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## Seeing your foot move changes muscle proprioceptive feedback

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49

50 **Abstract**

51 Multisensory effects are found when the input from single senses combines and this has been well-  
52 researched in the brain. Presently, we examined in humans the potential impact of visuo-  
53 proprioceptive interactions at the peripheral level, using microneurography, and compared it with a  
54 similar behavioral task. We used a paradigm where participants had either proprioceptive  
55 information only (no vision) or combined visual and proprioceptive signals (vision). We moved the  
56 foot to measure changes in the sensitivity of single muscle afferents, which can be altered by the  
57 descending fusimotor drive. Visual information interacted with proprioceptive information, where  
58 we found that for the same passive movement, the response of muscle afferents increased when the  
59 proprioceptive channel was the only source of information, as compared with when visual cues were  
60 added, regardless of the attentional level. Behaviorally, when participants looked at their foot  
61 moving, they more accurately judged differences between movement amplitudes, than in the  
62 absence of visual cues. These results impact our understanding of multisensory interactions  
63 throughout the nervous system, where the information from different senses can modify the  
64 sensitivity of peripheral receptors. This has clinical implications, where future strategies may  
65 modulate such visual signals during sensorimotor rehabilitation.

66

67 **Significance Statement**

68 It is well known that multisensory processes occur in the brain, yet we know little about the  
69 consequences of multisensory interactions at the spinal level. We recorded from single muscle  
70 afferents, while participants either saw or did not see their foot moving. We show that adding visual  
71 information reduces muscle afferent firing, probably via descending commands by fusimotor  
72 efference. These results impact sensorimotor rehabilitation, where clinical strategies using exercises  
73 without visual feedback may promote proprioceptive training.

74

75

76 **Introduction**

77 Perception is multimodal by nature and the central nervous system (CNS) integrates multiple  
78 sensory sources to produce coherent percepts (Kavounoudias, 2017). Combining spatially and  
79 temporally congruent multisensory cues is beneficial (Stein and Stanford, 2008), where combined  
80 vision and muscle proprioception can improve perceptual or motor responses (Blanchard et al.,  
81 2013; Guerraz et al., 2012; Reuschel et al., 2010; Rossetti et al., 1995; Sober and Sabes, 2003; Tardy-  
82 Gervet et al., 1986; Van Beers et al., 1999). These studies have shown that convergent inputs must  
83 be integrated properly to assess body configuration and any changes that may occur. Computational  
84 modeling, in particular the theoretical Bayesian framework, provides such an approach to predict  
85 perceptual enhancement due to multisensory integration, by postulating that the multisensory  
86 estimate of an event is given by the reliability-weighted average of each single-cue estimate (Ernst  
87 and Banks, 2002; Landy et al., 2011). Bayesian predictions have shown the optimal integration of  
88 vision and proprioception when evaluating arm movements (Reuschel et al., 2010), positions in  
89 space (Holmes and Spence, 2005; Tagliabue and McIntyre, 2013; Van Beers et al., 2002), and in  
90 performing pointing motor tasks (Sober and Sabes, 2003).

91

92 Interactions between sensory systems are found in the brain, including in the early stages of sensory  
93 information processing (Cappe et al., 2009; Hagura et al., 2009; Helbig et al., 2012; Kavounoudias et  
94 al., 2008; Klemen and Chambers, 2012). The sensitivity of muscle afferents can be modulated via  
95 central efference, which may mean that the periphery is subject to multisensory influences. The  
96 fusimotor system sends efferent  $\gamma$ -motoneurons from the spinal cord to the intrafusal fibers of  
97 muscle spindles (Awiszus and Schäfer, 1989; Ellaway et al., 2002, 2015; Murphy and Martin, 1993),  
98 where the positional sensitivity of muscle afferents is changed by  $\gamma$ -static fusimotor neurons and  
99 their velocity sensitivity by  $\gamma$ -dynamic fusimotor neurons (Matthews, 1981).

100

101 Since direct recordings of gamma efferents are rare in humans (Ribot et al., 1986), the influence of  
102 the fusimotor drive is classically assessed by recording the activity of single muscle afferents, whose  
103 modulation can likely be indirectly supported by a change in the fusimotor drive. Through this  
104 approach, microneurographic studies have shown that the fusimotor drive can influence muscle  
105 afferent firing depending on the attentional (Hospod et al., 2007; Ribot-Ciscar et al., 2009) or  
106 emotional (Ackerley et al., 2017) context. Hospod et al. (2007) showed a decrease in the dynamic  
107 sensitivity of primary muscle afferents when a participant's attention was selectively directed to the  
108 recognition of an imposed, complex, two-dimensional movement. Conversely, muscle afferent  
109 dynamic sensitivity has been observed to increase when the proprioceptive attention task was  
110 specifically oriented towards the movement velocity (Ribot-Ciscar et al., 2009). These studies show  
111 an independent static or dynamic fusimotor control of muscle spindle sensitivity in humans, which  
112 depends on the behavioral context.

113

114 There are few studies on the influence of vision on muscle proprioceptive sensitivity via the  
115 fusimotor drive. Wessberg and Vallbo (1995) compared muscle afferent activity from the hand  
116 during a visual tracking task that consisted of following a target displayed on a screen; during the  
117 reproduction of the same movement in the absence of visual control, no difference was reported. In  
118 contrast, Jones et al. (2001) showed that muscle afferent activity decreased in a visuo-motor  
119 adaptation task, where the displacement of a visual target was shifted, making the visual  
120 information incongruent with proprioceptive information from the moving hand. The decrease in  
121 proprioceptive sensitivity was interpreted as a strategy for resolving bisensory conflict. More  
122 recently, Dimitriou (2016) showed that the muscle spindle firing varied with adaptation state  
123 independently of muscle activity, making the gamma system a specific contributor to motor  
124 learning.

125

126 In these previous studies, vision was not directed towards the participant's own moving body, but  
127 towards a visual target (displaced by the participant's moving hand). In addition, these studies used  
128 active, rather than passive movements. Active movements are more representative of natural body  
129 conditions; however, passive movements are ideal to address muscle spindle sensitivity in the  
130 absence of concomitant activation of skeletomotor neurons (alpha-gamma coactivation). Presently,  
131 we investigated whether seeing your own foot move passively altered muscle proprioceptive  
132 feedback and how it might be related to perceptual performance. We designed a behavioral  
133 experiment to test whether movement amplitude discrimination was better when participants  
134 viewed their foot moving, as compared to only having muscle proprioception when participants kept  
135 their eyes closed. Further, we examined changes in muscle spindle sensitivity to similar passively-  
136 imposed foot movements, varying both vision and attention, where we hypothesized that muscle  
137 afferent firing would be modulated over these conditions.

138

#### 139 **Materials & Methods**

140 The present experiments were performed on healthy human volunteers, where written, informed  
141 consent was obtained and a random experimental design was used. The study was approved by the  
142 local ethics committee [Human subjects were recruited at a location which will be identified if the  
143 article is published] and performed in accordance with the Declaration of Helsinki. The study  
144 consisted of two series of experiments to investigate the multisensory effects of visual and  
145 proprioceptive processing: one using behavioral psychophysics and the other using the *in vivo*  
146 technique of microneurography. Fifteen volunteers (2 males; 26 years  $\pm$  5 SD) took part in the first  
147 behavioral experiment and thirteen (7 males; 26 years  $\pm$  6 SD) different volunteers took part in the  
148 second microneurographic experiment.

149

#### 150 **General experimental set-up**

151 In both experiments, the participants were seated in a semi-reclined armchair with their legs  
152 positioned in cushioned grooves, so that a standardized position could be maintained without  
153 muscle activity. The knee joint was at a flexion angle of  $\sim 120\text{-}130^\circ$ . The right foot rested on a  
154 stationary plate and the left foot rested and was held on a pedal connected to a computer-  
155 controlled robot, allowing sinusoidal foot plantar flexion/dorsiflexion movements to be imposed.  
156 The absence of concomitant muscle activity was monitored throughout the two experiments by  
157 recording surface electromyography (EMG). A pair of surface electrodes (Ag–AgCl, inter-electrode  
158 distance 2 cm) was placed over the tibialis anterior (TA) and another pair on gastrocnemius soleus  
159 (GS) muscle bellies during the behavioral experiment. In the microneurographic experiment, pairs of  
160 surface electrodes were placed over the TA (corresponding to afferents originating in TA and  
161 extensor digitorum longus (EDL) muscles) and peroneus longus (PL; corresponding to afferents  
162 originating in PL) muscle bellies. The location of each pair of electrodes was defined by asking the  
163 participant to isometrically contract the muscle under consideration and palpation of the muscle  
164 belly. The EMGs were band-pass filtered (30-3000 Hz), recorded with a high gain (x5000), and  
165 sampled at 10 kHz. Autonomic responses were recorded through electrodermal activity (EDA), using  
166 two surface electrodes placed on each side of the left hand (gain: x500, band-pass: 0.1-100 Hz,  
167 sampling frequency: 500 Hz). Physiological data were stored on a digital tape recorder (DTR 1802,  
168 Biologic, Claix, France) and processed off-line in Spike2 ([Spike2 Software](#), RRID:SCR\_000903). During  
169 all experiments, participants wore noise-cancelling headphones (Bose, Framingham, MA) to prevent  
170 extraneous sounds.

171

### 172 **Unitary muscle afferent recordings**

173 The *in vivo* technique of microneurography was used to record from the left common peroneal  
174 nerve at the popliteal fossa in humans (Bergenheim et al., 1999; Hagbarth and Vallbo, 1968). The  
175 nerve was located by palpation. Unitary muscle afferent activity was recorded differentially using an  
176 insulated tungsten microelectrode (impedance 0.3-1 M $\Omega$ , tip diameter  $\sim 5\ \mu\text{m}$ , length  $\sim 30\ \text{mm}$ ; FHC;

177 Bowdoin, ME). The recordings were monitored continuously using an oscilloscope and a  
178 loudspeaker. Neural activity was amplified (x100,000) and band-pass filtered (300-3000 Hz) to  
179 ensure an optimal signal-to-noise ratio, and sampled at 20 kHz. Muscle afferents were identified as  
180 primary endings on the basis of their irregular spontaneous activity, their high dynamic sensitivity to  
181 ramp-and-hold movements, and their silencing during passive muscle shortenings (Edin and Vallbo,  
182 1990). The activity from 24 single muscle spindle endings (21 type Ia muscle afferents and 3 type II)  
183 was recorded, but due to a loss of unit stability over time in some recordings, we gained full datasets  
184 over all conditions (vision, no vision, attention, no-attention) from 16 units (all type Ia). These  
185 originated in the extensor digitorum longus (EDL; n = 10), peroneus longus (PL; n = 3), and TA (n = 3)  
186 muscles. Microneurographic data were stored via digital tape recorder (DTR 1802, Biologic, Claix,  
187 France), along with the physiological data. Data were processed off-line by means of Spike 2  
188 software ([Spike2 Software](#), RRID:SCR\_000903).

189

## 190 **Procedure**

### 191 *Behavioral experiment*

192 Participants were required to discriminate the amplitude difference between two imposed  
193 movements of their left foot. The robot moved their foot - up-and-down twice, which then returned  
194 to its initial position (set at 20° and 40° from typical maximal dorsal and plantar flexions,  
195 respectively). The velocity was fixed at 5°/s. One of the movements was always the same reference  
196 movement, corresponding to an amplitude angle of 6.4° between the foot and the shin bone. Before  
197 each movement pair (repeated 15 times), participants were orally instructed to keep their eyes  
198 closed ('no vision', proprioceptive-only information) or have them open ('vision', combined and  
199 congruent visuo-proprioceptive information); vision and no vision trials were randomized. In the  
200 vision condition, the participants were required to look at their left foot moving. Each trial included  
201 the reference movement at 6.4° (given randomly the first or second movement) and another 'test'  
202 movement, which consisted of one of seven possible angles (5.1°, 5.6°, 6°, 6.4°, 6.8°, 7.2°, or 7.6°).

203 These angles were chosen on the basis of a previously defined pilot study (performed on 4  
204 participants not included in the main experiment), in order to identify angle amplitudes that make  
205 discrimination against the 6.4° reference very difficult (6 and 6.8°) or rather easy (5.1 and 7.6°) or of  
206 intermediate difficulty (5.6 and 7.2°). Participants had to decide whether the first or the second  
207 movement was the largest in amplitude. They answered orally 'one' or 'two', after the movements  
208 had finished, when prompted by the experimenter. Each angle was tested 30 times (15 times with  
209 closed eyes and 15 times with opened eyes) and resulted in a total of 210 movement comparisons  
210 (30 repetitions x 7 angles) per participant. All movement pairs were pseudo-randomized. Three  
211 minute breaks were systematically given after every 20 pairs of movement comparisons and the  
212 experimenter regularly checked whether the subject needed to take an extra break at any time to  
213 prevent fatigue and loss of motivation.

214

#### 215 *Microneurographic experiment*

216 Participants underwent similar passive foot displacements at the level of the ankle, where a series of  
217 30 sinusoidal plantar flexion/dorsiflexion movements (5° amplitude and 5°/s velocity, over ~1  
218 minute) were imposed during microneurographic recording. This longer foot movement protocol  
219 was chosen for the single unit microneurographic recording because it was important to analyze  
220 muscle afferent firing in the absence of muscle activity. A time pause of 30 s was given after each  
221 movement.

222

223 To investigate the effect of vision, the activity of each muscle afferent was recorded under four  
224 conditions presented in a pseudo-randomized order using a 2 x 2 factorial design, with vision (vision,  
225 no vision) and attention (attention, no attention) as experimental factors. Visual information was  
226 manipulated by asking the participant either to keep their eyes closed (no vision condition), or their  
227 eyes open with the instruction to watch the movement of their foot (vision condition). Attention was  
228 manipulated by asking the participants either to simply relax and not pay attention to their foot

229 moving (no attention condition) or they were instructed to pay attention to the movement of their  
230 foot (attention condition). To make sure that the participants were attentive, the participant was  
231 asked to judge whether it felt like the current sinusoidal movements were of larger amplitude than  
232 the previous ones. In fact, it was always the same passive movement imposed on the participant, to  
233 compare the response of muscle afferents to investigate a change in firing properties of the afferent  
234 fibers depending on the experimental conditions. Therefore, the same movement amplitude was  
235 used over all the four experimental conditions in the microneurographic study. We chose the lowest  
236 amplitude (5°) from the range of amplitudes previously tested in the present psychophysical study.  
237 Only one amplitude was used to minimize the duration of the experiment, as the longer the  
238 microneurographic recording, the higher the risk of losing the unit (e.g. due to electrode  
239 displacement) and thus not obtaining data. This is a common risk during microneurography in  
240 humans, which was more likely to occur presently due to the long-lasting trials used in this study (30  
241 cycles of 189 ankle movements, repeated). In addition, to avoid any implicit attention task, the no-  
242 attention and attention trials were blocked separately, and the no-attention block always preceded  
243 the attention block.

244

#### 245 **Data analysis**

246 Data were analyzed in MATLAB ([MATLAB](#), RRID:SCR\_001622) and compared statistically in SPSS  
247 ([SPSS](#), RRID:SCR\_002865) with a level of significance set at  $p < 0.05$ . For all statistical tests, effect  
248 sizes were determined using partial Eta-squared ( $\eta^2$ ). See the statistical table (Table 1) for further  
249 details of the tests carried out.

250

#### 251 *Behavioral experiment*

252 In order to evaluate and compare participants' performances across the two conditions (vision/no  
253 vision), we used an approach classically employed to estimate velocity discriminative thresholds of  
254 self-movements (Chancel et al., 2016; Ernst and Banks, 2002; Kingdom and Prins, 2010; Landelle et

255 al., 2018; Reuschel et al., 2010; Tagliabue and McIntyre, 2013; Wichmann and Hill, 2001). The  
256 psychometric data (i.e. the proportion of answers corresponding to movements found to be larger in  
257 amplitude than the reference) were fitted by a cumulative Gaussian function:

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

258 Here,  $x$  represents the movement angle (in degrees);  $\mu_\psi$  is the mean of the Gaussian, i.e. the point  
259 of subjective equality (PSE), that corresponds to the stimulation intensity leading the participant to  
260 perceive no difference between the reference and the test movements; and  $\sigma_\psi$  is the standard  
261 deviation of the curve (discrimination threshold), which is inversely related to the participant's  
262 discrimination sensitivity. A smaller  $\sigma_\psi$  value corresponds to higher discrimination sensitivity in the  
263 task and was used to measure their discrimination capability. The two indices, PSE and  $\sigma_\psi$ ,  
264 characterize the participant's performance, and  $\lambda$  accounts for stimulus-independent errors (e.g.  
265 due to participant lapses) and was restricted to small values ( $0 < \lambda < 0.06$ , Wichmann and Hill,  
266 2001). This parameter is not informative about the perceptual decision, thus we disregarded it for  
267 the subsequent analyses. Psignifit toolbox, implemented in MATLAB, was used to fit the  
268 psychometric curves. In this fitting procedure, bootstrap analysis was performed and the goodness-  
269 of-fit of the chosen model (i.e. the Gaussian function) was checked. As a result, the statistical power  
270 of the two parameters obtained to describe each participant's perception, mean and variance, was  
271 reinforced which leads to a reliable comparison between the different conditions both within and  
272 between participants (Wichman and Hill, 2001). Since the  $\sigma_\psi$  (beta) values can be assimilated as  
273 positively-skewed continuous variables modeled by a Gamma distribution, we used a non-  
274 parametric generalized linear model for repeated measured (GzLM) to compare these variables  
275 between the vision and no vision conditions.

276

277 *Microneurographic experiment*

278 The nerve spikes were inspected carefully for their single unit nature in an expanded time scale and  
279 then transformed into an instantaneous frequency curve (bin size = 0.005 s). The mean curve was  
280 obtained by averaging the response to 29 sinusoidal movements, where the first movement was  
281 excluded because of a dynamic response from the onset of the movement. Occasionally, some EMG  
282 activity (i.e. fluctuations in the steady EMG baseline) was found, despite the instruction for the  
283 participant to relax. When this occurred, the contaminated movement cycle was removed (cf.  
284 Ackerley et al., 2017). This occurred in only 5/64 runs (16 units x 4 conditions) and for each case, at  
285 least 85% of cycles were included. Measures were extracted from the averaged response, including  
286 the maximum and minimum frequency, and the difference between these two measures ('delta'),  
287 which was used as an index to characterize a unit's response in each condition (Ackerley et al.,  
288 2017). This measure was used to quantify the dynamic response of muscle afferents (Kakuda, 2000).

289

290 In line with other microneurographic studies of muscle afferent firing (e.g. Dimitriou, 2016), the data  
291 were normalized (z-transformed to give z-scores), so as to compare differences across the conditions  
292 over the individual afferents. Here, we obtained the delta per afferent/condition, which was then  
293 normalized by subtracting the mean delta, and this was divided by the delta standard deviation, for  
294 that afferent. This produced the number of standard deviations by which each condition differed  
295 from the mean value for each afferent tested. Statistical analyses were conducted on these  
296 normalized data, on the whole population of afferents, where the data were first checked for  
297 normality. A repeated measures two-way ANOVA was carried out in SPSS, to determine the effects  
298 of visual information and attention, and any interaction between these.

299

### 300 *Physiological indexes in both experiments*

301 The EMG and EDA activity were used to investigate whether the participant showed muscular or  
302 autonomic activity in the experiments. The direct current offset was removed from the EDA data and  
303 the EDA and EMG data were down-sampled to 2.5 kHz. For the psychophysical experiment, these

304 data were separated by visual condition, where data were epoched from the beginning of the  
305 movement to the end of a movement, per trial, resulting in 105 total trials for the combined visuo-  
306 proprioceptive information condition and 105 for the proprioceptive-only condition. For the  
307 microneurographic experiment, EMG (one EMG source was used, which depended on the muscle  
308 afferent recorded from) and EDA signals were extracted, per condition per participant, from the  
309 duration of the sinusoidal movement. For both signals, areas under the curves were measured to  
310 analyze the modulation of physiological signals across conditions. The mean values, per measure,  
311 were checked for normality and the visual conditions were compared by Student's paired t-tests in  
312 the behavioral experiment and the visual/attention conditions using repeated measures two-way  
313 ANOVA for the microneurography experiment.

314

## 315 **Results**

### 316 *Behavioral measurement of effect of visual information on movement discrimination*

317 Figure 1A shows an example of a participant's ability to discriminate the amplitude of their foot  
318 movement. The discrimination improved in the visuo-proprioceptive condition, compared to the  
319 proprioception-only condition, as shown by an increased slope of the visuo-proprioceptive  
320 psychometric curve. More precisely, the discrimination threshold  $\sigma$  (i.e., the increase in movement  
321 amplitude required to induce a perception of movement larger than the reference movement in  
322 84% of the trials with respect to 50% of the trials) was lower in the visuo-proprioceptive condition.  
323 The group data revealed that participants were on average able to discriminate the angle of their  
324 foot with higher precision in the vision condition, as compared to the no vision condition, as shown  
325 by a decrease in the discrimination level (Figure 1B). The discrimination threshold  $\sigma$  was significantly  
326 lower in the vision condition (mean  $\sigma = 0.66 \pm 0.04^\circ$  SEM) than in the no vision condition (mean  $\sigma =$   
327  $0.8 \pm 0.06^\circ$  SEM) (GzLM analysis slope = 0.242,  $t = 3.31$   $p < 0.001$ ; Figure 1B)<sup>a</sup>. No significant  
328 differences were found in the physiological measures (EMG, EDA) between the visual conditions  
329 (Table 2<sup>b</sup>).

330

331

*Please insert Figure 1 and Table 2 around here*

332

333 *Microneurography measurement of effect of visual information on movement encoding*

334 A total of 16 primary Ia muscle afferents were tested over the conditions where the participant  
335 viewed their foot moving (vision) or had their eyes closed (no vision), during a further task of paying  
336 attention to the movement (attention) or not (no attention). Figure 2 shows examples of unitary  
337 recordings from a muscle afferent over the conditions (Figure 2A), with the mean extracted change  
338 in instantaneous firing (delta) over the sinusoidal movement cycles per condition (Figure 2B). It can  
339 be seen in, both the individual cycles and in the unit's means, that there was a clear difference  
340 between the vision conditions, where the mean instantaneous firing frequency was lower with visual  
341 information, in both attention and no attention conditions.

342

343

*Please insert Figure 2 around here*

344

345 The same result was found in the group data (Figure 3). A repeated measures ANOVA on the delta z-  
346 scores showed a significant main effect of vision ( $F_{(1,15)} = 20.36$ ,  $p < 0.001$ , partial  $\eta^2 = 0.58$ ; Figure 3),  
347 but no significant effect of attention ( $F_{(1,15)} = 0.19$ ,  $p = 0.672$ , partial  $\eta^2 = 0.01$ ), nor an interaction  
348 between visual information and attention ( $F_{(1,15)} = 0.64$ ,  $p = 0.435$ , partial  $\eta^2 = 0.04$ )<sup>c</sup>. Therefore, a  
349 significant increase in delta was found when visual information was removed, but paying attention  
350 to the movement did not make a difference in the muscle afferent firing in this paradigm.

351

352 The physiological data (EMG, EDA) showed no significant differences between the conditions (Table  
353 3<sup>d</sup>). Here, for both EMG and EDA data, we found no significant effect of having visual information, or  
354 not, and neither was there an effect of whether the participant paid attention to the movement or  
355 simply relaxed, nor an interaction of these factors.

356

357

*Please Insert Figure 3 and Table 3 around here*

358

**359 Discussion**

360 Presently, we investigated the effect of congruent visual and/or proprioceptive signals on the  
361 processing of ankle movement. We found that visual information interacted with proprioceptive  
362 information, as seen in behavioral measures and in the responses of single muscle afferents. When  
363 participants saw their moving foot, they were more accurate in judging movement amplitude.  
364 Further, we found that the response from single muscle afferents was increased when the  
365 proprioceptive channel was the only source of sensory information, as compared to when the  
366 participant had the congruent visual input.

367

*368 Enhancement of visuo-proprioceptive perception*

369 Our behavioral results confirmed that combining visuo-proprioceptive information relating to self-  
370 body movements provided a perceptual enhancement, as there was a significant decrease in the  
371 threshold for discrimination when additional visual information was available. This corresponds well  
372 with many studies showing that combining congruent visuo-proprioceptive stimulation enhances the  
373 resulting perception, suggesting that both visual and proprioceptive cues are co-processed for  
374 kinesthetic purposes (Blanchard et al., 2013; Guerraz et al., 2012; Reuschel et al., 2010; Rossetti et  
375 al., 1995; Tardy-Gervet et al., 1986; Van Beers et al., 1999). For example, using the classical mirror  
376 paradigm, Guerraz et al. (2012) reported that when participants looked at the reflection of their  
377 moving left arm in a mirror, they felt an illusion of a concomitant displacement of their stationary,  
378 hidden right arm. When a congruent muscle vibration was added on the resting right arm, i.e.  
379 simulating a movement in the same direction as that of the visual moving arm, the velocity of the  
380 resulting illusion increased, showing the beneficial impact of multisensory inputs.

381

382 Vision and muscle proprioception may combine in movement perception, but it does not mean that  
383 the weights allocated to each of these sensory cues are equal. For example, under artificial  
384 conflicting visuo-proprioceptive conditions, where visual cues of the participants were deviated  
385 using prisms and participants had to place an unseen finger in the same position as their seen finger,  
386 visual information has been shown to override muscle proprioceptive information under full-light  
387 conditions. In contrast, proprioception dominates when vision input is severely reduced to a small  
388 light-emitting diode on the end of their finger, viewed in darkness (Plooy et al., 1998). Therefore, the  
389 exact behavioral context must be taken into account. According to the theoretical Bayesian  
390 framework, the CNS allocates relative weights to each sensory cue on its relative reliability to encode  
391 the perceptual event in a given context and their weighted combination can optimize the resulting  
392 perception (Ernst and Banks, 2002; Landy et al., 2011). Although our present experiment was not  
393 designed to test the optimality hypothesis, one may hypothesize that the discriminative  
394 enhancement we found in the bisensory condition may be explained by a weighted combination of  
395 both visual and proprioceptive information, as reported in other perceptual tasks (Reuschel et al.,  
396 2010; Van Beers et al., 1999).

397

#### 398 *Dynamic muscle spindle sensitivity increases in absence of vision*

399 It is generally assumed that multisensory integrative mechanisms take place in the brain, but the  
400 present findings show spinal effects, where visual signals were associated with decreases in the  
401 responses of the muscle afferents. We found that there was a decrease in the depth of modulation  
402 ( $\delta$ ) to repeated sinusoidal movements, when the participants viewed their foot moving. We  
403 verified that this change in muscle spindle sensitivity was not due to involuntary muscle activity, as  
404 the leg EMG activity recorded showed no significant differences across conditions. The effect of  
405 vision occurred independently of the attentional state of the participants, as manipulated via direct  
406 instructions to attend or not, where attention did not affect the  $\delta$ . Similarly, there was no  
407 significant interaction between vision and attention. Therefore, we postulate that in the present

408 experimental manipulation, attentional effects do not account for the changes in muscle spindle  
409 sensitivity in the different visual conditions. However, our manipulation of attention was explicit (i.e.  
410 we asked the participants to attend or not), which was in part constrained by the microneurography  
411 conditions where the participants are required to remain relaxed, and we were not able to confirm  
412 their attentional load. It may have been the case that participants may have simply disregarded the  
413 instruction to either attend or not attend; however, participants often reported the difficulty of the  
414 task, since the movements were actually all the same, which suggested that they really followed the  
415 instructions and executed the attentional task.

416

417 The absence of a change in muscle afferent activity with attention may appear contradictory with  
418 the results of previous studies, where it has been observed that a fusimotor-induced sensitization of  
419 muscle spindles occurs during proprioceptive attention tasks (Hospod et al., 2007; Ribot-Ciscar et al.,  
420 2009). However, the previous experiments were specifically designed to address the effect of  
421 attention, while here it was only a controlled parameter, and a difference between the difficulties of  
422 the present and previous tasks likely accounts for this. The present task was a simple comparison of  
423 movement amplitude at the end of the sinusoidal movements between attention conditions, which  
424 is far easier than the recognition of writing movements (Hospod et al., 2007) or classifying different  
425 movement amplitudes or velocities (Ribot-Ciscar et al., 2009).

426

427 We postulate that during the visual conditions, where the participant viewed their foot moving, the  
428 proprioceptive information, coupled with congruent visual signals, aids signal processing. In line with  
429 the Bayesian framework, a relative weighting of each visual and proprioceptive cue may account for  
430 the perceptual enhancement observed in our visuo-proprioceptive condition. The model predicts  
431 that if one sensory source becomes less reliable, the weight of the other one increases (Ernst and  
432 Banks, 2002). In the current study, when only proprioceptive information was available, the  
433 participant relied on one sensory source, where we found an increased sensitivity in firing of the

434 muscle afferents. Conversely, when congruent visual information was present, the relative visual  
435 weight increased, while that of the proprioception decreased. Vision plays a dominant role in spatial  
436 tasks, as reported in studies using the mirror paradigm, where seeing the reflection of one's moving  
437 arm in a mirror is sufficient to induce an illusion of a concomitant displacement of the other  
438 stationary, hidden arm (Guerraz et al. 2012). Furthermore, Chancel et al. (2016b) reported that  
439 illusions induced using the mirror paradigm can survive despite a marked visual impoverishment  
440 (obtained by covering between 0-100% of the mirror); the mirror illusion was significantly degraded  
441 only when the visual degradation was >84%, suggesting that even restricted visual information is  
442 sufficient to provide relevant kinesthetic cues. Future studies may be conducted to explore whether  
443 changing the reliability of the visual feedback by progressively degrading visual information results in  
444 an increase of muscle spindle sensitivity.

445

446 Previous microneurographic studies exploring the effect of vision on muscle proprioceptive  
447 information used external visual targets (Dimitriou, 2016; Jones et al., 2001; Wessberg and Vallbo,  
448 1995), in contrast to our experiment where the participant viewed their own passive movement.  
449 Jones et al. (2001) described a decrease in muscle afferent firing rate during incongruent muscle  
450 afferent and visual feedback, which was interpreted as a strategy for resolving bisensory conflict.  
451 Conversely, an increase in muscle afferent firing was more recently observed during a similar  
452 visuomotor task specifically during an imposed adaptation phase, making the fusimotor control a  
453 means of adjusting the human proprioceptive system to motor learning (Dimitriou, 2016).  
454 Interestingly, the latter study also observed a decrease in muscle spindle dynamic sensitivity in the  
455 washout stage, when visual feedback was again congruent with muscle feedback. In line with  
456 Dimitriou (2016), we found that the fusimotor drive selectively decreased muscle spindle sensitivity  
457 when muscle afferent feedback was accompanied by congruent visual cues. Although at first glance  
458 they might seem disparate, taken together, these recent studies and our present one accounted for  
459 a fusimotor control of muscle spindle sensitivity independent of the concurrent muscle activity,

460 which has long been debated (Vallbo et al., 1979). They all suggest that muscle spindle sensitivity  
461 may change according to its relevance to the context and, in particular, the presence or not of  
462 relevant visual cues.

463

464 The reweighting of proprioceptive information in the absence of visual signals can be related to the  
465 modulation observed in the primary somatosensory cortex depending on concomitant visual signals  
466 (Blakemore et al., 2005; Helbig et al., 2012). Using a design inspired by the Bayesian framework,  
467 Helbig et al. (2012) showed that during a task of shape identification, activation of the primary  
468 somatosensory cortex was modulated by the reliability of visual information within congruent visuo-  
469 tactile inputs. The less reliable the visual information, the more activity in the primary  
470 somatosensory cortex increased. In line with the modality appropriateness model (Welch and  
471 Warren, 1986) and the Bayesian framework (Ernst and Banks, 2002), one can assume that  
472 crossmodal processing is more likely to occur within the sensory pathway corresponding to the most  
473 accurate signal regarding the task, since this sensory signal is supposed to get a greater weight  
474 compared to the other less reliable signals.

475

476 Descending fusimotor influences from relevant visual cues may reduce the sensitivity of muscle  
477 afferents, reflecting a decrease in the proprioceptive contribution to encode the actual movement.  
478 Indeed, watching a video of one's own hand in movement is sufficient to elicit an illusory movement  
479 of participant's resting hand. By recording brain activity during this pure visually-induced kinesthetic  
480 illusion, Kaneko et al. (2015) found that the lateral premotor (PM) cortex and the supplementary  
481 motor area (SMA) were specifically activated together with the posterior parietal cortices and the  
482 insula. It is well known that the SMA and lateral PM are part of the motor system, with direct  
483 connections to M1, and descending output to the spinal cord (Dum and Strick, 1991; He et al., 1995;  
484 Maier, 2002; Picard and Strick, 2001, 1996). Further, the SMA and the lateral PM were not activated  
485 when participants viewed a video of someone else's own hand. Only relevant kinesthetic visual cues

486 may therefore influence proprioceptive sensitivity through descending motor commands that can  
487 modulate spinal fusimotor efference.

488

489 *Functional significance of the fusimotor modulation*

490 One may consider that the observed fusimotor effect is small, as compared to in animals; however,  
491 it has been repeatedly observed in humans (Ackerley et al., 2017; Burg et al., 1975; Dimitriou, 2016;  
492 Gandevia et al., 1994; Hospod et al., 2007; Jones et al., 2001; Ribot-Ciscar et al., 2009, 2000; Vallbo  
493 and Al-Falahe, 1990; Vallbo and Hulliger, 1981) and has been considered as intriguing when  
494 compared to animal data, where muscle spindle firing rates are ten times higher than in humans, as  
495 are the fusimotor-induced changes (Matthews, 1981). Whatever its amount, the observed effect was  
496 sufficient to significantly alter activity of muscle afferents and hence may have a functional impact  
497 on the resulting perception.

498

499 Moreover, the fact that our two experiments have been done with two different populations of  
500 participants may at first appear as a limitation of the present study. However, it is worth noting that  
501 there is commonly a high variability in the firing of muscle afferents, depending on the nature and  
502 number of intrafusal muscle fibers that are included, the fusimotor innervation received by the  
503 intrafusal fibers, and the location of the muscle spindle inside the muscle, where a receptor near the  
504 ankle joint will be more affected by the movement than another located more proximally in the EDL  
505 or TA muscles. Therefore, one can consider that the variability introduced by the use of different  
506 participants does not overly influence the outcome, with respect to the intra-subject variability, due  
507 to the technical challenge of recordings made in the same subject.

508 Our finding that afferent proprioceptive signals from ankle could be modulated by visual cues may  
509 be important for controlling postural balance (Burke and Eklund, 1977; Kavounoudias et al., 2001;  
510 Massion, 1992). High ankle proprioceptive acuity has been observed to be predictive of sport  
511 performance level in elite athletes such as dancers (Han et al., 2015b) and in balance performance of

512 the elderly (Goble et al., 2011). Similarly, better ankle proprioception is correlated with reduced  
513 ankle injuries (Han et al., 2015a), while after a complete loss of somatosensory afferents,  
514 deafferented patients present severe deficits in postural and motor tasks (Forget and Lamarre,  
515 1995). The central processing of ankle proprioceptive information with other sensory information  
516 enables optimal integration for balance control. When a source of information is used for other  
517 purposes, for example, if vision is used to track a target in the environment, the CNS uses a  
518 reweighting strategy relying on the most reliable sources of information to optimize balance control.  
519 We presently show that a relative reweighting of visual signals may occur by a recalibration at more  
520 peripheral levels of ankle proprioceptive inputs, via a direct setting of muscle receptor sensitivity by  
521 the CNS.

522

523 The present results may have further clinical impact on sensorimotor rehabilitation. Different  
524 interventions are used to improve ankle proprioception and balance control, particularly after ankle  
525 injury. While passive interventions, such as taping or compressing, do not seem to particularly  
526 improve proprioception, active interventions with task-specific paradigms are efficient, suggesting  
527 central processing modifications (Han et al., 2015b). The present results suggest that removing visual  
528 information may optimize the intervention, by providing the brain with increased proprioceptive  
529 information that may favor a better recovery of balance control.

530

531 In conclusion, we show that muscle afferent sensitivity can be altered in a context-dependent way  
532 via descending influences. Specifically, we show that when proprioceptive signals from a foot  
533 movement are coupled with congruent visual information, a decrease in muscle afferent firing was  
534 found. This decrease in the bisensory condition may reflect a re-weighting of the two sensory cues in  
535 favor of the visual source. Our study shows that the mechanisms of sensory reweighting are not  
536 limited to higher-level neural control in the brain, but that there are also spinal effects of  
537 multisensory processing between visual signals and proprioceptive coding. This opens up the

538 opportunity for the study of other multisensory effects below the level of the brain and impacts on  
539 our understanding of multisensory interactions throughout the central nervous system, which may  
540 also provide clinical therapeutic strategies for ameliorating visuo-sensorimotor disturbances.

541

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664

665 **Figure legends**

666 Figure 1. Behavioral effects of visual information on foot movement amplitude discrimination.

667 (A) An example of the mean psychometric curves for a single participant, where the slope is  
668 significantly steeper (smaller amplitude discrimination threshold) when they saw their foot moving.

669 (B) For the group ( $n = 15$  participants, shown in individual bars), there was a significant decrease in  
670 the discrimination threshold of movement amplitude when the participant watched their foot  
671 moving, as compared to having their eyes closed and only using proprioceptive information ( $* p <$   
672  $0.05$  and the mean discrimination levels are shown as boxes).

673 Figure contributions: Marie Chancel performed the experiment. Marie Chancel and Anne  
674 Kavounoudias analyzed the data

675

676 Figure 2. An example of muscle afferent firing, physiological measures, and the differences between  
677 conditions in a single participant.

678 (A) An example of three consecutive sinusoid movement cycles applied during each of the four  
679 visual/attention conditions. The minimum and maximum firing rates were extracted (gray arrows at  
680 the end of each example) and this mean firing rate change ( $\Delta$ ) was used to quantify the dynamic  
681 response of the muscle afferent, for each condition. In this example, a microneurographic recording  
682 was made from a primary muscle afferent (Ia) arising from extensor digitorum longus (EDL) muscle.

683 (B) For this muscle afferent, a clear difference in the  $\Delta$  can be seen between when the participant  
684 had visual or no visual information (standard deviation is shown per condition), regardless of the  
685 attention condition.

686 Figure contributions: Rochelle Ackerley, Edith Ribot-Ciscar and Jean-Marc Aimonetti performed the  
687 experiments. Rochelle Ackerley, Edith Ribot-Ciscar and Anne Kavounoudias analyzed the data

688

689 Figure 3. The mean effect of visual information and attention on muscle afferent movement  
690 encoding.

691 The group data of Ia muscle afferents ( $n = 16$ ) show a significant difference in the dynamic response  
692 of muscle afferents, as measured by the change in the minimum-to-maximum firing rates ( $\Delta$ ),

693 which was normalized via z-transform (means and SEMs are shown). A main effect was found for  
694 having visual information, where the delta was significantly lower with visual information, but no  
695 significant difference was found in the response between attention conditions, nor the interaction  
696 between vision and attention.

697 Figure contributions: Rochelle Ackerley, Edith Ribot-Ciscar and Jean-Marc Aimonetti performed the  
698 experiments. Rochelle Ackerley, Edith Ribot-Ciscar and Anne Kavounoudias analyzed the data

699

#### 700 **Table legends**

701 Table 1: Type and power of the statistical tests carried out in the psychophysics and  
702 microneurography experiments. Letters in the left column refer to values within the Results section.

703

704 Table 2: The mean values for the electromyography and electrodermal activity, with the standard  
705 error of the mean (SEM), as shown for the microneurography experiment. The electromyography  
706 and electrodermal responses are shown in arbitrary units (area under the curve) for the duration of  
707 the sinusoidal cycles per condition. There was no significant effect of vision, attention, or the  
708 interaction of these, as shown in the ANOVAs, where the partial  $\eta^2$  shows the size effects.

709

710 Table 3: The mean values for the electromyography and electrodermal activity, with the standard  
711 error of the mean (SEM), as shown for the behavioral experiment. The electromyography and  
712 electrodermal responses are shown in arbitrary units (area under the curve) for the total number of  
713 trials per condition. There was no significant effect of vision, as shown in the ANOVAs, where the  
714 partial  $\eta^2$  shows the size effects.

715

716

717

718 **Tables**

719

720 Table 1: Data structure for statistical analyses.

	<b>Data Structure</b>	<b>Type of Test</b>	<b>Power</b>
a	Behavioral amplitude discrimination level (n = 15 participants)	Generalized linear model (GzLM)	0.5
b	EMG and EDA data tests per condition/variable (n = 15 participants) for behavioral experiment	Student's paired t-test	0.5
c	Microneurography data for change in muscle afferent firing over conditions (n = 16 units)	Repeated measures two-way ANOVA	0.6
d	EMG and EDA data tests per variable (n = 16 recordings) for microneurography experiment	Repeated measures two-way ANOVA	0.6

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725

726 Table 2: Mean values and statistics for the physiological measures during microneurography  
 727 experiment.

	<b>Electromyography</b> <b>(mean ± SEM)</b>	<b>Electrodermal activity</b> <b>(mean ± SEM)</b>
No vision, relax	14105 ± 2927	45857 ± 1537
No vision, attention	14073 ± 2925	45828 ± 1502
Vision, relax	14105 ± 2899	45820 ± 1555
Vision, attention	14093 ± 2897	45723 ± 1556
ANOVA main effect Vision	$F_{(1,15)} = 3.45, p = 0.081,$ partial $\eta^2 = 0.20$	$F_{(1,15)} = 0.31, p = 0.568,$ partial $\eta^2 = 0.02$
ANOVA main effect Attention	$F_{(1,15)} = 0.34, p = 0.857,$ partial $\eta^2 = 0.01$	$F_{(1,15)} = 0.18, p = 0.679,$ partial $\eta^2 = 0.01$
ANOVA interaction Vision*Attention	$F_{(1,15)} = 0.17, p = 0.683,$ partial $\eta^2 = 0.01$	$F_{(1,15)} = 0.12, p = 0.739,$ partial $\eta^2 = 0.01$

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730 Table 3: Mean values and statistics for the physiological measures during behavioral experiment.

	<b>Electromyography TA</b> <b>(mean ± SEM)</b>	<b>Electromyography GS</b> <b>(mean ± SEM)</b>	<b>Electrodermal activity</b> <b>(mean ± SEM)</b>
Vision	9330 ± 1146	8478 ± 1766	8217 ± 1595
No vision	9237 ± 1076	8343 ± 1076	7827 ± 1237
paired t-test Vision vs No vision	$t(13) = 0.92, p = 0.385,$ partial $\eta^2 = 0.06$	$t(13) = 1.82, p = 0.092,$ partial $\eta^2 = 0.20$	$t(13) = 0.64, p = 0.531,$ partial $\eta^2 = 0.03$

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