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1 **Optimal visuo-tactile integration for velocity discrimination of self-hand**
2 **movements**

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17

18

19 **Running Head: Optimal visuo-tactile integration in kinesthesia**

20

21 **Author contributions**

22

23 All the authors conceived and designed the experiment; MC & CB performed the experiments, MC
24 analysed data; MC, CB, AM & AK interpreted results of experiments; AM conceived the model; MC
25 & AK drafted the manuscript; All the authors revised the manuscript.

26 **Abstract**

27

28 Illusory hand movements can be elicited by a textured disk or a visual pattern rotating under
29 one's hand, while proprioceptive inputs convey immobility information (Blanchard et al., 2013). Here
30 we investigated whether visuo-tactile integration can optimize velocity discrimination of illusory hand
31 movements in line with Bayesian predictions. We induced illusory movements in fifteen volunteers by
32 visual and/or tactile stimulation, delivered at six angular velocities. The participants had to compare
33 hand illusion velocities with a 5°/s hand reference movement in an alternative forced choice paradigm.
34 Results showed that the discrimination threshold decreased in visuo-tactile condition compared to
35 unimodal (visual or tactile) conditions, reflecting better bimodal discrimination. The perceptual
36 strength (gain) of the illusions also increased: the stimulation required to give rise to a 5°/s illusory
37 movement was slower in the visuo-tactile condition compared to each of the two unimodal conditions.
38 The Maximum Likelihood Estimation model satisfactorily predicted the improved discrimination
39 threshold, but not the increase in gain. When we added a zero-centered Prior, reflecting immobility
40 information, the Bayesian model did actually predict the gain increase, but systematically
41 overestimated it. Interestingly, the predicted gains better fit the visuo-tactile performances when a
42 proprioceptive *noise* was generated by co-vibrating antagonist wrist muscles. These findings show that
43 kinesthetic information of visual and tactile origins is optimally integrated to improve velocity
44 discrimination of self-hand movements. However, a Bayesian model alone could not fully describe the
45 illusory phenomenon pointing to the crucial importance of the omnipresent muscle proprioceptive cues
46 with respect to other sensory cues for kinesthesia.

47

48 Key-words: Illusions, Bayesian modeling, Kinesthesia, Multisensory integration, Muscle
49 proprioception

50

51 **New & Noteworthy**

52 The present study demonstrates for the first time that kinesthetic information of visual and tactile
53 origins are optimally integrated (Bayesian modeling) to improve velocity discrimination for self-hand
54 movement. We used an original paradigm consisting in similar illusory hand movements induced
55 through visual and tactile stimulation. By testing the role of other sources of information favoring non-
56 moving hand perception we also highlight the key contribution of the omnipresent muscle
57 proprioceptive information and its over-weighting for kinesthesia.

58

59 **Introduction**

60

61 To perceive our body movement in space, we can rely on several sensory inputs. Among them,
62 the involvement of muscle proprioception in kinesthesia has been widely investigated (for reviews see
63 McCloskey, 1978; Roll et al., 1990; Proske and Gandevia, 2012). The visual system also contributes
64 to the sense of movement, as evidenced byvection phenomenon, i.e. a kinesthetic percept elicited by a
65 visual moving scene scrolling in front of a participant (Brandt and Dichgans, 1972; Guerraz and
66 Bronstein, 2008) or under one's limb (Blanchard et al., 2013). Touch, like vision, also conveys
67 kinesthetic information with cutaneous receptors sensitive to the velocity of superficial brushing
68 applied to their receptive fields (Breugnot et al., 2006). Illusions of self-body movements can thus be
69 induced using a tactile stimulus rotating under the palm of the hand (Blanchard et al., 2011, 2013).

70 However, less is known about how these two sensory modalities interact to estimate self-body
71 motion. Many studies highlighted a perceptual benefit when two or more sensory signals are
72 combined, provided they are temporally and spatially congruent. Based on a probabilistic
73 representation of information and on the assumption that minimizing the variance of the combined
74 perceptual estimate is a primary goal of multisensory integration, the Optimal Cue Combination
75 framework has provided an efficient approach to predict the perceptual enhancement due to

76 multisensory integration (Landy et al., 2011). In particular, the Maximum Likelihood Estimation
77 (MLE) principle postulates that the multisensory estimate of an event is given by the reliability-
78 weighted average of each single-cue estimates (where reliability is defined as the inverse of variance).
79 MLE predictions have been successfully reported for several multisensory tasks, but mainly when the
80 object of perception is external to the body (Ernst and Banks, 2002; Alais and Burr, 2004; Wozny et
81 al., 2008; Gingras et al., 2009; Gori et al., 2011). Whether Bayesian rules can account for multisensory
82 integration subserving self-body perception has been less investigated, especially with regard to the
83 integration of visuo-tactile kinesthetic cues. Visual and vestibular information were found to be close-
84 to-optimally integrated in the perception of whole-body displacements (Fetsch et al., 2009; Vidal and
85 Bühlhoff, 2009; Prsa et al., 2012); as vision and proprioception when evaluating arm movements
86 (Reuschel et al., 2009), positions in space (VanBeers et al., 2002; Tagliabue and McIntyre, 2013), as
87 well as when performing pointing motor tasks (Sober and Sabes, 2003, 2005).

88 The present study aimed at further investigating whether visual and tactile signals are optimally
89 integrated when estimating self-hand movements. During natural movements, muscle proprioceptive
90 afferents are continuously activated and they cannot be selectively removed without impairing
91 concomitant cutaneous afferents (for instance, an ischemic block affects all large somatosensory fibers,
92 including both cutaneous and proprioceptive fibers (Diener et al., 1984). Therefore, it is usually
93 impossible to estimate the kinesthetic contribution of visuo-tactile modalities independently from
94 muscle proprioception. For this reason, we induced illusory movements rather than actual movements
95 using a visual and/or tactile moving background rotating under the hand, i.e. the participants felt that
96 their hand was passively rotated though it remained perfectly still. We estimated the perceptual benefit
97 of visuo-tactile stimulation compared to each unimodal stimulation in a discriminative test of self-hand
98 movement velocity, and then compared it to the MLE predictions.

99 However, in our experiment, participants were aware that their hand was not actually moving,
100 and this cognitive component was further strengthened by a proprioceptive feedback from the wrist
101 muscles conveying static information. This Prior knowledge combined with static muscle

102 proprioceptive cues might explain why the perceived velocity of the illusory movements was about six
103 times less than the actual velocity of the stimulation (Blanchard et al. 2013). In the Bayesian
104 framework, sensory illusions have been successfully explained as the result of an optimal combination
105 between noisy sensory information and stimulus-independent Prior knowledge. For example, a Prior
106 favoring low-speed motion can account for several visual illusory phenomena observed in motion
107 vision (Weiss et al., 2002; Montagnini et al., 2007). Studies about self-body perception used a
108 Gaussian low-speed Prior distribution to account for top-down expectations that influence perceptual
109 performance (Jürgens and Becker, 2006; Laurens and Droulez, 2006; Dokka et al., 2010; Clemens et
110 al., 2011).

111 Therefore we tested a Bayesian model including a Gaussian Prior distribution, as well as a
112 proprioceptive Likelihood, both centered on zero, in order to account for the strong belief in favor of
113 immobility and for the omnipresent static information from muscle spindle endings. The combination
114 of these two Gaussian distributions centered on zero should provide a theoretical ground for the very
115 low gain of the illusory hand-motion perception. For the sake of simplicity, we will refer to this
116 combined information as zero-centered Prior. We also manipulated this Prior static information by
117 disturbing proprioceptive feedback. To this end, we equally applied a co-vibration onto the
118 participants' antagonist wrist muscles (*Noisy* condition). We expected to make the muscle
119 proprioceptive inputs less reliable, and consequently to lower the weight of the static information taken
120 into account in the Prior distribution and to increase the gain of illusory perception.

121

122 **Method**

123

124 *Participants*

125 Twenty right-handed volunteers (14 women) with no history of neurological disease agreed to
126 participate to this study. They all gave their informed consent, conforming to the Helsinki declaration,

127 and the experiment was approved by the local Ethics Committee (CCP Marseille Sud 1 #RCB 2010-
128 A00359-30). Five of them did not experience any illusory perception during the tactile stimulation and
129 were therefore not included in the complete series of experiments and analysis.

130

131 *Stimuli (Fig. 1)*

132 Tactile stimulation was delivered by a motorized disk (40 cm in diameter) covered with cotton
133 twill (8.5 ribs/cm), which is a material known to efficiently activate cutaneous receptors (Breugnot et
134 al., 2006). The disk rotated under the participant's right hand in a counterclockwise direction with a
135 constant angular velocity ranging from 10 to 45 °/s (Fig. 1B).

136 Visual stimulation consisted of a projection of a black and white pattern on the disk. To give the
137 participant the feeling that the pattern was moving in the background, i.e. under his/her hand, a black
138 mask adjusted to the size of each participant's hand was included in the video and prevented the
139 pattern from being projected onto his/her hand. The pattern was rotating around the participant's right
140 hand with a constant counterclockwise angular velocity ranging from 10 to 45 °/s (Fig. 1C).

141 These two types of stimulation were delivered for six seconds either separately (unimodal conditions)
142 or simultaneously (bimodal condition) at six different velocities (10, 20, 25, 30, 35, and 45 °/s). These
143 stimulation velocities were chosen based on a previous study (Blanchard et al., 2013) to induce
144 efficient illusory movements with a perceived velocity well distributed around 5 °/s (reference
145 velocity).

146 In the *Noisy* conditions, muscle proprioception was disturbed using low amplitude mechanical
147 vibration (0.5 mm peak-to-peak) set at a constant low frequency (20 Hz). We used two vibrators each
148 made of a biaxial DC motor with eccentric masses forming a 5-cm long and 2-cm in diameter cylinder.
149 As shown on Figure 1D, they were fixed on both sides of the participant's right wrist to stimulate
150 equally and simultaneously two antagonist muscle groups: the *longus pollicis* and the *extensor carpi*
151 *ulnaris* muscles. Indeed, microneurographic studies showed that such low amplitude vibration
152 preferentially activates muscle spindle primary endings. Roll et al (1989) have shown that in 10 to 100

153 Hz vibration range, primary muscle spindle endings respond with a frequency of discharge equal to the
154 vibration frequency (with a 1 : 1 mode of response), resulting in a masking effect of spontaneous
155 natural discharges, usually ranged between 3 to 15 Hz in the absence of vibratory stimulation (Roll et
156 al., 1989). When applied onto a single muscle group, vibration stimulation can elicit an illusory
157 sensation of limb movement but any illusion is cancelled when a concomitant vibration is equally
158 applied onto antagonist muscles (Calvin-Figuière et al., 1999). Therefore, by equally co-stimulating
159 wrist antagonist muscles, we expected to disturb proprioceptive afferents without inducing any illusory
160 sensation of movement. The stimuli were delivered using a National Instruments card (NI PCI-6229)
161 and a specifically designed software implemented in LabView (V.2010).

162

163 *Insert Figure 1 around here*

164

165 *Procedure*

166 Participants sat on an adjustable chair in front of a fixed table with arm-rests immobilizing their
167 forearms, their left hand resting on the table and their right hand on the motorized disk. A small
168 abutment in the disk center placed between their index and middle finger kept their hand from moving
169 with the disk when it rotated. Head movements were limited thanks to a chin- and chest-rest allowing
170 participants to relax and sit comfortably. The experiment took place in the dark and participants wore
171 headphones to block external noise, as well as shutter glasses partially occluding their visual field and
172 reducing it to the disk surface only.

173 *Training phase*

174 Before the experimental session, each participant underwent two training sessions. First, a 15
175 minute session consisted of 150 trials of separate tactile and visual stimulation applied at medium
176 velocity (25 °/s). To be included in the experiment, the participants had to feel illusory hand rotations
177 in at least 80 % of the trials.

178 Then, the participants were trained to perform a reproducible 5 °/s clockwise hand rotation. During this
179 second 15 minute session, with their middle fingers they had to follow a red line moving at 5 °/s that
180 was repeatedly projected onto the disk every 7.5 seconds. Participants were asked to memorize the
181 movement using all the available information (tactile, visual and proprioceptive feedback, plus efferent
182 motor command). This 5 °/s movement was chosen as the reference to which participants would have
183 to compare their perception during the discrimination test phase.

184

185

186 *Discrimination test phase*

187 The experimental test consisted of a 2-AFC (alternative forced choice) discrimination
188 task with constant stimuli. A stimulation condition (visual, tactile or combined) and the
189 reference movement were presented by pairs in random order. The participants were instructed
190 to say out loud whether the illusory movement they perceived was faster or slower than the
191 reference movement.

192 The reference movement executed during the experimental test was similar to that performed
193 during the training phase except that the red line appeared only during the first and the last of the 6
194 seconds of the movement duration to prevent the participants from using only visual feedback.

195 Three stimulation conditions were randomly intermixed within the experimental sessions: two
196 unimodal conditions (tactile T, visual V) and one bimodal condition (visuo-tactile VT). For each
197 stimulation condition, 6 intensities were tested and presented immediately before or after the reference
198 movement. All stimuli lasted 6 seconds (as the reference movement) and the inter-stimulus intervals
199 ranged between 1.7 and 2.3 seconds. Before each reference/stimulation pair, a white line was projected
200 to make sure that participants always positioned their hand in the same orientation. Participants were
201 instructed to focus on their hand to estimate as accurately as possible whether the illusory movement
202 they perceived was faster or slower than the reference movement they executed just before or just after
203 each stimulus. They had to keep their eyes open, except if a green screen appeared signaling them to

204 close their eyes before a tactile-only stimulus. At the end of each pair (reference/stimulation)
205 presentation, participants had 2 seconds to answer (“*faster*” or “*slower*”) and 3 seconds (\pm 300 ms)
206 before a new pair was presented. The presentation order of the 18 stimulation conditions was
207 counterbalanced for each subject.

208 During the *Standard* condition test, participants were asked to compare 270
209 reference/stimulation pairs (3 conditions * 6 intensities * 15 trials) divided into four sessions of 10
210 minutes each performed on two different days (at the same time during the day). Thirteen of the fifteen
211 participants were tested in four additional *Noisy* condition sessions of 10 minutes during which the
212 same block of 270 pairs of reference/stimulation was presented while participants underwent co-
213 vibrations of their antagonist wrist muscles.

214

215 ***Movement acquisition and kinematic analysis***

216 Participants were asked to compare the velocity of each illusory movement they experienced
217 during the unimodal and bimodal stimulation conditions with the velocity of the same reference
218 movement, consisting of a clockwise rotation of the right hand at 5 °/s that they actively performed just
219 before or just after every stimulus. All reference movements were recorded using an optical motion
220 capture system (CODAmotion, Charnwood Dynamics, Rothley, UK) composed of 3 infrared ‘active’
221 markers and one camera to track the 3D marker positions (sampling frequency: 10 Hz). Markers were
222 attached to the participants’ middle finger, on the top of their hand back, and on the last third of their
223 forearm to capture the angular rotation of their wrist during the reference movement execution.

224 For each participant, the mean angular velocity of hand movements was extracted with the
225 Codamotion Analysis software (V6.78.2). Reproducibility of the reference movement across the 270
226 trials during the *Standard* experiment was further tested by a one-way ANOVA for each participant
227 with the session (4 sessions) as experimental factor for the *Standard* condition (without vibration) and
228 the *Noisy* condition (with co-vibration stimulation). As expected, no significant difference in the mean
229 velocity of the reference movement was found between sessions whatever the participant neither in the

230 *Standard* nor the *Noisy* condition. Note that individual variability estimated from the four sessions
 231 ranged between 0.22 and 0.37 °/s. We further verified the precision of estimation of the reference
 232 movement in a complementary experiment performed on ten naïve participants consisting in a
 233 discrimination task between several self-hand rotations actively executed. Participants were asked to
 234 compare the velocity of the fixed reference movement set at 5°/s (like in the main experiments) with 8
 235 other hand movement velocities (3.5°/s, 4 °/s, 4.5 °/s, 4.75 °/s, 5.25 °/s, 5.5 °/s, 6 °/s, or 6.5 °/s). Again,
 236 the estimated variability was found to be small (ranging from 0.33 to 0.79 °/s).

237 A one-way ANOVA was also performed to ensure that reference movement was not
 238 significantly different between participants (*Standard* condition: $F(3, 42) = 1.05$, $P = .38$; *Noisy*
 239 condition: $F(3, 36) = 0.21$, $P = .89$). Finally, a Student’s paired t test was used to ensure the
 240 reproducibility of the reference movement between the *Standard* condition and the *Noisy* condition.
 241 There was no significant difference between these conditions ($\text{mean}_{\text{Standard}} = 4.6 \pm 0.08$ °/s $\text{mean}_{\text{Noisy}} =$
 242 4.7 ± 0.07 °/s; $P = .34$), suggesting that participants referred on average to the same velocity of
 243 reference movement in both conditions.

244 ***Data analysis***

245 In order to evaluate and compare participants’ perceptual performance across the three
 246 stimulation conditions (T, V, VT), the psychometric data (i.e. the proportion of “faster than the
 247 reference” answers at different stimulation intensities) were fitted by a cumulative Gaussian function:

$$248 \quad P(x) = \lambda + (1 - 2\lambda) \frac{1}{\sigma_\psi \sqrt{2\pi}} \int_{-\infty}^x e^{-\frac{(y-\mu_\psi)^2}{2\sigma_\psi^2}} dy$$

249 where x represents the stimulus velocity (in degrees per second); μ_ψ is the mean of the Gaussian, i.e.
 250 the Point of Subjective Equality (PSE) that corresponds to the stimulation intensity leading the
 251 participant to perceive an illusory movement on average as fast as the reference set at 5 °/s; σ_ψ is the
 252 standard deviation of the curve, or discrimination threshold, which is inversely related to the
 253 participant’s discrimination sensitivity. In other words, a smaller σ_ψ value corresponds to a higher
 254 sensitivity in the discrimination task. The two indices, PSE and σ_ψ , characterize the participant’s

255 performance. λ accounts for stimulus-independent errors due to participant's lapses and was restricted
256 to small values ($0 < \lambda < 0.06$, Wichmann and Hill, 2001), This parameter is not informative about the
257 perceptual decision, thus we disregarded it for the following analyses. Psignifit toolbox implemented
258 on Matlab software (© 1994-2014 The MathWorks, Inc.) was used to fit the psychometric curves
259 (Wichmann and Hill, 2001).

260 To compare discrimination sensitivity across the three stimulation conditions (T, V and VT),
261 we performed a one-way repeated-measures ANOVA with Tukey post-hoc tests on σ_ψ values. In
262 addition, for each participant, the enhancement of the visuo-tactile discrimination sensitivity over the
263 best unisensory one was assessed using the multisensory index (MSI) as defined by (Stein et al., 2009).
264 Since an improvement of discrimination sensitivity corresponded to a decrease in σ value, the MSI was
265 computed as follows:

$$266 \quad MSI(\sigma_\psi) = \frac{Min(\sigma_{\psi T}; \sigma_{\psi V}) - \sigma_{\psi VT}}{Min(\sigma_{\psi T}; \sigma_{\psi V})}$$

267 To quantify the perceptual strength of the illusions, the gain of the responses in the different
268 stimulation conditions was assessed as follow (in percentage):

$$269 \quad Gain = \frac{V_{ref}}{PSE} * 100$$

270 with the reference velocity V_{ref} set at 5 °/s.

271

272 For the fifteen participants, we compared the response gains between the three sensory stimuli (T,
273 V and VT) using a one-way repeated-measure ANOVA with Tukey post-hoc tests. For the thirteen
274 participants that underwent the *Noisy* condition, a two-way repeated-measure ANOVA was also
275 performed on the illusion gains to test the effect of the sensory stimulation (T, V and VT) and the
276 experimental condition (*Standard* vs *Noisy*).

277 The enhancement or depression of the visuo-tactile response gain over the best unisensory
278 response gain was computed using the multisensory index (MSI) as defined by (Stein et al., 2009)

279

$$280 \quad MSI (Gain) = \frac{Gain_{VT} - \text{Max}(Gain_T; Gain_V)}{Gain_{VT}} * 100$$

281

282

283 **Models**

284 *The Maximum Likelihood Estimate model used to predict optimal multimodal discrimination*
285 *performance*

286 ***Insert Figure 2 around here***

287

288 As illustrated in Figure 2, the minimum-variance linear combination model (often referred to as
289 Maximum Likelihood Estimate (MLE) model) predicts how an “optimal observer” would combine two
290 unbiased sensory signals to optimize the resulting perception (in the sense of minimizing its variance)
291 relative to the two unimodal representations. According to MLE rules (which are just one particular
292 instantiation of the more general Bayesian framework, see Landy et al. 2011), the optimal perceptual
293 estimate in visuo-tactile stimulation can be described by the normalized product of the unimodal
294 Likelihood distributions $P(\vartheta_T|\vartheta)$ and $P(\vartheta_V|\vartheta)$, with the underlying assumption that visual and tactile
295 sources are conditionally independent variables affected by Gaussian noise:

$$296 \quad (1) \quad P(\vartheta_{VT}|\vartheta) \propto P(\vartheta_T|\vartheta) * P(\vartheta_V|\vartheta)$$

297 where ϑ_T , ϑ_V and ϑ_{VT} are the tactile, visual and visuo-tactile estimates of hand velocity for a given
298 value of stimulation velocity ϑ .

299 The visuo-tactile Likelihood resulting from the normalized multiplication of the two unimodal
300 Gaussians is a Gaussian distribution itself, with a variance σ^2_{VT} related to the unimodal variances
301 through the following equation

$$302 \quad (2) \quad \frac{1}{\sigma^2_{VT}} = \frac{1}{\sigma^2_V} + \frac{1}{\sigma^2_T}$$

303 Therefore, equation 2 implies that if the two sensory signals are optimally integrated, the visuo-tactile
304 variance is smaller than the variance of either modality in isolation, thus leading to a sensitivity
305 enhancement.

306 The MLE model and its predictions can easily be tested on the behavioral data of a multisensory
307 discrimination experiment. It can be shown that the same relation presented in equation 2 for the
308 variance of the sensory likelihood does actually apply to the standard deviation (σ_ψ) of the estimated
309 cumulative-Gaussian psychometric curve (i.e. its discrimination threshold). In particular, in this study,
310 predicted and observed visuo-tactile discrimination thresholds were compared in order to determine if
311 the integration of vision and touch was optimal with regard to the discriminative sensitivity of the
312 participants.

313 It should be noticed that in the present experimental context, the uncertainty related to the reference
314 movement velocity estimation could account for a portion of the estimated discrimination threshold σ_ψ .
315 We will address this issue in the next session.

316

317 *A Bayesian model to account for the low-perceptual gain of movement illusions*

318 In the present study, kinesthetic illusions of hand movements were induced while participants were
319 aware that their hand was actually not moving. This Prior knowledge was also supported by muscle
320 proprioceptive feedback from their stationary wrist. The conflict between this static information and
321 the moving tactile or visual information may account for the extremely low gain of the velocity
322 illusions with respect to the actual velocity of the moving stimuli (Blanchard et al., 2013).

323 In order to account for the low gain of the uni- and multimodal illusions, a more complex Bayesian
324 model was elaborated including a zero-centered Gaussian Likelihood accounting for muscle
325 proprioceptive cues and a Gaussian Prior distribution centered on zero too. The combination of those
326 two distributions is also a zero-centered Gaussian distribution. Therefore, to preserve the model
327 parsimony, we will treat these distinct contributions as a single probability distribution and we will
328 refer to it as “Prior” throughout the present manuscript.

329 The sensory Likelihood and the Prior distributions are combined according to Bayes' rule to obtain
 330 the Posterior distribution:

$$331 \quad (3) \quad P(\vartheta|\vartheta_i) \propto P(\vartheta_i|\vartheta) * P(\vartheta)$$

332 with $P(\vartheta)$ = Prior probability distribution of hand velocity, $P(\vartheta_i|\vartheta)$ = sensory Likelihood for the
 333 modality i , and $i = T, V$ or VT .

334 The parameters (mean and variance) of the Bayesian Gaussian distributions are linked by the
 335 following relations:

$$336 \quad (4) \quad \left\{ \begin{array}{l} \frac{\mu_{Post_i}}{\sigma^2_{Post_i}} = \frac{\mu_i}{\sigma^2_i} + \frac{\mu_{prior}}{\sigma^2_{Prior}} \\ \\ \frac{1}{\sigma^2_{Post_i}} = \frac{1}{\sigma^2_i} + \frac{1}{\sigma^2_{Prior}} \end{array} \right.$$

339 with $i = T, V$ or VT , $\mu_{Prior} = 0$ °/s, σ^2_{Prior} is the unknown variance of the Prior (assumed to be constant
 340 throughout the different experimental conditions), μ_i the mean of the Likelihood, σ^2_i the unknown
 341 variance of the Likelihood and, similarly, μ_{Post_i} and $\sigma^2_{Post_i}$ are the mean and variance of the Posterior
 342 distribution. In line with most Bayesian models, we assumed that the Likelihood mean exactly matches
 343 the velocity stimulation ($\mu_i = \vartheta_i$) as it represents the first stage of (presumably unbiased) sensory
 344 encoding of global motion information. We also assumed that σ^2_i does not depend on velocity in the
 345 considered range. Although this last assumption is probably not true in general (e.g. Stocker &
 346 Simoncelli 2006), it seems to be a reasonable approximation for the relatively small range of
 347 stimulation velocities considered here.

348 Given all the above-mentioned assumptions, the estimated parameters of the psychometric function
 349 can be put in relation to the parameters of the hidden Bayesian distributions. A Bayesian ideal observer
 350 uses the information provided by the Posterior distribution to formulate a perceptual judgment, such as
 351 the velocity discrimination in our study. As shown in Figure 3, the proportion of judgments of the type

352 “test faster than reference” is equal to the integral of the Posterior distribution over the interval
353 $]V_{ref}; +\infty[$

354 *Insert Figure 3 around here*

355

356 Let us consider two values of the stimulation velocity that correspond to the critical parameters of the
357 psychometric curve, namely the PSE and the value at which $\Psi = 0.84$ which corresponds by
358 definition to $(PSE + \sigma_\psi)$.

359 When the test velocity $\vartheta_i = PSE$ the ideal observer perceives on average by definition a velocity
360 equivalent to the reference velocity V_{ref} . Thus the mean (and most likely value) of the Posterior
361 distribution μ_{Post} is equal to V_{ref} .

362 On the other hand, when the test velocity is $\vartheta_i = PSE + \sigma_\psi$, the integral under the Posterior is 0.84,
363 which - on the ground of the assumption of normality - implies that its mean μ_{Post} is equal to $(V_{ref} +$
364 $\sigma_{post})$.

365 By substituting these equalities in the system of equations 4, we obtained the expression of the
366 variance of the three Bayesian distributions as a function of the parameters of the psychometric curve
367 (PSE_i, σ_i) and of V_{ref} .

368 (5)
$$\frac{1}{\sigma^2_i} = \frac{PSE_i}{V_{ref}} * \frac{1}{\sigma^2_{\psi_i}}$$

369

370 (6)
$$\frac{1}{\sigma^2_{Prior}} = \frac{PSE_i}{V_{ref}} * \frac{1}{\sigma^2_{\psi_i}} * \left(\frac{PSE_i}{V_{ref}} - 1 \right)$$

371

372 (7)
$$\frac{1}{\sigma^2_{Post}} = \frac{PSE_i^2}{V_{ref}^2} * \frac{1}{\sigma^2_{\psi_i}}$$

373

374 Note that these equations hold for each type of stimulation (T, V or VT). The variance of the Prior
375 distribution was thus estimated (through Equation 6) for each of the unimodal conditions V and T.
376 Consistent with our assumption of a constant Gaussian Prior noise across experimental conditions, we
377 verified that the σ_{Prior} estimated by the “tactile” and the “visual” equation (6) did not differ
378 significantly (Student’s paired *t*-test: $P = .063$). We used the mean of the Prior variance estimated from
379 the visual and tactile psychometric parameters (Equation 6) for the later steps (see also Fig. 4; Step 1).
380 We then applied the MLE predictions for the estimate of the Likelihood variance in the condition of
381 visuo-tactile stimulation (Equation 2) and then inverted the Equations 5, 6 and 7, relating the Bayesian
382 to the psychometric parameters, in order to predict the bimodal point of subjective equality PSE_{VT}
383 (Fig. 4; Step 2),

$$384 \quad (8) \quad PSE_{VT}^{pred} = V_{ref} * \left(1 + \frac{\sigma_{VT}^2}{\sigma_{Prior}^2} \right)$$

385 where both σ_{VT}^2 and σ_{Prior}^2 can be expressed as functions of the unimodal psychometric parameters.
386 For all participants, the predicted gain G_{VT} of the visuo-tactile illusion in the *Standard* condition could
387 finally be compared to the observed visuo-tactile gain.

388 As previously pointed out, the uncertainty related to the estimation of the reference movement velocity
389 could account for a portion of the perceptual variability in our hand-velocity discrimination task,
390 whatever the sensory stimulation. Therefore we assessed its influence by including the individual
391 variability of the reference movement reproduction (see Methods section) in the estimation of the
392 global uncertainty for the velocity discrimination task. However, doing so increased the complexity of
393 the model without improving the predictions, nor changing the core results. For the sake of parsimony,
394 we will only briefly present the impact of this additional component of perceptual uncertainty on the
395 predictions at the end of the Result section.

396
397 In addition, the same analysis was performed on perceptual responses elicited in the *Noisy*
398 condition, where co-vibration was applied onto antagonist wrist muscles to disturb static muscle

399 proprioceptive feedback. The variance of the Prior σ^2_{Prior} in the *Noisy* condition was estimated and the
400 visuo-tactile illusion gain G_{VT} was predicted.

401 The relative contribution of the Prior in the final perception was also assessed by computing the
402 relative weight of the Prior with respect to the visual and tactile weights, as follows:

$$403 \quad \omega_{Prior} = \frac{\sigma_{Prior}^{-2}}{\sigma_{Prior}^{-2} + \sigma_T^{-2} + \sigma_V^{-2}}$$

404

405 The relative weights of the Prior obtained in *Standard* and *Noisy* conditions were compared using a
406 Student's paired t-test.

407 Finally, to test whether the model better fit the visuo-tactile performances in the *Noisy* condition
408 compared to the *Standard* condition, the differences between predicted and observed gains in the two
409 conditions were compared using a Student's paired t-test.

410 *Insert Figure 4 around here*

411

412 **Results**

413

414 *Discriminative ability for hand movement velocity based on visual and/or tactile inputs*

415 As expected, for all the participants included in the study, the counterclockwise rotation of the
416 visual and/or tactile stimulation gave rise to an illusory sensation of rotation of their stimulated hand,
417 which was always oriented in the opposite direction, i.e. clockwise. For each stimulation condition (T,
418 V, VT) randomly applied at six different velocities, participants reported whether the illusion was
419 faster or slower than the 5 °/s clockwise reference rotation they actively performed just before or just
420 after the stimulation delivery. To compare the participants' performance in the velocity discrimination
421 task between tactile, visual, and visuo-tactile stimulation, the probability of perceiving the illusion as
422 faster than the reference movement was fitted by a cumulative Gaussian function for the tested
423 stimulus velocities to obtain three individual psychometric curves.

424 As shown in the example of Figure 5A, the participant experienced an illusory movement with
425 a velocity close to the 5 °/s reference when the tactile or the visual stimulation was rotating around
426 29.8 °/s and 28.8 °/s, respectively. The participant's ability to discriminate the velocity of his/her hand
427 movement improved in the visuo-tactile condition compared to the unimodal ones, as attested by an
428 increased slope of the visuo-tactile psychometric curve. More precisely, the discrimination threshold σ
429 (i.e. the increase in stimulation velocity required to induce an illusory movement faster than the
430 reference movement in 84 % of the trials with respect to 50 % of the trials) was lower in the visuo-
431 tactile condition (mean $\sigma_{VT} = 6.02 \pm 2.19$ °/s) than in the unimodal conditions (mean $\sigma_T = 8.67 \pm 3.6$
432 °/s; mean $\sigma_V = 7.68 \pm 3.5$ °/s). In other words, the decrease in σ value reflected the fact that the
433 velocity discrimination ability of this participant increased in the visuo-tactile condition.

434 These individual results were confirmed at the group level (Fig. 5B). Performances in velocity
435 discrimination changed according to the stimulation condition ($F(2, 28) = 12.375, P = .00014$). The
436 mean σ decreased significantly in the visuo-tactile condition in comparison with the tactile (post-hoc
437 test: $P < .001$) and visual conditions (post-hoc test: $P = .0025$). Discrimination thresholds for the
438 velocity discrimination task did not significantly differ between the two unimodal conditions ($P = .58$).

439 In order to quantify the benefit resulting from visuo-tactile stimulation, the multisensory index
440 (MSI) was calculated individually for the σ values. This index, expressed in percentage, reveals for
441 each participant the enhancement (or depression) of the multisensory sensitivity over the best
442 unisensory response (Stein et al., 2009). For eleven of the thirteen participants, the multisensory
443 response showed a positive benefit on the discriminative threshold σ . Quantitatively, the visuo-tactile
444 σ values for those eleven participants were lower than the lowest of the unimodal σ , with an MSI
445 ranging between 3 % and 40 % (Fig. 5C). Only two among 15 participants did not show an
446 improvement of their discriminative sensibility in the visuo-tactile condition.

447

448 As depicted in Figure 2, the MLE model predicts an improved discrimination performance in the
449 multimodal condition. The MLE-predicted visuo-tactile σ values were estimated for each participant
450 on the basis of his/her performances in the two unimodal conditions. As illustrated in Figure 5D,
451 comparing these estimates to the experimental observations during the visuo-tactile condition showed
452 that the data estimates did not differ significantly from the observed σ values (Student's Paired t test, P
453 = .55). Note that including the variability of the reference reproduction task in the model did not
454 change the predictions of the discriminative thresholds in any appreciable way (0.9 % of difference in
455 the worst case...).

456

Insert Figure 5 around here

457

458 *A low-perceptual gain for movement illusions*

459 *Standard condition*

460 In the individual results presented in Figure 6A, illusory movement was perceived at a velocity
461 close to the 5 °/s reference when the tactile or the visual stimulation was rotating at about 29 °/s, with a
462 point of subjective equality (PSE) estimated at 28.8 and 29.8 °/s, respectively. When the two kinds of
463 stimulation were combined, the velocity of the stimulation required to evoke an illusion close to the 5
464 °/s reference dropped to 20.5 °/s (Fig. 6A). The decrease in PSE reflected the fact that the participant
465 perceived a faster illusory movement with combined visual and tactile stimulation compared to only
466 one kind of stimulation. These results can also be expressed in terms of response gain, classically
467 defined as the ratio between the perceived illusion velocity and the actual velocity of the stimulus (see
468 Method section). A value of 100 % would indicate that the participant perceived a hand movement at
469 the same velocity as the actual stimulation velocity. In our experimental paradigm, the gains of the
470 illusions were always much lower than 100 %. They were on average about 19.9 % (± 2.7 % SD) and
471 18.4 % (± 2.9 % SD) for the tactile and visual stimulation, respectively. During visuo-tactile

472 stimulation, the gain significantly increased, up to 23.7 % (± 3.5 % SD) in comparison with unimodal
473 tactile (post-hoc test: $P = .0004$) and visual (post-hoc test: $P < .0001$) stimulations: illusion velocity got
474 closer to the actual stimulation velocity in visuo-tactile condition (Fig. 6B). A more detailed analysis
475 showed that the multimodal gain increased for all participants except one (Fig. 6C). This increase was
476 also attested by positive MSI values, ranging from 1 % to 40 % for 14 of the 15 participants (mean
477 MSI = 14 % \pm 13).

478 *Insert Figure 6 around here*

479

480 To account for these low-perceptual gains, we then considered a more complex model than the MLE,
481 including the influence of the “non-moving hand information” *a priori* present in our experimental
482 paradigm. Indeed, in addition to the omnipresent proprioceptive static cue, participants were always
483 aware that their hands were not actually moving. By modeling the “non-moving hand information” as
484 a Gaussian distribution centered on zero, the variance of this Prior was first estimated through the
485 observed data obtained in the two unimodal conditions (Fig. 3 & 4 Step 1). In line with our assumption
486 that the Prior distribution should be constant over the various sensory conditions, we found that the
487 variance estimates based on each single sensory performance did not differ significantly ($P = .18$).

488 The visuo-tactile Likelihood was then predicted by combining the estimated Prior distribution with the
489 estimated unisensory Likelihoods (see Fig. 3 & 4 Step 2).

490 This model predicted that the gain of the illusion in the visuo-tactile condition would improve
491 compared to the unimodal ones. However, the observed increase in gain was less than that predicted by
492 the model (Fig. 6D). By taking into account the variability of the reference movement perception in the
493 model, predictions were not improved (they became actually worse, in the worst case, discrepancies
494 between observations and predictions of the gain went from 3.9 % to 9.8 %), but the discrepancy
495 between data and model predictions did not qualitatively change, highlighting in all cases an
496 overestimation of the gain increase by the Bayesian complete model.

497

498 *Noisy condition*

499 To further explore the influence of the “non-moving hand” cues in our paradigm, the same
500 experiment was performed while muscle proprioception was disturbed by equivalent vibrations applied
501 on antagonist wrist muscles involved in left-right hand movement: the right *pollicis longus* and *carpi*
502 *ulnaris extensor* muscles. Applied on antagonist muscles with the same low frequency, mechanical
503 vibration equally activates muscle spindle endings, masking natural muscle spindle afferents without
504 giving rise to any relevant movement information (Roll et al., 1989; Calvin-Figuère et al., 1999).
505 Before the beginning of each experimental session, we ensured that muscle co-vibration did not induce
506 any movement sensation.

507 During co-vibration, all the participants were still able to experience the illusory movement
508 elicited by the tactile and/or visual stimulation. In the *Noisy* condition, the stimulus velocity required
509 for the illusory movement to reach a velocity close to the reference value was lower than that
510 previously observed in the *Standard* condition where no vibration was applied. A two-way ANOVA
511 analysis showed that the gains of the perceptual illusions increased significantly in the *Noisy*
512 conditions compared to the *Standard* ones (Main effect of condition ($F(1, 12) = 26.003$; $P = .00026$).
513 When the two *Noisy* and *Standard* conditions were confounded, the gain observed in the visuo-tactile
514 conditions was significantly higher than those observed in the tactile and visual conditions ($F(2, 24) =$
515 25.37 ; $P < .0001$) (Fig.7). No significant interactions were found between the condition (*Noisy* vs
516 *Standard*) and stimulation (T, V, VT) factors.

517

518 ***Insert Figure 7 around here***

519

520 As in the previous *Standard* experiment, we estimated the variance of the Prior based on unimodal
521 responses collected during co-vibration. With degraded muscle proprioceptive information, the
522 influence of the “non moving hand” information modeled by the Prior was supposed to be reduced in
523 the *Noisy* conditions. As expected, for the 13 participants tested, the relative weight of the Prior

524 (compared to the tactile and visual relative weight) was lower in the *Noisy* experiment (0.89 ± 0.03)
525 than in the *Standard* one (0.95 ± 0.017 ; Student's paired *t* test: $P = .011$).

526 In addition, the predicted gains of the visuo-tactile responses were estimated on the basis of the
527 unimodal and Prior distributions obtained with concomitant co-vibration. Although the predicted gains
528 were still higher than those observed experimentally, the discrepancy between data and model
529 predictions was reduced in the *Noisy* experiment with respect to the *Standard* one (Student's paired *t*
530 test: $P = .019$; see Figure 8).

531 *Insert Figure 8 around here*

532

533 **Discussion**

534 *Optimal visuo-tactile integration in velocity discrimination of self-hand movements*

535 The present study shows that visual and tactile motion cues can be equivalently used by the
536 CNS (central nervous system) to discriminate the velocity of self-hand movements. By combining both
537 types of stimulation at the same velocity, one can assume that we generated congruent multisensory
538 signals, as during actual hand movements. As expected, we observed a multimodal benefit provided by
539 the combination of visual and tactile motion cues when participants evaluated the velocity of self-hand
540 illusion rotation. This behavioral improvement was first of all attested by a better discrimination ability
541 (a lower discrimination threshold) in bimodal than in unimodal conditions.

542 The perceptual benefit of combined vision and touch had mainly been estimated when one has
543 to assess properties of an external object like its size (Ernst and Banks, 2002) or its speed (Bensmaia et
544 al., 2006; Gori et al., 2011). In those studies, as in the present one, the multimodal benefit is well
545 predicted by the MLE principle suggesting that vision and touch are combined in an optimal way when
546 discriminating perceived self-hand velocity.

547 Moreover, participants' ability to discriminate the velocity of an illusory hand movement was
548 equivalent when based on the rotation of either the tactile disk or the visual background with a

549 discrimination threshold about 8 °/s for both conditions. This is consistent with the study by Gori et al.
550 (2011) showing equal sensitivities to discriminate the velocity of external motion signals of tactile or
551 visual origin. One can thus hypothesize that common inferential processes take place in situations of
552 visuo-tactile integration in the context of velocity discrimination, whether the perceived object is the
553 self or an external object.

554 *Influence of the non-moving hand Prior in the low-perceptual gain of movement illusions*

555 A strong difference emerges for the absolute estimation of the velocity depending on whether
556 visual and tactile motion signals are related to an external object or to self-body. Whereas velocity
557 estimation of a tactile stream on a fingertip is close to the actual velocity of the moving object
558 (Bensmaia et al., 2006), velocity of the perceived self-hand movement in the present experiment was
559 drastically underestimated with a perceived movement speed always lower than 30 % of the actual
560 visual or tactile stimulation velocity. One plausible explanation is that since proprioceptive afferents
561 from participants' wrist muscles informed the CNS that the hand was not actually moving, the sensory
562 conflict might have resulted in a slower perception of hand rotation. To account for this unavoidable
563 proprioceptive feedback together with the fact that participants knew that their hand was actually not
564 moving, we developed a Bayesian model including a Prior term defined as the product of two
565 Gaussian distributions (the Proprioceptive static sensory Likelihood and the cognitive Prior) centered
566 on zero. We postulated that, when visual or tactile stimulation was applied, the final perception of
567 illusory hand movement resulted from the combination of the visual, tactile or visuo-tactile motion
568 cues with this zero-centered Prior. Our parameter-free Bayesian model successfully predicted a gain
569 increase in visuo-tactile illusions compared to unimodal ones. In the Bayesian framework this effect is
570 explained by the stronger weight of the sensory information when two modalities are optimally
571 combined and hence reliability is increased. In a self-angular displacement estimation task, Jürgens
572 and Becker (2006) had postulated a Prior favoring a particular rotation speed to account for the
573 velocity-dependent bias observed in the participants judgments. Albeit that study did not test a
574 quantitative prediction on the observed bias reduction in multisensory stimulation, the authors'

575 conclusions are consistent with ours and point to a probabilistic integration of sensory representations
576 with a prior knowledge as postulated by Bayes theory. However, the observed gain increase in the
577 present experiment did not match the predicted values, which were over-estimated. In the following
578 section we discuss some possible explanations.

579

580 *Suboptimal multisensory integration: insights into the underlying mechanisms*

581 Deviations from optimal integration predictions have already been reported in cases of sensory
582 conflicts, when sensory information is strongly non-coherent across different modalities. Suboptimal
583 cue weights have been reported in conflictual situations where visual and vestibular inputs are
584 manipulated to give incongruent spatial information relative to passively imposed body rotations (Prsa
585 et al., 2012). In the latter case, participants over-weighted the visual cues to discriminate the angle of
586 imposed rotations. Conversely, vestibular cues were found excessively preponderant to visual cues in a
587 heading perception task (Fetsch et al., 2009).

588 In the present experiment, several explanations may account for the suboptimal benefit on the
589 perceptual gain for visuo-tactile stimulation.

590 First, it has been shown that in case of extreme conflict, integration can be prevented, favoring
591 segregation of the multisensory information (Bresciani et al., 2004; Roach et al., 2006; Körding et al.,
592 2007; van Dam et al., 2014). Accordingly, causal inference models predict a variable degree of
593 multisensory integration according to the probability of the incoming signals to be causally related to a
594 common origin in the world (Körding et al., 2007). In the present study, one can speculate that, if the
595 statistical inference process assigns high weight to a single cause (proprioception, vision and touch all
596 originating from the same true source), then one would indeed find a strengthening of the illusion
597 when a second moving cue is added to the first one. On the other hand, having two moving sensory
598 cues instead of one may increase the conflict between static and movement information, thus leading
599 to a lower weight for the common origin hypothesis. In the latter case, this conflict increase may have
600 degraded multisensory integration and may then have led the participants to partly attribute the visual

601 and tactile motion cues to a different origin, in the environment, rather than their own body. However,
602 a change in causal attribution does not seem to fully explain the present results since it is not consistent
603 with the observation of an increased (although suboptimal) gain in the visuo-tactile condition and also
604 the fact that all the participants reported more salient illusory hand movements in bimodal compared to
605 unimodal conditions. Lastly, segregation is more likely to occur for large discrepancies between cues.
606 Therefore future studies should be conducted to test whether increasing the conflict between static and
607 motion information (using higher velocity stimulation) results in a greater deviation from optimality.

608 Regardless of the conflict between static and motion cues, a second explanation for the
609 overestimation of the bimodal gain improvement can be considered. One can speculate that there is an
610 illusory percept that is being used for a behavioral report and simultaneously a non-reported judgment
611 of background motion and those may interact. In this context, combining visual and tactile cues leads
612 to a decrease in the variability of the velocity estimate, both for self-body movements (as suggested by
613 our psychophysical results) and for external object motions (Gori et al, 2011). As a consequence, if
614 participants have a more coherent percept of the rotation of the environment under their hand, this
615 should in turn facilitate the attribution of the movement to the environment rather than to the hand
616 during the bimodal condition compared to the unimodal conditions, and finally result in sub-optimal
617 performances as compared to Bayesian predictions. Nevertheless, this argument alone fails to explain
618 the observed improvement of gain predictions in the *Noisy* condition. Indeed, muscle proprioceptive
619 noise should not have affected the way external object motion was perceived.

620 Finally, taking into account the crucial role of muscle proprioception in kinesthesia, the
621 suboptimality in the present study can be interpreted as a weighting bias in favor of this modality.
622 Biases toward one sensory cue in multisensory conflicting situations that cannot be explained by a
623 Bayesian weighting process can rather be attributed to a recalibration mechanism (Adams et al., 2001;
624 Block and Bastian, 2011; Wozny and Shams, 2011; Prsa et al., 2012). To solve the discrepancy
625 between two sensory estimates, the brain may choose to realign all the sensory estimates with respect
626 to the most appropriate one. This interpretation is consistent with the *appropriateness principle* (Welch

627 et al., 1980): discrepancies between senses tend to be resolved in favor of the modality not only
628 generally more reliable, but also more appropriate to the task at hand. Recently, Block and Bastian
629 (2011) demonstrated that the weighting and realigning strategies are two independent processes that
630 might occur in conjunction.

631 In the present experiment, the conflict increase between static and movement information may
632 lead to an apparent suboptimal estimation of the illusion velocity due to a recalibration of the visuo-
633 tactile estimation with respect to the static proprioceptive information. Indeed, the CNS may rely more
634 on less ambiguous information, which is muscle proprioceptive information, rather than on visual or
635 tactile information which can both relate to either self-body or environmental changes. Such a
636 recalibration mechanism could thus explain why the perceptual benefit of the bimodal situation was
637 lower than predicted.

638 To test this hypothesis, we degraded muscle proprioceptive signals in order to reduce the reliability of
639 the static information. Natural messages from muscle spindles were masked thanks to a concomitant
640 vibration applied onto the wrist antagonist muscles (Roll et al., 1989). Such vibration efficiently
641 degraded the information of hand immobility: the velocity required to give rise to an illusory
642 movement with a velocity close to the reference value was lower than previously observed in the
643 *Standard* condition (with no vibration). In other words, the same visual or tactile stimulation gave rise
644 to faster illusory movements when muscle proprioception was masked by the vibration. Using the
645 mirror paradigm, Guerraz et al. (2012) consistently reported that the illusory movement sensation of
646 one arm evoked by the reflection on a mirror of the contralateral moving arm increased with a
647 proprioceptive masking of the arm subjected to kinesthetic illusion.

648 As expected, the proprioceptive noise enabled our model to better fit the observed illusion
649 gains. However, the model predictions still over-estimated the visuo-tactile benefit on gain, suggesting
650 that attenuating muscle proprioceptive feedback was not sufficient. This quantitative discrepancy may
651 be due to incomplete masking of proprioceptive afferents through our non-invasive stimulation. In
652 addition, static information cannot be completely cancelled, since the participants were always aware

653 that no actual hand movement was occurring during the experiment. This cognitive component might
654 have pushed towards a sensory realignment in conjunction with a greater muscular proprioception
655 reweighting in the visuo-tactile estimation of illusory hand movements.

656

657 *Physiological evidence for visuo-tactile integration and Bayesian inferences*

658 A large number of studies performed in animals and humans have recently provided compelling
659 evidence for the neural substrates of multisensory integrative processing, including in the early stages of sensory
660 information processing (for reviews see Cappe et al., 2009; Klemen and Chambers, 2012). Bimodal neurons
661 sensitive to both visual and tactile stimuli applied on the hand have been found in the premotor and parietal
662 areas of the monkey (Graziano & Gross, 1998; Grefkes & Fink, 2005), when spatially congruent stimuli from
663 different origins are simultaneously presented to the animal. Neuroimaging studies further support that
664 heteromodal brain regions are specifically activated in the presence of different sensory inputs (Calvert, 2001;
665 Downar et al., 2000; Gentile et al., 2011; Kavounoudias et al., 2008; Macaluso & Driver, 2001). By applying
666 coincident visual and tactile stimuli on human hands, Gentile et al. (2011) used fMRI to show the involvement
667 of the premotor cortex and intraparietal sulcus in visuo-tactile integration processing, supporting observations
668 previously reported in monkeys. More generally, the inferior parietal cortex has been found to subserve visuo-
669 tactile integrative processing for object motion coding in peripersonal space (Bremmer et al., 2001; Grefkes and
670 Fink, 2005) as well as for coding self-body awareness (Kammers et al., 2009; Tsakiris, 2010).

671 Interestingly, direct or indirect interactions between primary sensory areas have been recently evidenced
672 (Ghazanfar & Schroeder, 2006; Cappe et al., 2009). Recently, using an elegant design inspired by the Bayesian
673 framework, Helbig et al. (2012) showed that during a task of shape identification, activation of the primary
674 somatosensory cortex can be modulated by the reliability of visual information within congruent visuo-tactile
675 inputs. The more reliable the visual information, the less activity in S1 increased.

676 Meanwhile, computational modelling approaches have demonstrated that a simple linear summation of neural
677 population activity may account for optimal Bayesian computations (Knill & Pouget, 2004; Ma et al., 2006;
678 Fetsch et al., 2013). By recording single neurones sensitive to both vestibular and visual stimuli within the
679 dorsal medial superior temporal area (MSTd) in monkeys, a brain region activated during self-body motion,

680 Morgan et al. (2008) provided evidence for the neural basis of Bayesian computations in kinesthesia. During
681 presentation of multisensory stimulation, MSTd neurones displayed responses that were well fit by a weighted
682 linear sum of vestibular and visual unimodal responses.

683 Altogether these observations support the assumption that the level of activation of primary sensory regions
684 may reflect the relative weight of the sensory cues, and that the perceptual enhancement due to convergent
685 multisensory information might be achieved through a multistage integration processing involving dedicated
686 heteromodal brain regions as well as direct interactions between primary sensory areas. Although the cerebral
687 networks responsible for visuo-tactile integration involved in self-body movement perception remain to be
688 identified, neural recordings from visuo-vestibular cortical regions support the assumption of a Bayesian-like
689 multisensory integration at the cortical level, bridging the gap between neurophysiological, computational and
690 behavioural approaches.

691

692 **Conclusion**

693 The present findings show for the first time that kinesthetic information from visual and tactile
694 origins is optimally integrated to improve speed discriminative ability for self-hand movement
695 perception. In addition, by inducing illusory movement sensations, we created an artificial conflict
696 between static muscle proprioceptive information and moving tactile and/or visual information. Such
697 sensory conflict might explain the low-perceptual gains of the observed illusions, as attested by the
698 increase in illusion gain when muscle proprioception was masked. However, we observed an over-
699 weighting in favor of the *non-moving hand cues* that cannot be fully predicted by a Bayesian optimal
700 weighting process including a Prior favoring hand immobility. An additional recalibration strategy
701 favoring the less ambiguous information in conflictual situations might explain such bias toward the
702 static proprioceptive cues that are omnipresent and play a crucial rule for kinesthesia.

703

704

705

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713

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716

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839 **Figure Captions**

840

841 **Figure 1: Experimental set-up and stimulation devices**

842 A: Experimental set-up including stimulation devices and motion capture system (CODAmotion) to
843 record actual right hand movements in the reference movement condition. B: Textured-disk used as
844 tactile stimulation. C: Visual pattern displayed by a video projector (see A). D: Mechanical vibrators
845 applied onto two antagonist wrist muscles (*pollicis longus* and *extensor carpi ulnaris*) to disturb
846 muscle proprioceptive inputs (MP) in the *Noisy* condition
847 Participants exposed to a counterclockwise rotation of the tactile and/or visual stimuli had to report
848 whether the induced clockwise illusion of hand rotation they perceived was faster or slower than the
849 velocity of the reference movement they actively executed before or after each stimulation.

850

851 **Figure 2: Schematic representation of the MLE principle**

852 In order to estimate self-hand movement velocity, the CNS is supposed to proceed as an inference
853 machine: following MLE rules, unisensory cues (noisy, normally-distributed representations of the
854 stimulation velocity ϑ_T and ϑ_V on the basis of each sensory modality, touch and vision) are optimally
855 combined to determine the minimum-variance visuo-tactile perceptual estimate ϑ_{VT} . The right panel
856 illustrates the MLE prediction for the visuo-tactile Likelihood (with variance σ^2_{VT} , black curve)
857 resulting from the optimal combination of unimodal Likelihoods (σ^2_T , σ^2_V , dark grey and light grey
858 curves, respectively).

859

860 **Figure 3: Relationship between Bayesian and psychometric functions**

861 A and B represent two different relevant conditions of stimulations (1 and 2) used to determine the
862 discriminative threshold: the PSE (A) and the intensity leading to 84.13 % of “faster than the reference
863 velocity” answer (B). V_{ref} is the velocity of the reference movement (5 °/s). σ_{Post} , μ_{Post} and μ_i are

864 parameters of the Bayesian functions, respectively the standard deviation and mean of the Posterior
865 distribution and the mean of the Likelihood function (assumed equal to the stimulation velocity). σ_ψ
866 and PSE are the psychophysical, measured parameters, respectively the variance and the mean of the
867 psychometric function. We remind that the PSE is defined as the point of subjective equality, i.e. the
868 stimulation intensity eliciting an illusory movement faster than the reference 50 % of the time. These
869 relations allow to estimate all the parameters of the hidden Bayesian functions as a function of the
870 psychometric parameters (see in Models).

871

872 **Figure 4: Schematic representation of the key steps for predicting visuo-tactile gain on**
873 **the basis of a Prior-equipped Bayesian model.**

874 **Step 1: Prior variability estimation:** the standard deviation (σ_{Prior}) of the Prior distribution (black
875 curve, centered on the null velocity) is estimated for each participant using (through Equation 6) the
876 psychometric parameters estimated in unimodal visual (orange curves) and tactile (blue curves)
877 conditions.

878 **Step 2: Prediction of visuo-tactile gain:** the expected PSE (Point of subjective equality) in visuo-
879 tactile stimulation (mean of the visuo-tactile Likelihood depicted by the dashed green curve) is
880 predicted on the basis of the estimate of the Prior variance (step 1), the MLE-estimate for σ^2_{VT} and
881 Equation 7. The visuo-tactile gain is simply derived from the PSE (see definition in Method).

882

883 **Figure 5: Comparison of velocity discrimination thresholds during tactile, visual and**
884 **visuo-tactile stimulation**

885 **A. Extraction of σ from psychometric curves:** Psychometric curves of one representative participant
886 obtained by fitting the probabilities of perceiving the illusion as faster than the reference movement
887 with a cumulative Gaussian distribution for the tactile stimulation (T, blue curve), visual stimulation

888 (V, yellow curve), and visuo-tactile stimulation (VT, green curve). The discrimination threshold, σ , is
889 the difference between the stimulation velocities leading to the «faster» answer 84.13 % of the times
890 and 50 % of the times, and it is inversely related to the slope of the psychometric function.

891 **B. Mean σ in bi- or unimodal stimulation:** Mean individual values of σ (grey bars) and mean (\pm SD)
892 values of σ extracted from the whole population data (N = 15) for tactile (blue square), visual (yellow
893 square), and visuo-tactile (green square) stimulation. For the mean σ values, significant differences
894 were found between the bimodal and each of the two unimodal conditions (* $P < .05$; ** $P < .01$).

895 **C. Multisensory Index for σ :** individual (grey bars) and mean Multisensory Index (MSI; green
896 square) for σ (N = 15 participants). Positive and negative values correspond respectively to a
897 multisensory benefit or loss in the discrimination performance of the participants with respect to their
898 most efficient unimodal performance.

899 **D. Comparison between observed and MLE-predicted σ :** Comparison between observed σ in visuo-
900 tactile stimulation and σ predicted by the MLE model for the 15 participants (S1 to S15). The green
901 diamonds correspond to the observed data and the error bars are the standard deviation. No significant
902 difference was found between predictions and observations of σ ($P = .55$, ns). Light green rectangles
903 represent 95 % CIs computed using the following bootstrap procedure. Choice data were resampled
904 across repetitions (with replacement) and refitted 1000 times to create sample-distributions of the
905 threshold for each psychometric function and for the predicted visuo-tactile parameters. The CIs were
906 directly estimated from these bootstrap-samples (percentile method).

907

908 **Figure 6: Comparison of the gains of the perceptual responses during tactile, visual and**
909 **visuo-tactile stimulation**

910 **A. Extraction of PSE from psychometric curves:** Psychometric curves of one participant obtained
911 by fitting the probability of perceiving the illusion as “faster than the reference” movement with a

912 cumulative Gaussian distribution for the tactile stimulation (T, blue curve), visual stimulation (V,
913 yellow curve), and visuo-tactile stimulation (VT, green curve). The PSE (Point of Subjective Equality)
914 corresponds to the stimulation velocity leading to the «faster than the reference» answer 50 % of the
915 time.

916 **B. Mean Gain in bi- or unimodal stimulation:** Mean individual values of gain (grey bars) and mean
917 (\pm SD) values of gain calculated as the ratio between the reference velocity, V_{ref} , and the actual
918 velocity of the visual (yellow bars), tactile (blue bars) and visuo-tactile (green bars) stimulation at the
919 PSE. For the mean gain values, significant differences were found between the bimodal and each of
920 the two unimodal conditions (* $P < .05$; ** $P < .01$).

921 **C. Multisensory Index for Gain:** Individual (grey bars) and mean Multisensory Index (MSI; green
922 square) of illusion gains (N=15 participants). Positive and negative values correspond respectively to a
923 multisensory increase or decrease in the gain of the perceptual illusions of the participants with respect
924 to the best unimodal performance.

925 **D. Comparison between observed and Bayesian predicted Gain:** Comparison between observed
926 gain in visuo-tactile stimulation and gain predicted by the Bayesian model with a zero-centered Prior
927 for the 15 participants (S1 to S15). The green diamonds correspond to the observed data and the error
928 bars are the standard deviation. The increase of the bimodal gain was predicted but over-estimated by
929 the model. Light green rectangles represent 95 % CIs computed using the following bootstrap
930 procedure. Choice data were resampled across repetitions (with replacement) and refitted 1000 times
931 to create sample-distributions of the threshold for each psychometric function and for the predicted
932 visuo-tactile parameters. The CIs were directly estimated from these bootstrap-samples (percentile
933 method).

934

935

936

937 **Figure 7: Comparison of illusion gains between *Standard* and *Noisy* conditions**

938 Mean gain (\pm SEM) of the discrimination responses induced by tactile (T, squares), visuo-tactile (VT,
939 triangles), and visual (V, diamonds) stimulation for the *Standard* (plain grey) and the *Noisy* (hatched
940 grey) conditions. Note that illusion gains observed in the *Noisy* conditions, in which muscle
941 proprioception afferents were masked by an ago-antagonist co-vibration, were significantly higher than
942 those in the *Standard* conditions whatever the stimulation (T, V, VT). * $P < .05$; ** $P < .01$

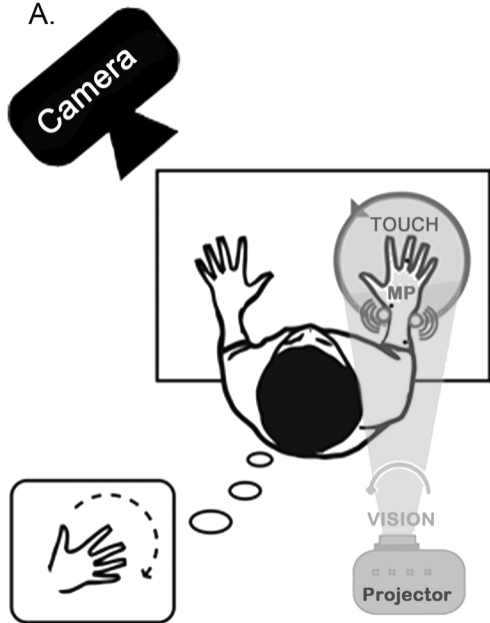
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944 **Figure 8: Comparison of the Bayesian predictions for the *Standard* and *Noisy* conditions**

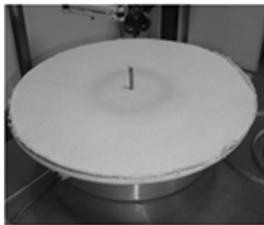
945 **A. Bayesian prediction vs observation in Noisy condition:** Comparison between observed gains in
946 visuo-tactile stimulation and gains predicted by the Bayesian model in the *Noisy* condition for the 13
947 participants (S1 to S13). The dots correspond to individual observed data and the error bars are the
948 standard deviation. represent 95 % CIs computed using the following bootstrap procedure. Choice data
949 were resampled across repetitions (with replacement) and refitted 1000 times to create sample-
950 distributions of the threshold for each psychometric function and for the predicted visuo-tactile
951 parameters. The CIs were directly estimated from these bootstrap-samples (percentile method).
952 Increase of the visuo-tactile gain was better predicted than in the *Standard* condition but remained
953 over-estimated by the model.

954 **B. Difference between prediction and observation $\text{Gain}_{\text{pred}} - \text{Gain}_{\text{obs}}$:** The quantitative difference
955 between model predictions and empirically obtained values of visuo-tactile gain was significantly
956 smaller in the *Noisy* condition compared to the *Standard* condition ($P < .05$).

A.



B.



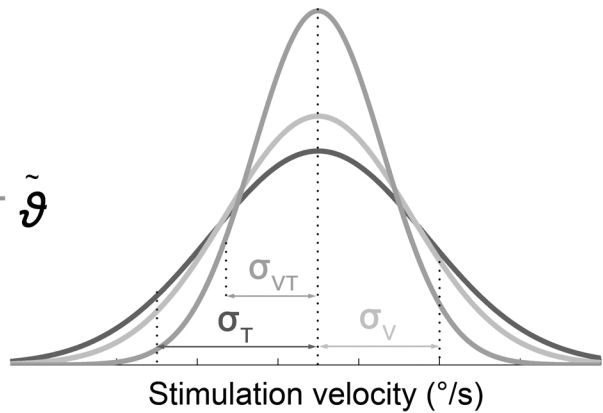
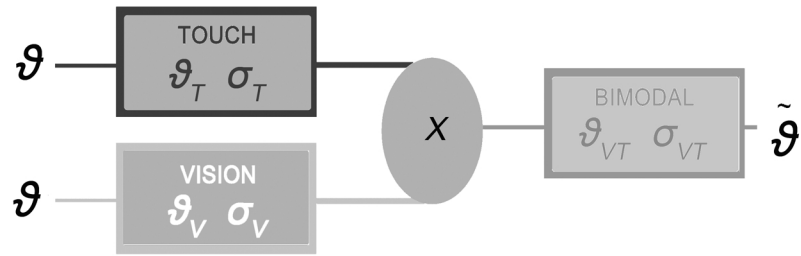
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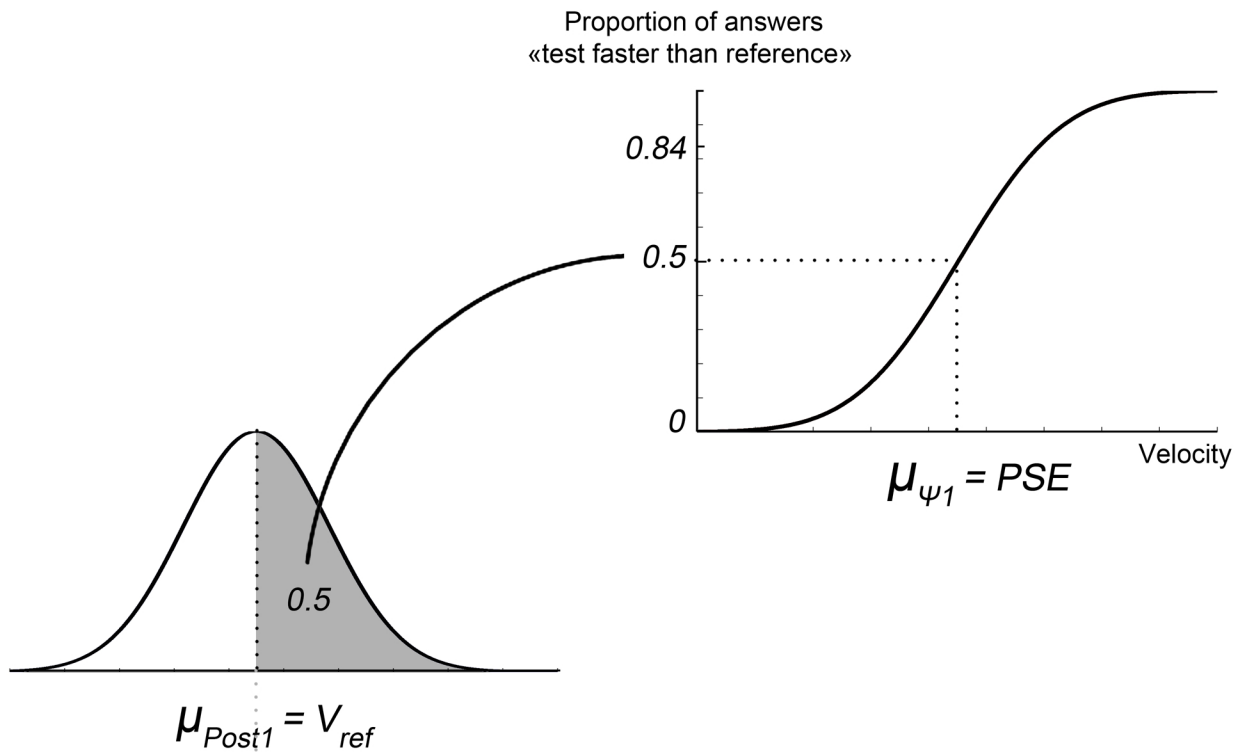
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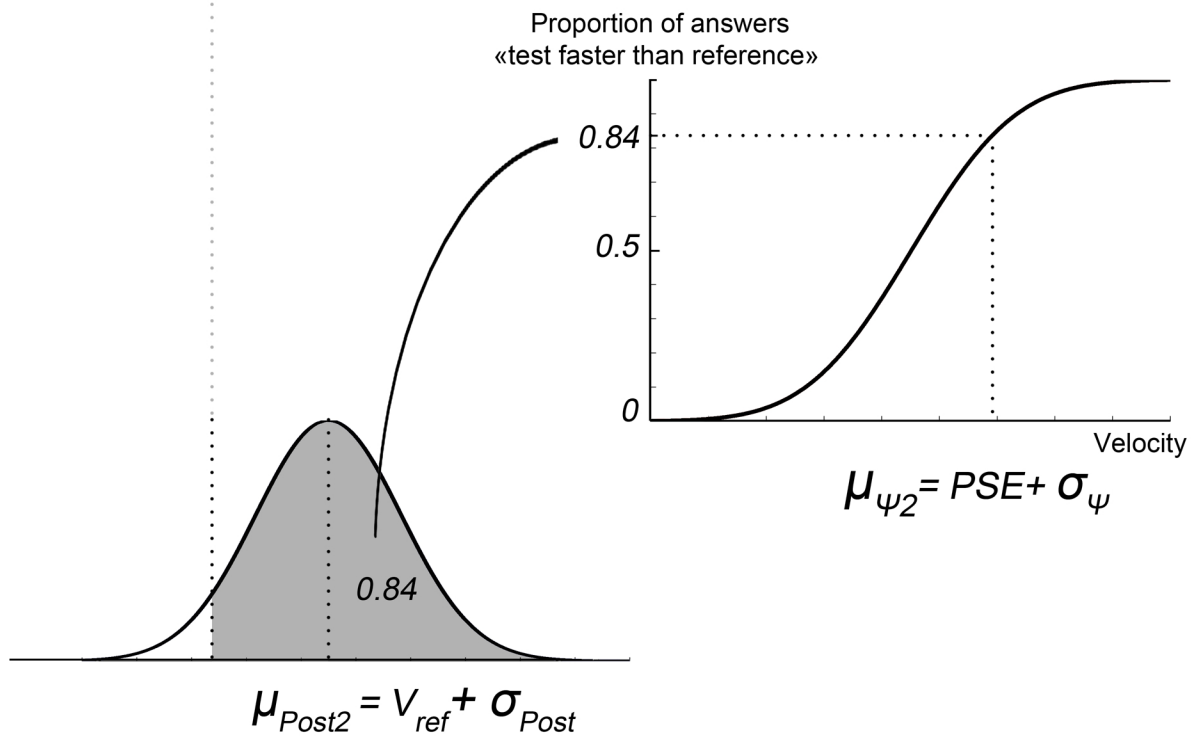
MLE principle



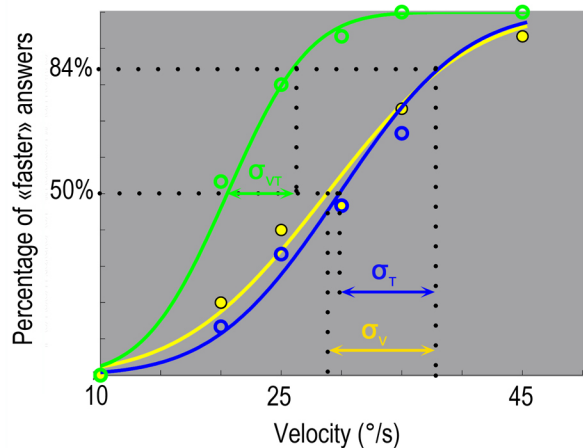
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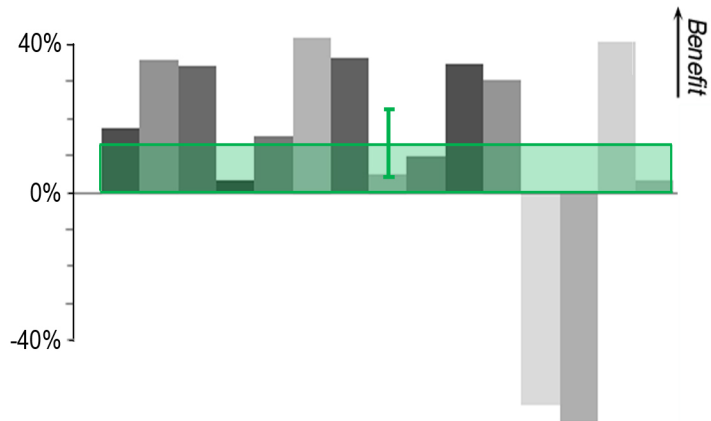
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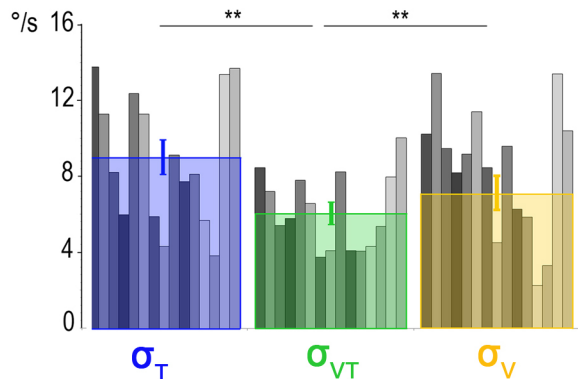
A σ extraction from psychometric curves



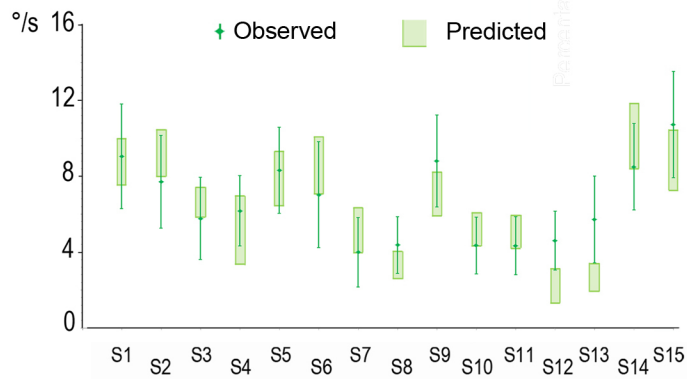
C Multisensory index for σ



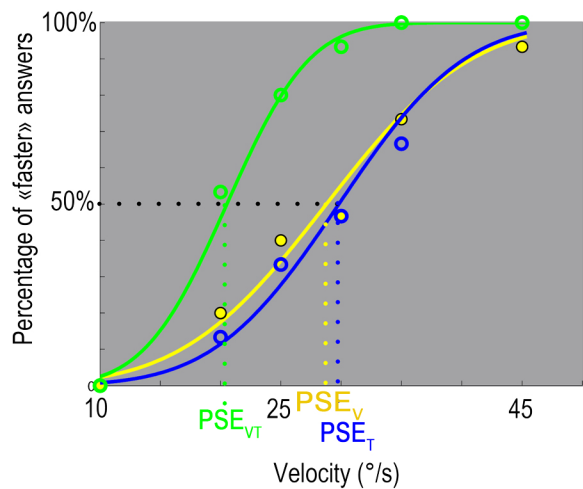
B Mean σ under bi- or unimodal stimulation



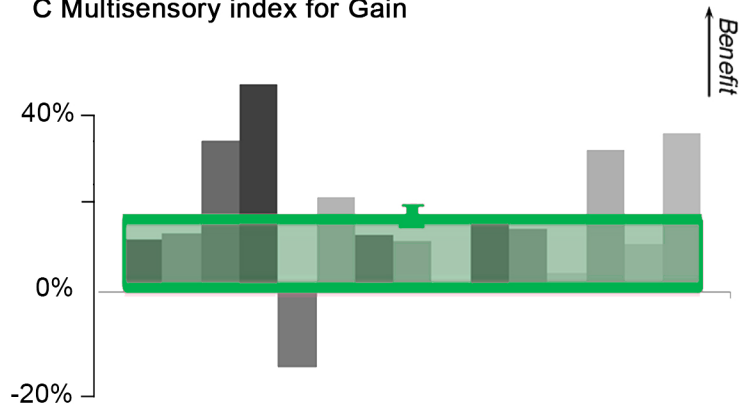
D Observed and MLE-predicted σ



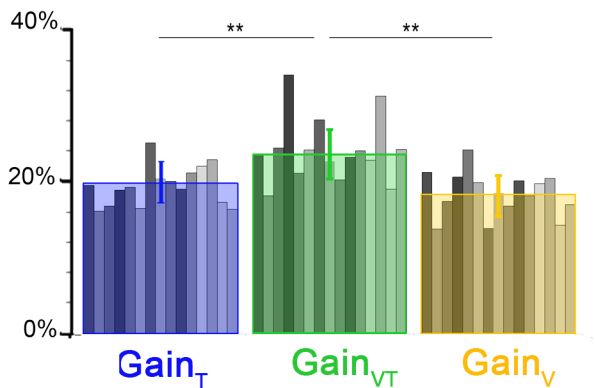
A PSE extraction from psychometric curves



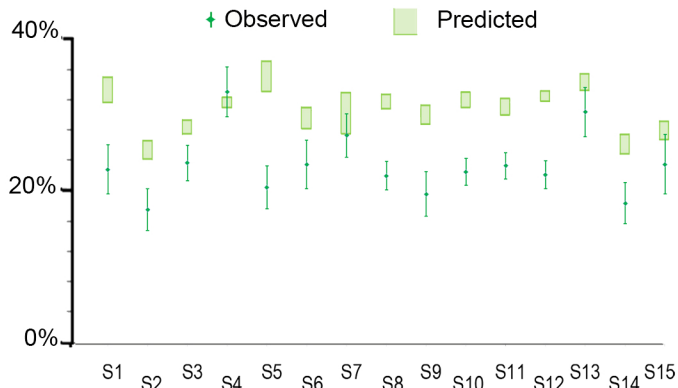
C Multisensory index for Gain



B Mean Gain under bi- or unimodal stimulation



D Observed and Bayesian predicted Gain



Illusion gain

