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► To cite this version:

Estelle Nakul, Diane Deroualle, Marion Montava, Jean-Pierre Lavielle, Christophe Lopez. Observing the self and other in motion modulates the excitability of vestibulocollic reflexes. 2022. hal-03820009

HAL Id: hal-03820009

<https://amu.hal.science/hal-03820009>

Preprint submitted on 18 Oct 2022

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1 **Observing the self and other in motion modulates the**
2 **excitability of vestibulocollic reflexes**

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15

16 **Abbreviated title:** Social modulation of the excitability of vestibulocollic reflexes

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18 Number of pages: 26

19 Number of figures: 4, Number of tables: 1

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35

36 **Abstract**

37 Vestibular inputs from the inner ear are at the basis of the vestibulo-spinal and vestibulocollic
38 reflexes involved in balance control. Studies have focused on how attentional load and emotions
39 influence balance, but low-level social cues, such as observing human bodies in motion, have
40 been neglected. Yet, individuals observing another person in a challenging posture or in motion
41 can experience imbalance, indicating that sensorimotor resonance between self and others is
42 involved. The present study examines how the observation of videos depicting human bodies
43 in motion modulates well-established neurophysiological signatures of vestibular information
44 processing. The excitability of vestibulocollic reflexes was assessed by analyzing the waveform
45 of vestibular-evoked myogenic potentials (VEMPs) over the sternocleidomastoid and trapezius
46 muscles of 25 healthy participants (13 females, 12 males). Here we show that observing human
47 bodies undergoing passive whole-body rotations reduced the VEMPs amplitude when
48 compared to observing an object. Importantly, the modulation depended on the person depicted
49 in the video as VEMPs were reduced when observing oneself, compared to someone else being
50 moved. Direction-specific effects and electromyography recordings ruled out non-specific
51 emotional and attentional effects. These results show that the vestibular system is sensitive to
52 observing human bodies in motion, establishing new connections between social neuroscience
53 and vestibular neurophysiology.

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55

56 **Significance Statement**

57 Vestibulocollic reflexes are thought to be consistent and of short latency. Yet, previous results
58 show that observing conspecifics influences balance. We combined approaches from social
59 neuroscience and vestibular electrophysiology to describe how the observation of self and other
60 bodies in motion influences vestibular information processing. The results show that observing
61 human bodies in motion reduces the amplitude of vestibulocollic reflexes involved in the
62 stabilization of the head and balance. These results establish new relations between the sense
63 of balance and social cognition and challenge classical views in vestibular neuroscience.

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69 Introduction

70 Vestibular signals originating from the inner ear are essential for multisensory self-motion
71 perception and accurate balance control¹. These signals trigger stabilizing reflexes in postural
72 and neck muscles when the body is translated or rotated, and damage to the inner ear impairs
73 body orientation and stabilization². The vestibular control of balance and of head stabilization
74 in space is supported by projections from the vestibular nerve to the vestibular nuclei in the
75 brainstem, and then to alpha and gamma motoneurons³. Vestibulo-spinal and vestibulocollic
76 reflexes that maintain balance and stabilize the head in space are consistent and of short
77 latency⁴⁻⁶. In humans, vestibulocollic reflexes are now classically studied by recording
78 vestibular-evoked myogenic potentials (VEMPs) over cervical muscles. Cervical VEMPs
79 consist of inhibitory reflexes evoked by auditory clicks⁷ or by electrical impulses over the
80 vestibular nerve^{7,8} and are characterized by a biphasic p13-n23 wave⁹. Although the pattern of
81 excitatory and inhibitory connections between the different vestibular receptors and neck
82 muscles is well described^{6,10}, there is scarce description of how cognitive, emotional and
83 environmental factors influence vestibulocollic reflexes¹¹.

84 Recent evidence suggests that self-motion perception and vestibular reflexes are not as
85 immune to emotions and cognition, as it is sometimes posited. For example, postural threats on
86 participants standing on an elevated platform, increase the amplitude of cervical VEMPs¹².
87 Moreover, participants involved in a cognitive task while standing or walking show a decreased
88 balance¹³, whereas patients with phobic postural vertigo exhibit a balance behavior that is closer
89 to controls when distracted with a cognitive dual task¹⁴. To date, there has been little research
90 about the effects of the observation of conspecifics on vestibular perception and cognition, as
91 is typical for other sensory systems¹⁵. It has been shown that observing another person in a
92 challenging posture or in motion may evoke an imbalance in the observer¹⁶. Furthermore,
93 observing videos of bodies being passively rotated on a motorized chair modulated performance
94 in a self-motion detection task^{16,17}. Of note, patients with peripheral vestibular disorders report
95 discomfort and poorer balance control when surrounded by crowds of people moving around
96 them^{15,18,19}, but the underpinnings of the influence of other motion observation on vestibular
97 information processing are still unknown.

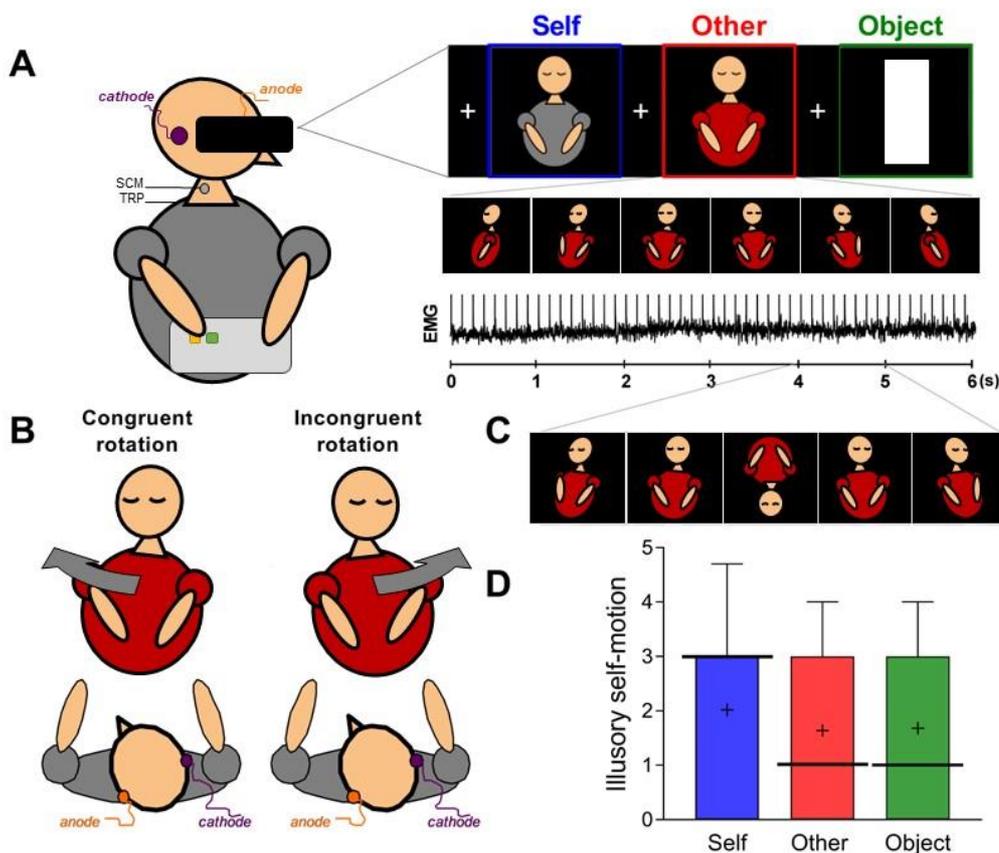
98 In the present study, healthy participants observed videos of human bodies or an object
99 undergoing passive whole-body motion while we assessed the excitability of vestibulocollic
100 reflexes by evoking cervical VEMPs with galvanic vestibular stimulation. We hypothesized
101 that observing the passive motion of one's own body, of another unknown body, or an object,

102 would modulate VEMPs waveforms differently. We also analyzed how empathy traits²⁰ related
103 to VEMPs modulation. This was motivated by behavioral data showing that empathy influenced
104 self-motion perception abilities during the observation of other bodies in motion¹⁷. Personality
105 traits were also shown to modulate brain response to vestibular stimulation²¹.

106 We found that observing the passive motion of human bodies (self and other) or of an
107 object have different effects on VEMPs, supporting our assumption that vestibular information
108 processing can be modulated by self-other representations, a crucial feature of social cognition.

109

110 Results



111

112 **Fig 1. Experimental setup and procedures.** A. Binaural galvanic vestibular stimulation (GVS) and
113 electromyographic (EMG) recordings recorded over the sternocleidomastoid (SCM) and the trapezius
114 (TRP) muscles. Participants actively maintained their head flexed towards the torso and rotated towards
115 the anode to contract the SCM and the TRP under the cathode. Six-second videos showing the passive
116 rotation of the participant (“Self videos”), an unknown person (“Other videos”), or a white object
117 (“Object videos”) were presented in a head-mounted display. GVS was applied during the videos and
118 electric artefacts were visible on the EMG signal. B. “Congruent rotation” showed rotations in the
119 direction matching what participants would have seen of their initial head rotation in a mirror, whereas

120 “Incongruent rotations” showed rotations in the opposite direction (specular congruency). **C.** Example
121 of the vertical inversion of the image (100 ms; 1.5 s, 3 s or 4.5 s after the video onset), present in 25%
122 of the videos. **D.** Box-and-Whisker plots illustrate the intensity (0 = “not at all”; 7 = “absolutely felt
123 something”) of illusory self-motion for each category of Videos. The top and bottom ends of the whisker
124 represent the 90th and 10th percentiles of the distribution, the bold horizontal line represents the median
125 and the black cross represents the mean.

126

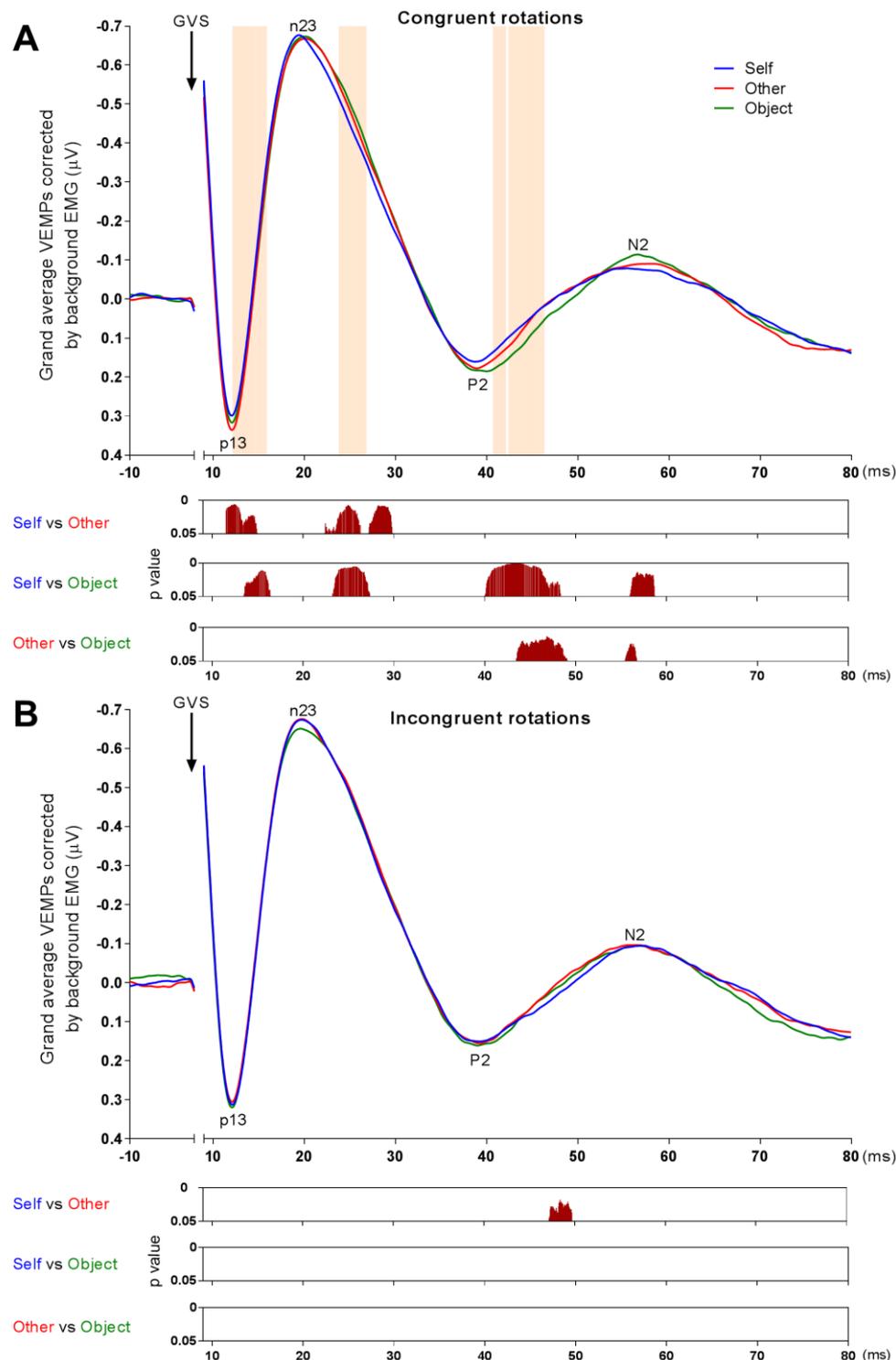
127 **Self-reports and behavioral results**

128 Participants experienced moderate illusory self-motion when observing passive rotations of a
129 body/object (**Figure 1D**). Some participants reported that Self videos evoked “a motion of the
130 head, like in a mirror”, or “the sensation of being rotated”. By contrast, participants did not
131 report self-motion during Other videos (e.g., “I was looking at the other person being rotated,
132 but I did not have the sensation I was rotated”). Friedman’s ANOVA revealed a near-significant
133 main effect of Video on illusory self-motion ($\chi^2(2) = 5.49$, $p = 0.06$). Two-sided Wilcoxon
134 signed-rank tests showed marginally higher illusory self-motion for Self than Other videos (Z
135 = 1.83, $p = 0.068$) and for Self than Object videos ($Z = 1.86$, $p = 0.06$), whereas illusory self-
136 motion was similar for Other and Object videos ($Z = 0$, $p = 1$). There was no significant effect
137 of Direction of rotation on illusory self-motion ($\chi^2(1) = 1.0$, $p = 0.32$).

138 Participants detected the inversion of the images in the videos with a mean accuracy of
139 98%, indicating that they attended to the task. There was a near-significant effect of the Video
140 on accuracy ($\chi^2(2) = 5.75$, $p = 0.06$) and no effect of the Direction of rotation ($\chi^2(1) = 0.53$, $p =$
141 0.47). When exploring the statistical trend of the effect of Video, we found that accuracy did
142 not differ between categories of videos (Self vs. Other: $Z = 0.24$, $p = 0.81$; Self vs. Object: $Z =$
143 1.7, $p = 0.09$; Other vs. Object: $Z = 1.6$, $p = 0.11$).

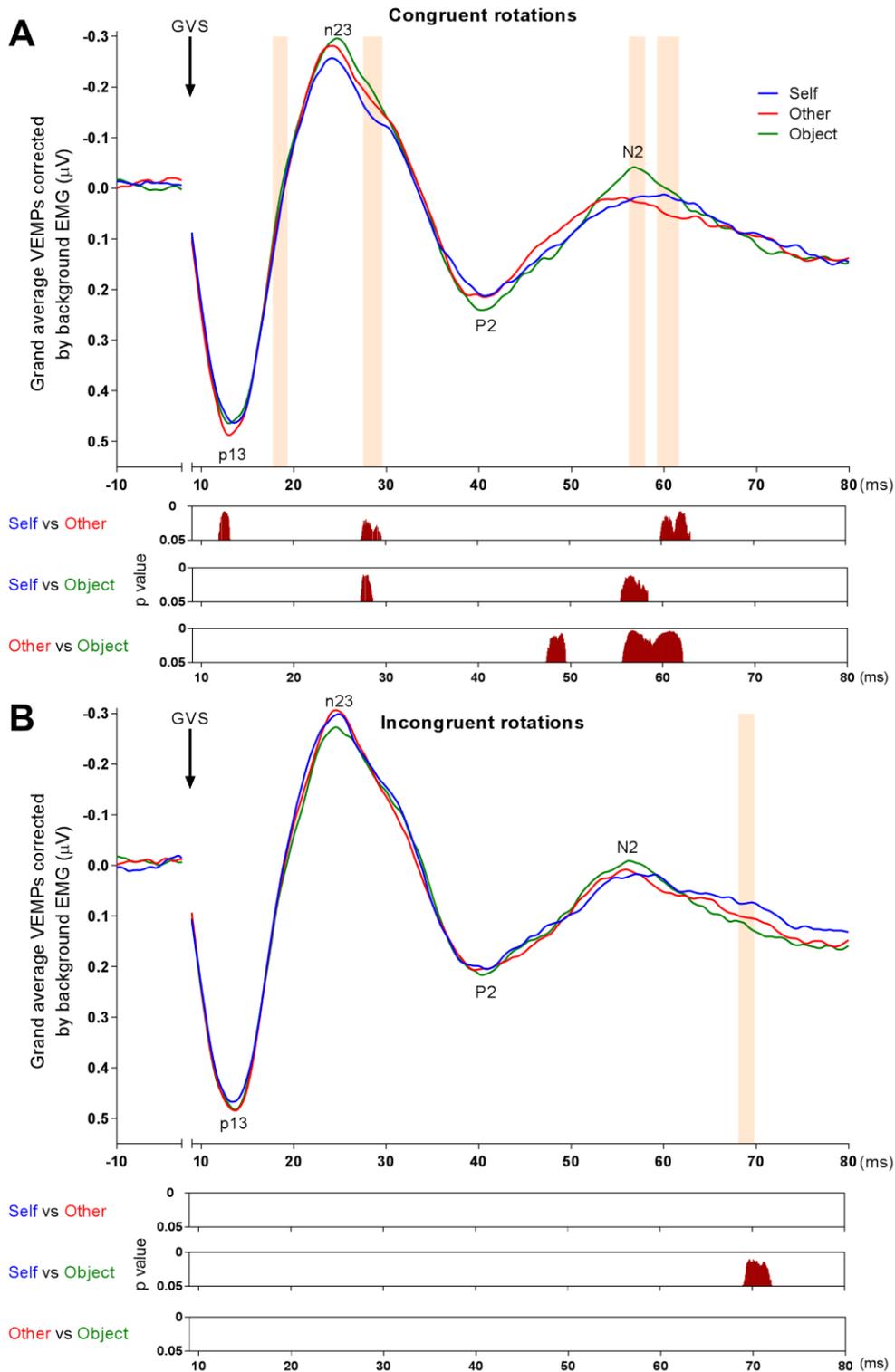
144

145 **VEMPs waveform analyses**



146

147 **Fig 2. VEMPs recorded over the SCM muscle.** Grand-average VEMPs ($n = 24$) are showed separately
148 for Congruent rotations (A) and Incongruent rotations (B) for each category of Videos. Colored areas in
149 the upper panel show periods with a significant main effect of the Videos (Friedman's ANOVA). The
150 three lower panels present results from post-hoc analyses (Wilcoxon signed-rank test). Analyses were
151 corrected for temporal autocorrelation by using the constraints of 20 consecutive data points reaching
152 the 0.05 level of significance.



153

154 **Fig 3. VEMPs recorded over the TRP muscle.** Grand-average VEMPs ($n = 20$) are showed separately
155 for Congruent rotations (A) and Incongruent rotations (B) for each category of Videos. Same
156 conventions as for Figure 2.

157

158 **Figures 2 and 3** illustrate the effect of Video (Friedman's ANOVAs) on the corrected VEMP
159 amplitude over the SCM and TRP muscles, separately for Congruent and Incongruent rotations.
160 Different patterns of modulation by the Video were found for Congruent and Incongruent
161 rotations. For Congruent rotations, we found a significant main effect of the Video for both
162 SCM and TRP muscles in time windows spanning the p13 wave (SCM muscle: 62 consecutive
163 significant data points [csdp.] at $p < 0.05$, from 12.1 to 15.0 ms; TRP muscle: 26 csdp., 17.8–
164 19.3 ms), the decreasing portion after the peak of component n23 (SCM: 50 csdp., 23.8–26.8
165 ms; TRP: 34 csdp., 27.5–29.5 ms), and the decreasing portion after the peak of P2 (SCM: 24
166 csdp., 40.7–42.1 ms, followed by 65 csdp., 42.4–46.3 ms), as shown by the colored areas
167 superimposed on VEMPs waveforms in **Figures 2A and 3A**. There was also a main effect of
168 Video spanning the peak of component N2 on the TRP muscle (29 csdp., 56.2–57.9 ms,
169 followed by 39 csdp., 59.3–61.6 ms). By contrast, Friedman's ANOVAs for the Incongruent
170 rotations yielded no effect of the Video on the VEMPs amplitude during the p13-n23 biphasic
171 wave, and the P2–N2 (**Figures 2B and 3B**). There were only 28 csdp. from 68.1 to 69.8 ms,
172 thus after the later components, for the TRP muscle. Accordingly, we report below only results
173 from post-hoc analyses comparing the waveform of the VEMPs between each category of
174 Videos in the Congruent rotation condition.

175 We explored the main effect of Videos using Wilcoxon signed-rank tests (**Figures 2 and**
176 **3**). Overall, the analysis shows an attenuation of the VEMP during the observation of Self
177 videos when compared to the observation of Other videos, revealing a modulation of the
178 excitability of vestibulocollic reflexes by the person depicted in the video. This attenuation of
179 the VEMPs was found for segments of the waveform spanning the p13-n23, as well as for the
180 P2 and N2. When compared to Other videos, the amplitude of the peak of the p13 for Self
181 videos was significantly reduced for both the SCM muscle (57 csdp., 11.5–15.0 ms) and TRP
182 muscle (21 csdp., 11.9–13.1 ms). Similarly, the amplitude of the portion after the peak of the
183 n23 was significantly reduced for Self videos when compared to Other videos for both SCM
184 muscle (66 csdp., 22.4–26.4 ms, and 44 csdp., 27.2–29.8 ms) and TRP muscle (37 csdp., 27.3–
185 29.5 ms). The amplitude of the N2 on the TRP muscle was also reduced during Self videos
186 when compared to Other videos (54 csdp., 59.9–63.1 ms).

187 When compared to Object videos, observation of Self videos showed a significantly
188 reduced p13 amplitude for the SCM muscle (49 csdp., 13.5–16.4 ms), as well as significantly
189 reduced portion after the peak of the n23 for both muscles (SCM: 68 csdp., 23.2–27.3 ms; TRP:
190 22 csdp., 27.3–28.6 ms). The P2 amplitude was also significantly reduced for Self videos when

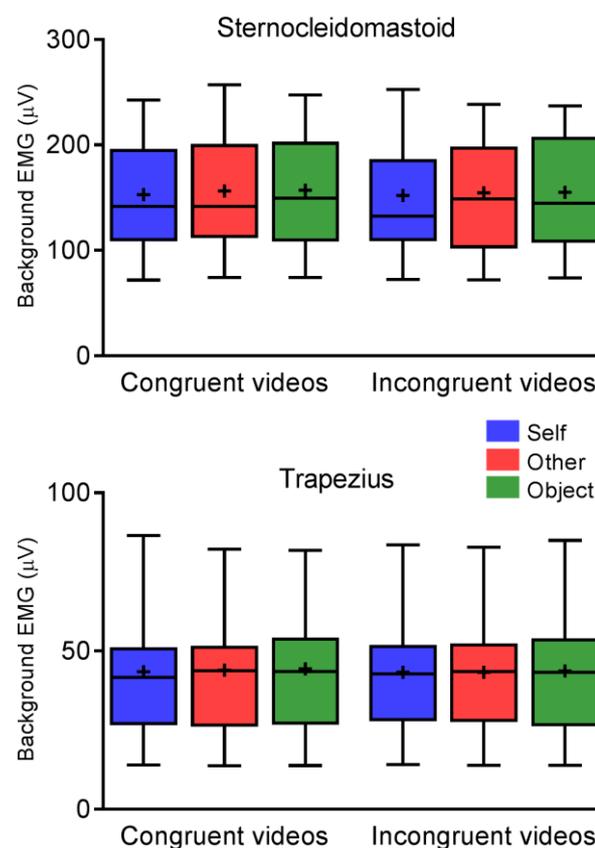
191 compared to Object videos (SCM: 138 csdp., 40.0–48.3 ms) and this was also the case of the
192 N2 amplitude (SCM: 46 csdp., 56.0–58.7 ms; TRP: 49 csdp., 55.4–58.3 ms).

193 The amplitude of the p13-n23 biphasic wave did not differ between the Other videos
194 and the Object videos, suggesting that the attenuation of the early component reported above
195 involves specifically the observation of self-motion. We note that the amplitude of the later
196 components P2 and N2 recorded over both muscles was reduced for the Other videos when
197 compared to the Object videos (P2 component: SCM, 93 csdp., 43.4–49.1 ms; TRP, 36 csdp.,
198 47.4–49.5 ms and N2 component: SCM, 22 csdp., 55.4–56.7 ms; TRP, 109 csdp., 55.6–62.2
199 ms).

200

201 Control for background EMG activity

202



203

204 **Fig 4. Background EMG activity.** Box-and-Whisker plots illustrate the background EMG activity
205 calculated over 6-s periods of video observation, for both SCM (upper panel) and TRP (bottom panel)
206 muscles. The top and bottom ends of the whisker represent the 90th and 10th percentiles of the
207 distribution, the bold horizontal line inside the box represents the median, the black cross represents the
208 mean.

209

210 There was no main effect of the Videos on the background EMG (**Figure 4**) on the SCM muscle
 211 (Friedman’s ANOVA, Congruent rotations: $\chi^2(2) = 5.58$, $p = 0.61$; Incongruent rotations: $\chi^2(2)$
 212 $= 1.0$, $p = 0.61$) nor on the TRP muscle (Congruent rotations: $\chi^2(2) = 3.44$, $p = 0.18$; Incongruent
 213 rotations: $\chi^2(2) = 2.24$, $p = 0.33$).

214

215 **Correlations between VEMP amplitude and empathy scores**

216

		Empathic concern		Perspective taking	
		SCM	TRP	SCM	TRP
Congruent rotations	Self videos	$\tau = 0.40$ $p = 0.006^*$	$\tau = 0.27$ $p = 0.10$	$\tau = -0.15$ $p = 0.29$	$\tau = -0.02$ $p = 0.89$
	Other videos	$\tau = 0.43$ $p = 0.003^*$	$\tau = 0.27$ $p = 0.10$	$\tau = -0.13$ $p = 0.37$	$\tau = -0.01$ $p = 0.95$
	Object videos	$\tau = 0.43$ $p = 0.003^*$	$\tau = 0.20$ $p = 0.22$	$\tau = -0.09$ $p = 0.56$	$\tau = 0.04$ $p = 0.79$
	Self videos	$\tau = 0.42$ $p = 0.004^*$	$\tau = 0.30$ $p = 0.06$	$\tau = -0.15$ $p = 0.29$	$\tau = -0.07$ $p = 0.64$
	Other videos	$\tau = 0.43$ $p = 0.003^*$	$\tau = 0.25$ $p = 0.12$	$\tau = -0.17$ $p = 0.25$	$\tau = -0.05$ $p = 0.74$
	Object videos	$\tau = 0.44$ $p = 0.002^*$	$\tau = 0.29$ $p = 0.08$	$\tau = -0.14$ $p = 0.34$	$\tau = -0.03$ $p = 0.84$

217

218 **Table 1.** Correlation between individual peak-to-peak p13-n23 amplitude and scores to the *empathic*
 219 *concern* and *perspective taking* subscales of the IRI (Kendall’s tau test). Significant results at $p < 0.05$
 220 are highlighted with an asterisk.

221

222 The individual peak-to-peak p13-n23 amplitude on the SCM muscle correlated positively with
223 the *empathic concern* scale for all Videos and both Directions of rotation (Kendall's tau test, τ
224 ≥ 0.40 , all $p \leq 0.006$) (**Table 1**). Thus, participants with higher empathic concern were those
225 who tend to have larger vestibulocollic responses, irrespective of the video presented.

226

227 **Discussion**

228 Our results provide original neurophysiological evidence that the excitability of vestibulocollic
229 reflexes is sensitive to observing human bodies in motion, establishing connections between
230 the so far distinct fields of social neuroscience and vestibular neurophysiology²². Although
231 previous studies reported that attention²³, motor imagery²⁴ and emotions^{12,25,26} can influence
232 the amplitude of vestibulo-spinal, vestibulocollic and oculomotor reflexes, the tasks and stimuli
233 used in previous studies were devoid of self- and other-related visual information.

234

235 Observing the passive rotation of the self reduced the p13-n23, compared to observing the same
236 rotation of another body or an object. However, observing the rotation of another body did not
237 modulate the p13-n23 significantly, compared to an object. As for the somatosensory
238 system^{27,28}, it seems that there is something special about viewing one's own body that
239 modulates vestibular information processing.

240 Self information processing and self awareness has been associated with the insula^{29,30},
241 with the precuneus, posterior cingulate cortex, temporoparietal junction, and the medial and
242 anterior prefrontal cortex³¹. These areas overlap with several core regions of the vestibular
243 cortex, such as the operculo-insular complex, temporoparietal junction and cingulate cortex^{32,33}.
244 Observing videos of the self may activate areas involved in both self-representations and
245 vestibular information processing. We note that participants may also have recalled previous
246 experience of vestibular sensations during the rotation of their own body. Such recall of
247 vestibular sensations has been associated with bilateral activations of the inferior frontal gyri,
248 anterior operculum, middle cingulate cortex, premotor cortex and anterior insula³⁴. By
249 activating cortical areas involved in self-representations, vestibular information processing and
250 recall of self-motion, observing Self videos may have modulated VEMPs waveform through
251 direct or indirect projections from the cortex to the vestibular nuclei^{35,36}. Indeed, electrical
252 stimulation of the multisensory vestibular cortex have been shown to activate or inhibit
253 responses in the cat vestibular nuclei and these stimulations influenced vestibulo-spinal,
254 vestibulocollic and oculomotor reflexes^{37,38}.

255 Furthermore, electrophysiological recordings in monkeys showed that active head
256 rotation strongly decreases the firing rate of vestibular nuclei neurons, compared to passive self-
257 motion^{39,40}. We propose that observing Self videos (while maintaining the head rotated towards
258 the anode) triggers partly similar neurophysiological mechanisms to active self-motion and
259 decreases the excitability of vestibulocollic reflexes. Indeed, we found a trend for stronger
260 illusory self-motion for the observation of Self videos, which could be misinterpreted as active
261 self-rotation.

262 Finally, we found that observing the passive rotation of the self also reduced the P2 and
263 N2 responses, compared to observing another body (SCM) and an object (SCM and TRP).
264 There is a controversy as to whether components following the n23 are of vestibular origin.
265 Most authors proposed that later components are not of vestibular origin, as they survive after
266 vestibular neurectomy⁴¹, whereas others reported opposite findings for the TRP muscles⁴². As
267 most clinical and theoretical studies have disregarded those later components, it is unknown
268 how P2 and N2 can be modulated by cognitive and emotional factors. The P2 and N2 are likely
269 of multisensory origin, including vestibular, cochlear and somatosensory origins⁴². The
270 modulation of the P2 and N2 components by low level information about self and other bodies
271 is a new finding. It may reflect more complex multisensory mechanisms related to self-other
272 resonances, i.e. the modulation of sensorimotor processing when observing bodies.

273
274 Just as observing other bodies in motion can have a detrimental effect on the observer's
275 balance^{16,43} and self-motion perception¹⁷, we found that observing another body undergoing
276 passive motion reduced VEMPs waveform when compared to observing an object in motion.
277 Surprisingly, the VEMP attenuation was found for components P2 and N2, but not for the early
278 p13-n23 component.

279 The fact that observing both Self and Other videos decreased the P2-N2 amplitude – but
280 to a lower extent for the conspecifics – indicates a modulation of the late VEMP components
281 by self-other representations. This suggests that sensorimotor resonance between self and others
282 also applies to the vestibular system. Sensorimotor resonance refers to the fact that observing
283 another person receiving a sensory stimulation changes our processing of the same stimulation.
284 It has been described extensively for other senses than the vestibular system and relies on
285 common structures processing self and other sensory information⁴⁴⁻⁴⁷. Observing bodies
286 undergoing passive whole-body motion may activate self and other representations and self-
287 other resonance, modulating activity in the vestibular nuclei and decreasing the excitability of
288 vestibulocollic reflexes through corticofugal projections.

289

290 Interestingly, the VEMPs waveform was only modulated by videos presenting Congruent
291 rotations. First, this direction-specific effect rules out non-specific emotional and attentional
292 modulation of the excitability of vestibulocollic reflexes. Second, it suggests that a specular
293 congruency between the actual head position on the trunk and the direction of the observed
294 rotation is more likely to influence the excitability of vestibulocollic reflexes. This is consistent
295 with behavioral data suggesting that sensorimotor resonance becomes more important when the
296 observed body posture or movement is compatible with the observer's motor stabilization
297 strategy⁴⁸ and that third-person perspective taking is facilitated when the observer and the seen
298 conspecific share a common body posture⁴⁹. As vestibular nuclei neurons are sensitive to the
299 position of the head on the trunk⁵⁰, our data suggest that the specular congruency between visual
300 and neck somatosensory signals facilitates the inhibition of vestibular nuclei neurons projecting
301 to the spinal cord.

302

303 We found that the p13-n23 amplitude on the SCM, the muscles most strongly involved in the
304 head rotation towards the cathode, was positively correlated with *empathic concern*, for all
305 categories of videos. This suggests a general effect of empathy on the excitability of
306 vestibulocollic reflexes, irrespective of the person observed. A recent functional magnetic
307 resonance imaging study has linked the strength of visuo-vestibular responses to personality
308 traits, with stronger responses in the vestibular nuclei and parieto-insular cortex of participants
309 with higher neuroticism (i.e. more nervous participants) and larger responses in the amygdala
310 of more introverted individuals^{21,51}. Our data are in line with such a general effect of personality
311 traits on vestibular information processing, extending previously defined interplay between
312 emotional and social neural networks with the vestibular neural network⁵²⁻⁵⁴. A study¹⁷ revealed
313 that empathy scores positively correlated with the congruent vs. incongruent latency difference
314 to detect passive self-motion when simultaneously observing Others or Objects videos, but not
315 Self videos. This suggests that personality traits impact multisensory self-motion perception
316 (based on visual and vestibular signals) and vestibulocollic reflexes with different effects
317 depending on the person depicted in the video. Thus, self-motion perception may involve more
318 fine-grained multisensory – and social – regulation mechanisms³⁹ than the excitability of
319 vestibulocollic reflexes.

320

321 Our results show that vestibular information processing is sensitive to observing human bodies
322 in motion, establishing new connections between research in social and vestibular neuroscience.

323 From an evolutionary perspective, the present findings suggest that the human balance system
324 evolved to react differently to moving objects and conspecifics. Similar studies in non-human
325 primates could put our results in a comparative perspective and provide detailed information
326 about the neurophysiological mechanisms involved. We note that previous studies of sensory
327 processing in a social context have manipulated higher-level features of self-other resonance,
328 such as political ideas, ethnicity, or pleasantness of the others^{55,56}. While this was beyond the
329 scope of the present investigation, our results may lead the way to the study of self-motion
330 perception and vestibular information processing as a function of such social features. Finally,
331 studies of the interplay between self-other representations, higher-level social features and
332 vestibular information processing may have important applications for understanding balance
333 disorders and improving their rehabilitation.

334

335 **Methods**

336

337 **Participants**

338 Twenty-five healthy volunteers participated (13 females; mean age \pm SD: 23 \pm 3 years), of
339 whom 24 participants were right-handed (mean laterality quotient \pm SD: 83 \pm 16 %; Edinburgh
340 Handedness inventory⁵⁷) and one was left-handed (-40 %). They had normal or corrected-to-
341 normal vision and declared no history of vestibular, neurological, or psychiatric disease. All
342 participants provided written informed consent prior to participation. Experimental procedures
343 were approved by the local Ethics Committee (Comité de Protection des Personnes Sud-
344 Méditerranée II, 2011-A01221-40) and followed the ethical recommendations laid down in the
345 Declaration of Helsinki.

346

347 **Visual stimuli**

348 Visual stimuli consisted of videos showing the passive rotation of the participant (“Self
349 videos”), of an unknown, age- and gender-matched person (“Other videos”), or of a white
350 rectangular cuboid (“Object videos”), installed on the same rotating chair (Robulab 80,
351 Robosoft SA, Bidart, France) (**Figure 1A**). Self-videos were recorded before electrophysiology
352 recordings. Participants were seated on a rotating chair with their hands on their laps, eyes
353 closed and a neutral face. A video camera (Sony HDR-XR160, Sony, Surrey, United Kingdom)
354 placed 1.65 m in front of the participants recorded the rotation of their entire body on the chair.
355 A black fabric behind the chair excluded all visual references from the background. Participants

356 were rotated passively in the clockwise and counterclockwise direction around their
357 longitudinal axis during 6 s with a sinusoidal velocity profile and a peak velocity of 18 °/s. The
358 Other videos were recorded using the same procedures and with the same motion profile. An
359 actor and an actress, who did not take part in the electrophysiology experiment, helped to create
360 the videos depicting an unknown male and female body. The unknown body shown in the video
361 was age-matched because our participants were all within the same age range. Object-videos
362 were created following the same procedures, i.e. by rotating the white rectangular cuboid placed
363 on the rotating chair. The rectangular cuboid was made of cardboard and had about the same
364 height (84×31×31 cm) as the participants when seated on the chair. All videos were edited to
365 last 6 s and were cropped to display the participant/actor from their head to their lower legs
366 (when facing the camera) using Adobe Premiere Pro CC 2015. Participants were first seen from
367 the side, and at the middle of the rotation (3 s), they were facing the camera (**Figure 1A**). During
368 the experiment, videos were showed in a head-mounted display with a 30° horizontal field-of-
369 view (LDI-100BE, Sony). This allowed us to maintain visual stimuli fixed in a head-centered
370 coordinate system.

371

372 **Galvanic vestibular stimulation**

373 Transmastoid galvanic vestibular stimulation (GVS) was used to evoke VEMPs recorded over
374 two neck muscles^{8,58}. A pair of carbon and rubber electrodes (4 × 2.5 cm, Plate electrode EF
375 10, Physiomed Electromedizin AG, Schnaittach, Germany) inserted in wet sponges was
376 maintained on the skin covering the opposite mastoid processes using a cohesive contention
377 strip around the head. Thirteen participants (7 females) had left cathodal/right anodal GVS
378 configuration, whereas 12 participants (6 females) had right cathodal/left anodal GVS
379 configuration. GVS consisted in series of square-wave pulses of 2 ms delivered at 8 Hz with an
380 intensity of 3.2 to 5.0 mA (depending of the participant's skin sensitivity; mean intensity ± SD:
381 4.7 ± 0.7 mA) by a Grass S88 stimulator (Grass Instrument Co, Quincy, Massachusetts, USA)
382 coupled to a constant current and isolating unit (Grass PSIU-6B). Short-duration GVS does not
383 evoke self-motion perception. GVS was preferred over acoustic air-conducted stimulation of
384 otolithic receptors as it provides more physiologically valid inputs related to bilateral
385 stimulation of the vestibular receptors. GVS increases the firing rate in the vestibular afferents
386 under the cathode, while decreasing the firing rate in the afferents under the anode⁵⁹.

387

388

389 **Electromyography recordings**

390 VEMPs were recorded over the sternocleidomastoid (SCM) and trapezius (TRP) muscles
391 following previously described procedures^{8,12}. Active electrodes (FLAT Active electrode,
392 Biosemi Inc., Amsterdam, Netherlands) were placed at the junction of the upper and middle
393 thirds of the SCM ipsilateral to the cathode and at the intersection between the upper and middle
394 muscle fibers on the TRP ipsilateral to the cathode. In our system, the Common Mode Sense
395 (CMS) and Driven Right Leg (DRL) electrodes replace the single standard ground electrode
396 and form a feedback loop to increase the signal-to-noise ratio. CMS-DRL electrodes were
397 placed 2 cm apart over the C7 vertebra. A reference electrode was placed on the sternum.
398 Preamplified electromyographic signals (EMG) were sampled at 16 kHz with a bandwidth of
399 0.16–3200 Hz and analyzed offline using custom-made scripts in Matlab R2015b (The
400 MathWorks Inc., Natick, USA).

401 As cervical VEMPs are inhibitory responses of the ipsilateral neck muscles, participants
402 were required to maintain tonic activation of the SCM and TRP ipsilateral to the cathode. They
403 sat on a chair whose backrest was tilted $\sim 45^\circ$ backward. Participants actively maintained their
404 head flexed towards the torso and rotated it $\sim 80^\circ$ towards the anode (the amplitude of head
405 rotation was adapted to each participant to be as comfortable as possible). This contracted the
406 SCM, and to a lower extent the TRP, under the cathode (**Figure 1A**). Participants were trained
407 to maintain a stable muscular contraction before the experiment. In addition, the experimenter
408 controlled the participant's head position and level of muscle contraction on the visual display
409 of the recording software (Actiview 7.03, Biosemi Inc., Amsterdam, Holland) throughout the
410 experiment.

411

412 **Convention for the direction of rotation of the body/object in the videos**

413 The direction of rotation of the body/object in the video was not referred to as clockwise and
414 counterclockwise rotation, as there was no specific hypothesis about differences between those
415 directions. By contrast, vestibular perception depends on the congruency between the direction
416 of rotation of the body/object in the video and the actual direction of rotation of the observer's
417 body¹⁷. As VEMPs were recorded with the participant's head maintained rotated towards the
418 anode, we defined the direction of rotation of the body/object in the video according to the
419 congruency of the observed rotation with the initial rotation of the participants' head (**Figure**
420 **1B**). According to our convention, videos with "Congruent rotations" showed rotations in the
421 direction matching what participants would have seen of their initial head rotation in a mirror,

422 whereas videos with “Incongruent rotations” showed rotations in the opposite direction. Thus,
423 Congruent rotations were rotations towards the anode, whereas Incongruent rotations were
424 rotations towards the cathode.

425

426 **Experimental procedures**

427 Each category of video (Self, Other, and Object) was presented 24 times for Congruent
428 rotations, and 24 times for Incongruent rotations, resulting in a total of 144 visual stimuli per
429 participant. Visual stimuli were presented in a randomized order in 18 blocks of 8 videos. Each
430 block of visual stimuli started with the presentation of a white fixation cross on a black
431 background for 500 ms, followed by a video. After each video a fixation cross was presented
432 for 500 ms plus the response time to the detection task described below (with a maximum of 1
433 s). This resulted in a maximal duration of 56.5 s per block. Participants were asked to fixate on
434 the cross presented between videos and to fixate on the body/object at the center of the screen
435 during the videos. GVS pulses began with the video onset and were applied at 8 Hz during 6 s.
436 Thus, 48 GVS pulses were presented during a video, resulting in a total of 1152 vestibular
437 stimulation per category of video and direction of rotation. This high number of stimulation,
438 compared to previous electrophysiological studies, ensured a good signal-to-noise ratio. Video
439 presentation and GVS application were controlled by Superlab 4.5 (Cedrus Corporation, San
440 Pedro, USA). Participants maintained a stable muscle contraction during each block of visual
441 stimuli and rested as long as they wanted to relax their neck between consecutive blocks of
442 visual stimuli.

443 To maintain their alertness during the recordings, participants were involved in a two-
444 alternative forced choice task. In 25% of the videos, images were inverted vertically for 100
445 ms, starting at 1.5 s, 3 s or 4.5 s after the video onset (**Figure 1C**). Participants were asked to
446 observe the body/object being rotated and to indicate as quickly and accurately as possible
447 whether the video was, or was not, temporarily presented upside-down. They were instructed
448 to answer during the fixation cross following the video, and we confirmed that no answer was
449 given during the videos. Participants responded on two buttons of a response pad (RB-830,
450 Cedrus Corporation, San Pedro, USA) with their right middle and index fingers (13 subjects
451 responded 'yes' with their middle finger, 12 responded 'yes' with their index finger). Before the
452 recordings, participants trained to the task on 10 trials without GVS.

453

454

455 **Illusory self-motion questionnaire**

456 At the end of the experiment, participants filled out a questionnaire about illusory self-motion.
457 For both directions of rotation (Congruent, Incongruent), participants answered the question
458 “Did you feel a sensation of motion of your own body when observing the videos of yourself/the
459 other person/the object?” Answers were given on a 7-point Likert scale ranging from “not at
460 all” to “absolutely felt something”. Participants could indicate whether the illusory motion was
461 in the same direction as the observed motion and add comments. Participants answered this
462 questionnaire once about their average experience of the whole electrophysiology experiment.

463

464 **Interpersonal reactivity index**

465 Participants completed the Interpersonal Reactivity Index^{20,60}. Our analyses focused on the
466 relation between VEMP amplitude and two subscales of the IRI measuring self-reported
467 empathic concern and perspective taking. Both scales have been showed to correlate with
468 implicit perspective taking⁶¹. The *empathic concern scale* includes seven questions assessing
469 “other-oriented feelings of sympathy and concern for unfortunate others”, while the *perspective*
470 *taking scale* includes seven questions assessing “the tendency to spontaneously adopt the
471 psychological point of view of others”²⁰. Ratings were completed on a 5-point scale ranging
472 from “describes me very well” to “does not represent me very well”.

473

474 **Data recording and analysis**

475 EMG signals were referenced to the electrode placed on the sternum and band-pass filtered
476 (0.1–1000 Hz). All GVS pulses applied during the same category of videos (Self, Other, Object)
477 and with the same direction of rotation (Congruent, Incongruent) were pooled together to
478 calculate an average VEMP for each participant. VEMPs were calculated on epochs starting 25
479 ms before GVS pulses until 100 ms post-stimulus and were baseline-corrected by the average
480 unrectified EMG during the 25 ms pre-stimulus. Epochs whose baseline (unrectified EMG)
481 exceeded the mean \pm 3 SD of the baseline were excluded, and the same was done for the
482 rectified signal in the 100 ms post-stimulus. After data pre-processing, VEMPs on the SCM
483 muscles were calculated on (mean \pm SD): 1047 \pm 101 GVS pulses for Self videos, 1049 \pm 92
484 pulses for Other videos, and 1052 \pm 92 pulses for Object videos (no effect of the category of
485 videos, Friedman’s ANOVA: $\chi^2(2) = 0.67$, $p = 0.72$). VEMPs on the TRP muscles were
486 calculated on 868 \pm 65 GVS pulses for Self videos, 865 \pm 71 pulses for Other videos, and 866
487 \pm 66 pulses for Object videos (no effect of the category of videos, $\chi^2(2) = 0.67$, $p = 0.72$).

488 It is known that the level of background muscle activation is linearly correlated with
489 VEMP amplitude^{8,62}. Thus, we normalized each epoch by the average rectified EMG during
490 the 25 ms pre-stimulus to account for the level of background EMG^{12,63,64}. We compared SCM
491 and TRP contraction for each category of videos and both rotations by calculating the average
492 background EMG over the 25 ms pre-stimulus.

493 GVS evokes VEMPs with shorter latency⁸ than acoustic stimulation of otolithic
494 receptors, as GVS bypasses the mechano-electrical transduction. Yet, we named “p13-n23” the
495 first biphasic response on the SCM and TRP muscles in accordance with responses to acoustic
496 stimulation⁸. In our study, the p13-n23 component was identified as the first salient positive-
497 negative peak complex within a time window of 8 to 25 ms after GVS onset⁶⁵. In our sample
498 of participants, VEMPs were detectable over the SCM of 24 participants and over the TRP of
499 20 participants. Only their data were considered for subsequent analyses.

500 For each muscle, mean responses from these participants were averaged to obtain grand-
501 average VEMPs for each category of videos and each direction of rotation. As most of the
502 dependent variables were not normally distributed, we used non-parametric Friedman’s
503 ANOVA and Wilcoxon signed-rank tests to conduct waveform analyses of grand-average
504 VEMPs, as done for event-related potentials in electroencephalographic investigations of
505 sensory and cognitive processing⁶⁶⁻⁶⁸. This approach allows a point-by-point analysis of the
506 exact time course of the vestibulospinal reflex, without *a priori* hypotheses about the timing of
507 the differences (only two points, the peaks of the p13 and n23, are classically analyzed). We
508 corrected for temporal autocorrelation by using the constraints of 20 consecutive data points
509 reaching the 0.05 level of significance^{66,69}. Waveform analyses were conducted within 9 to 80
510 ms after GVS onset to span on waves of interest, that is on the p13 and n23 components, as
511 well as later components (P2 and N2).

512 Finally, to analyze relations between VEMPs and empathy, we measured the peak-to-
513 peak amplitude of the individual p13-n23 response^{8,12} and calculated the correlation coefficient
514 of this amplitude with empathic concern and perspective taking scores.

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684

685 **Acknowledgements:** The research leading to these results has received funding from
686 the People Programme (Marie Curie Actions) of the European Union’s Seventh Framework
687 Programme (FP7/2007–2013) under REA Grant agreement number 333607 (‘BODILYSELF,
688 vestibular and multisensory investigations of bodily self-consciousness’). The authors thank
689 Ali Gharbi and Guy Escoffier for technical assistance, and Dr. Manuel Vidal for his help with
690 the rotating chair.

691

692 **Author contributions:**

693 All authors participated to the experimental design. E.N. and D.D. recorded the data, E.N.
694 analyzed the data. E.N., D.D. and C.L. contributed to statistical analysis. E.N. and C.L. wrote
695 the main manuscript text. E.N. prepared Figs. 1–4 and Table 1. All authors reviewed the
696 manuscript. Funding was provided by C.L.

697

698 **Additional information:** The authors declare no competing interests.