regression line is
 814 computed. The response precision is associated to the response dispersion around the regression line:
 815 root mean squared residual.

816 **Figure 4:** Orientation of the subjects' hand as function of the target inclination, in the three experimental
 817 conditions. Each line represents data from a single subject and each point represent the average of the
 818 three responses made by a given subject for one target orientation. Black points show what would be the
 819 responses corresponding to null error.

820 **Figure 5:** Quantification of subjects' average performance in the three experimental conditions, in terms
821 of accuracy (*Accu*), total average shift of the responses (*Bias*), contraction of the responses toward the
822 vertical (*Contr*) and variability of the responses (*Prec*). Vertical whiskers represent the 0.95 confidence
823 intervals. Stars represent the results of the Newman-Keuls post-hoc tests. (** $p < 0.001$; * $p < 0.01$).

824 **Figure 6:** Subject responses to each target orientation in the *Inter/Mirror* and *Inter/Parallel* conditions.
825 The responses for the trials with and without conflict are represented separately. Thick lines are the
826 average responses (transparent areas' width represent the standard error) of all subjects, combining
827 trials with left and right head tilt. Green arrows represent the measured responses' deviations due to the
828 tilt of the visual scene.

829 **Figure 7:** Results of the present *Inter/Mirror* Vs *Inter/Parallel* experiment (black) compared with the
830 results obtained in our previous *Intra-* Vs *Inter-* manual experiment (light gray) (Tagliabue and McIntyre
831 2013). A) Deviations induced by an imperceptible tilt of the visual scene. The results are expressed as a
832 percentage of the theoretical deviation expected if subjects aligned the response with respect to the visual
833 scene. B) Response precision, *Prec*. Vertical whiskers represent the 0.95 confidence intervals. Stars
834 represent the results of the t-test comparison with the nominal 0% value and of the t-test analyses testing
835 the differences between the two experimental conditions. (** $p < 0.01$; * $p < 0.05$).

836 **Figure 8:** Simplified graphical representation of putative sensory information flow during the following
837 three different experimental conditions.

838 ***Intra:*** The proprioceptive signals coming from the right hand supinator (Sup) and pronator (Pron)
839 muscles during the target memorization can be directly compared with the proprioceptive signals coming
840 from the same muscles during the response phase. In order to achieve the task's goal the brain modifies
841 the hand orientation to minimize the difference between the corresponding target and response signals.

842 ***Inter/Mirror:*** The proprioceptive signals coming from the left hand supinator (Sup) and pronator (Pron)
843 muscles during the target memorization can be directly compared with the proprioceptive signals coming
844 from the homologous muscles of the right hand during the response phase. The task can be therefore
845 achieved as in the *Intra* condition.







846 ***Inter/Parallel:*** The task cannot be achieved by simply matching the proprioceptive signals from the
847 homologous muscles of the left and right arm. The brain has to combine the supinator and pronator signal
848 to build a representation of the right and left hand orientation than can be indirectly compared. Such
849 reconstruction of the hands' orientation can take advantage of using additional sensory signals such of
850 proprioceptive signals coming from other parts of the body, gravitational signal and visual scene
851 information, effectively performing the comparison in multiple reference frames.

852 The red color represents the elements affected by the tilt of the visual scene. Blue and black colors
853 represent the proprioceptive and gravitational signals, which are supposedly not affected by the sensory
854 conflict.

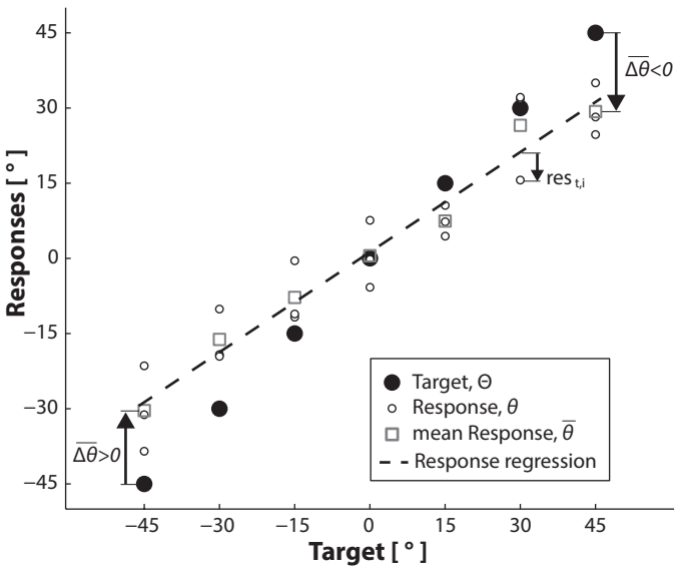
855 **Figure 9:** A) Potential curve, V , function of the phase angle between the two hands, ϕ , proposed by Haken,
856 Kelso and Bunz (1985) to represent spontaneous transitions from anti-phase ($\phi = \pi$) to in-phase ($\phi = 0$)
857 rhythmic movements. The state of the system can be described as a ball rolling along this curve. The
858 arrows represent intrinsic noise of the system, which tend to perturb the system. In the HKB model the
859 noise did not vary as a function of ϕ .

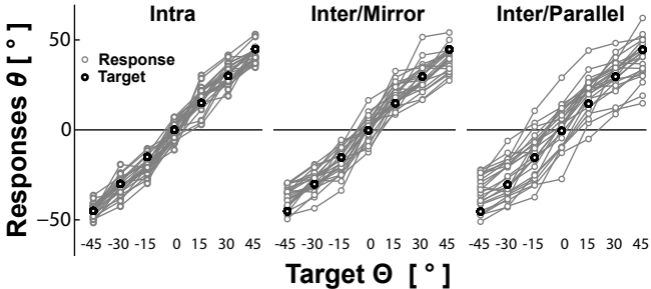
860 B) Example of an alternative representation of rhythmic movements dynamics. As an extreme case, the in-
861 and anti-phase movements correspond to similar minima of the potential function. The system noise is
862 function of ϕ and more precisely it is larger for the anti-phase than for the in-phase movements.

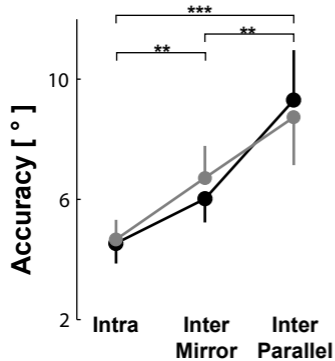
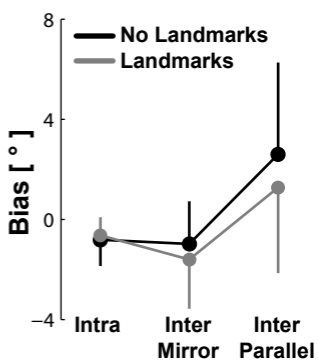
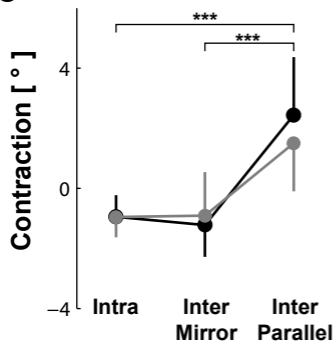
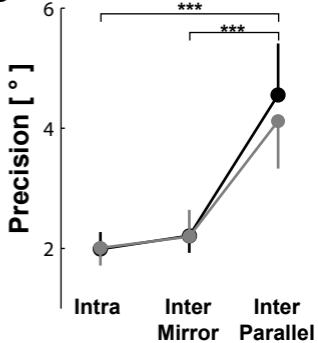
A

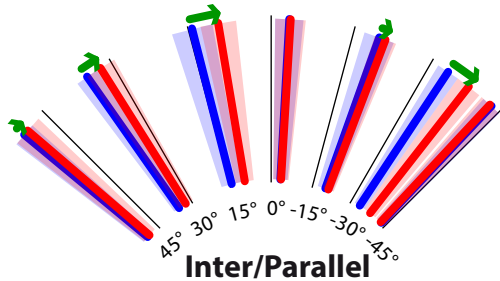
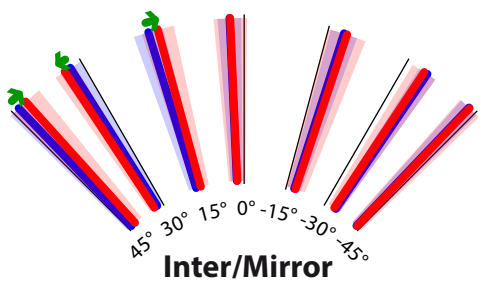
	Memorisation	Response	Inter hemisph.	Joint-angle transform.
Intra			NO	NO
Inter/Mirror			YES	NO
Inter/Parallel			YES	YES

B



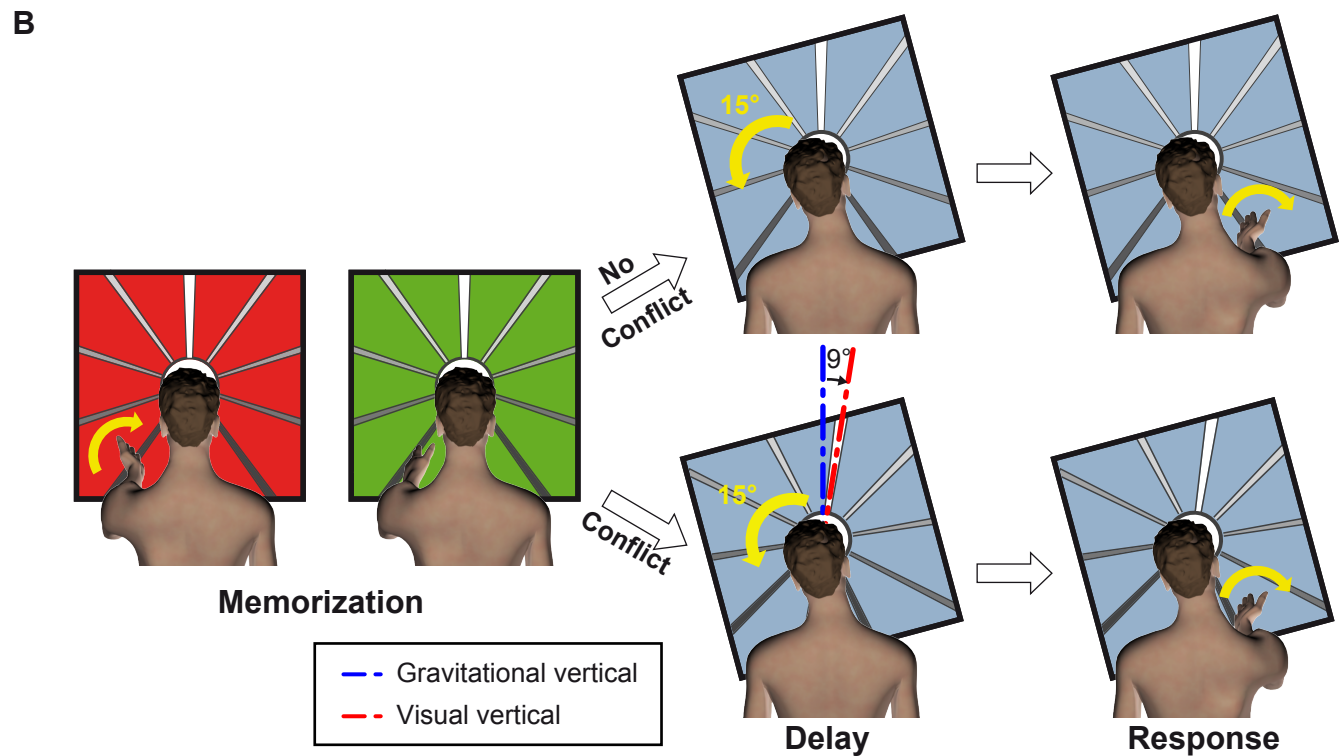
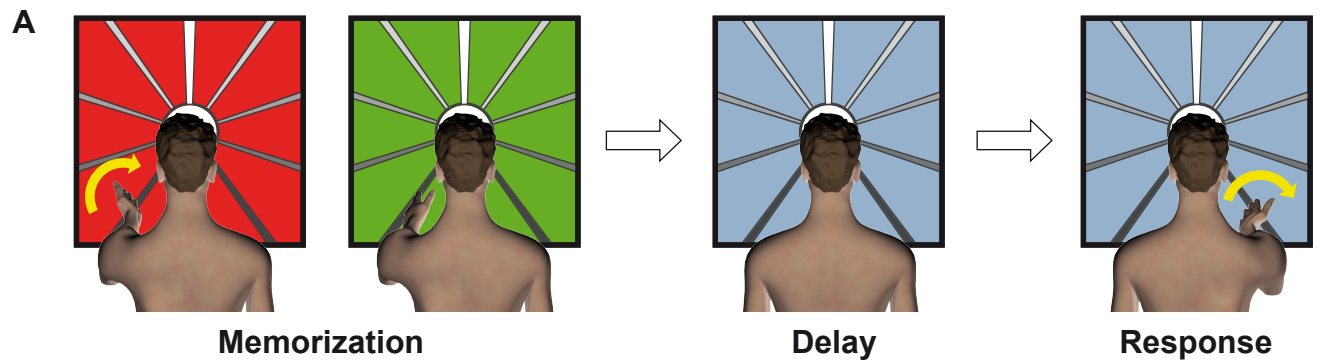


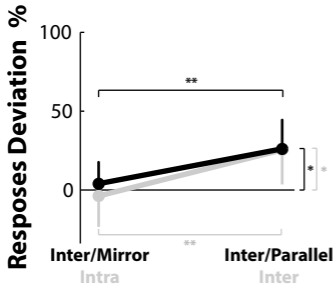
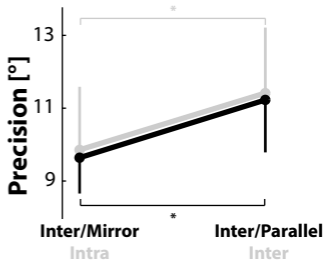
A**B****C****D**



— Target — No Conflict

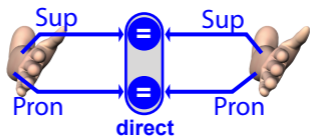
— Conflict → Deviation



A**B**

Intra

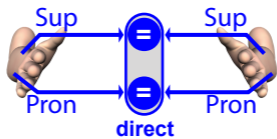
Response



Target

Inter/Mirror

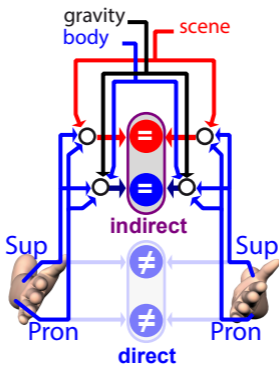
Response



Target

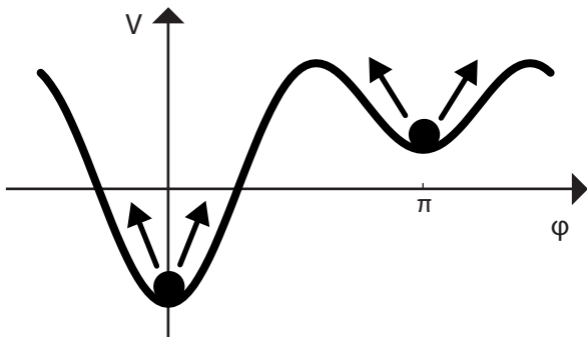
Inter/Parallel

Response



Target

A



B

