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Motor adaptation distorts visual space

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Abstract

It has been suggested that the human visual system exploits an adaptable metric to implement a precise but plastic spatial representation. Indeed, adapting to a dense dot-texture reduces the apparent separation of subsequently presented dots pairs. Whether this metric is purely visual or shared between senses is still unknown. Here we present a new cross-modal after-effect revealing that the metric with which the visual system computes the relative spatial position of objects is shared with the motor system. A few seconds of mid-air self-produced tapping movements (adaptation) yielded a robust compression of the apparent separation of dot pairs subsequently displayed around the tapping region. This visuo-motor spatial metric could reflect an efficient functional architecture to program and execute actions aimed at efficient interaction with the objects in the environment.

Introduction

Encoding the position of visual objects in the external world is an essential requirement for navigating and interacting with the environment. A fundamental organizing principle of the visual system is retinotopy: signals from different parts of the visual field activate different portions of the retina and this spatially organized activity is preserved along the visual processing hierarchy. This organization

28 of the spatial maps allows the visual system to precisely reconstruct an internal representation of the
29 spatial layout of the external environment, resulting in an extremely accurate ability to perceive
30 objects' spatial positions. Despite such a well-organized representation, the construction of spatial
31 maps poses several challenges to the visual system in terms of stability, given the continuously
32 changing visual inputs yielded by eye and head movements. Moreover, in spite of very accurate
33 performances in spatial judgments tasks, the neural representation of space seems to be not
34 completely hard-wired as it is susceptible to strong distortions induced by contextual information.
35 One of the most common techniques for investigating how sensory processes are prone to contextual
36 information is sensory adaptation, a form of short-term plasticity induced by a sustained exposure to
37 a particular stimulus, such as a steadily drifting pattern (Clifford et al., 2007; Mollon, 1974;
38 Thompson & Burr, 2009; Webster, 2011). Adaptation is a very generalized property of perceptual
39 systems applying to most of visual and non-visual features; thus, adaptation paradigms have proven
40 to be fundamental psychophysical tools for studying several perceptual properties, including spatial
41 coding. For example, the perceived position of a visual object can be markedly distorted as a
42 consequence of motion adaptation, an effect known as positional motion after-effect (PMAE)
43 (McKeefry, Lavers, & McGraw, 2006; Nishida & Johnston, 1999; Snowden, 1998; Turi & Burr,
44 2012; Whitney & Cavanagh, 2003).

45 Recently, Hisakata and coll. (2016) reported a new visual adaptation effect, able to distort space
46 representation. In their work, the authors demonstrated that, after a few seconds of exposure
47 (adaptation) to a dense dot-array, the perceived distance between two successively presented dots was
48 robustly compressed. This result is of particular interest as it elegantly reveals that the human visual
49 system exploits an adaptable metric to implement the internal representation of space. However,
50 despite being valuable, Hisakata's work was confined within the visual system whilst, in everyday
51 life, we continuously and actively interact with a multisensory environment, which raises the question
52 whether this flexible visual spatial map might be linked to the motor system. To answer this question,
53 we took advantage of a new technique (named motor adaptation) that has been previously proved to

54 be able to distort two different visual dimensions, perceived numerosity and duration (Anobile,
55 Arrighi, Togoli, & Burr, 2016; Anobile, Domenici, Togoli, Burr, & Arrighi, 2019). The technique
56 consisted of a short motor adaptation phase in which subjects were required to produce a series of
57 mid-air tapping movements performed around a specific location with no concurrent visual, haptic or
58 auditory feedbacks. Results indicate that, as a consequence of motor adaptation, visual arrays or
59 sequences of flashes were perceived as containing fewer elements/events than they actually did.
60 Similarly, motor adaptation was found to distort the perceived duration of a moving grating, thus
61 expanding the interaction between the perceptual and the motor system in the processing of perceived
62 time. Interestingly, all aforesaid motor adaptation effects were spatially selective and only distorted
63 the representation of stimuli presented within $\approx 10^\circ$ around the tapping region, suggesting that motor
64 adaptation effects occur at the sensory rather than cognitive representations of such magnitudes.
65 Given that motor adaptation has been proved to be a sensitive and effective tool to unveil visuo-motor
66 interactions, the aim of the current work is to exploit such a technique to test whether the
67 representation of visual space is also linked with the motor system. The hypothesis is straightforward:
68 if the visual spatial map interacts with the motor system, the motor adaptation should be able to affect
69 visual spatial processing. Contrarily, if visual perception of spatial distances only relies on visual
70 information, no effect of motor adaptation should be detected.

71

72 **Methods**

73 **Participants**

74 A total of 21 adults (all naïve, except one of the authors) all with normal or corrected-to-normal vision
75 (mean age= 24.85, 17 right-handed, 4 left-handed) participated in the motor adaptation experiment.
76 A subset of 9 of them also participated in the visual adaptation experiment. All participants gave
77 written informed consent. The experimental procedures were approved by the local ethics committee
78 (Comitato Etico Pediatrico Regionale – Azienda Ospedaliero-Universitaria Meyer – Firenze FI).

79

80 **Apparatus**

81 Stimuli were created with Psychophysics toolbox for Matlab (Brainard, 1997; Kleiner, Brainard, &
82 Pelli, 2007; Pelli, 1997) and displayed on a 60Hz – 23” LCD monitor (Acer S23IHL) placed
83 horizontally at a viewing distance of 57 cm. When required, hand movements were monitored by an
84 infrared motion sensor device (Leap motion controller – <https://www.leapmotion.com/>) running at
85 60Hz. Subjects were tested in a quiet and dark room, to minimize visual and auditory feedback.

86

87 **Stimuli and procedure**

88 Visual perception of spatial distance was psychophysically measured with a discrimination task
89 (2AFC). In all experiments, the stimuli for the discrimination task consisted in briefly and
90 simultaneously presented pairs of black dots (duration 100ms, size 10 pixels diameter) centered 10°
91 left and right relatively from a central fixation point (the same used by Hisakata et al. (2016)). The
92 dot distance of the reference stimulus was kept constant across trials to 4° while the test stimulus
93 varied trial by trial. The value of the test stimulus was decided with the method of the constant stimuli
94 by randomly selecting, trial-by-trial, a value between 3° to 5° by steps of 0.33° (3°, 3.33°, 3.66°, 4°,
95 4.33°, 4.66°, 5°) roughly presenting each value an equal amount of time.

96 The orientation of two dot pairs was the same on a given trial but randomized (0°-360°, steps of 1°)
97 across trials. In the motor adaptation experiment, the test stimulus was always presented on the
98 dominant-hand side. In the visual adaptation experiment, within each trial session the positions of
99 test and reference were kept constant (i.e. right and left respectively) but in half of the sessions the
100 positions of test and reference were reversed. In all cases, the test was presented in the same location
101 where the adapter had previously been displayed. Participants were asked to indicate which one of
102 the two dot pairs appeared to be shorter and to guess if unsure. For the motor adaptation experiment,
103 participants provided their responses verbally (left-right) and an experimenter (blind to the stimuli)
104 recorded them by a key press. Participants generally completed each experiment on a separate day.
105 The adaptation conditions were always performed after the baseline (to prevent artifacts due to

106 possible relatively long-term adaptation effects). All trials of a given condition (e.g. adaptation or no
107 adaptation) were blocked together.

108

109 **Motor adaptation**

110 As in Anobile et al. (2016; 2019), in the motor adaptation phase, subjects were asked to tap as fast as
111 possible behind the screen with their hand floating between the monitor and the desk (without
112 touching any surface). Participants tapped with their dominant hand for 6 seconds on each trial. The
113 tapping movements were an “up-down” movement of one finger, with the hand concealed by the
114 monitor itself. Tapping movements were monitored by a Leap motion controller (Fig. 1B). All trials
115 in which the subject’s hand was not correctly positioned were automatically aborted. Similarly to
116 Anobile et al. (2016; 2019), the tapping rate averaged across subjects was around 6 Hz (5.89 Hz ,
117 SD= 0.68, min = 4.91, max= 7.53). During the adaptation phase, only the central fixation point was
118 presented on the screen and a change of its color signaled the subjects to stop tapping. Then, after
119 500 ms the visual dot stimuli were presented and participants provided their response. Each
120 participant completed 190 trials (100 for the baseline and 90 for the adaptation condition respectively)
121 divided into 5 separate blocks. Each test value was presented roughly equally, 7 and 6 times in the
122 baseline and adaptation conditions respectively.

123

124

125 **Visual Adaptation**

126 This was a replication of the Hisikata et al. (2016) experiment (Fig. 1A). In the adaptation condition,
127 the test phase was preceded by 60 seconds of visual adaptation (with a 5 seconds top-up at the
128 beginning of the remaining trials). The adapter consisted of a square texture (15°x15°) containing
129 100 black dots (10 pixels in diameter). The position of each dot was defined with a random horizontal
130 and vertical displacement (up to +/- 30 arcmin) and was updated every 300 ms. Each participant
131 completed 300 trials (100 for the baseline and 200 for the adaptation condition respectively) divided

132 into 10 separate blocks. Each test value was presented roughly equally, 7 and 14 times in the baseline
133 and adaptation conditions respectively.

134

135 **Statistical analysis**

136 The proportion of trials where the reference appeared “shorter” than the test was plotted against the
137 test dot pair distance and fitted with cumulative Gaussian error functions. The 50% point of the error
138 functions estimates the point of subjective equality (PSE). The spatial delta between dots needed to
139 move from 50% to 75% of correct responses was defined as JND (just notable difference) which was
140 normalized by PSE gave Weber Fraction, an index of sensory precision.

141 Total adaptation magnitude was measured as the difference between the PSEs measured in the
142 adaption and baseline condition. The effects induced by visual and motor adaptation were analyzed
143 by frequentist and Bayesians ANOVAs. Effect size was reporter as η^2 and significance by p-values
144 and Bayes Factor. Bayes factor is the ratio of the likelihood probabilities of the two models H1/H0,
145 where H1 is the likelihood of a difference between PSEs calculated in the baseline and in the
146 adaptation condition, and H0 the likelihood that the difference does not exist. BF were calculated by
147 JASP (Version 0.8.6) software and reported by transforming the BF_{10} (as provided by the software)
148 into the Log_{10} of BF_{10} (LBF). By convention, a $LBF > 0.5$ it is considered substantial evidence in
149 favor of the existence of the effect, and $LBF < -0.5$ substantial evidence in favor of it not existing.

150 In order to quantitatively compare the magnitude of adaptation effect between the visual and motor
151 adaptation, given the different sample size and the statistically different amount of variance (Levene’s
152 test $p= 0.01$), we applied an assumption free bootstrap test. On each of 10,000 iterations and
153 separately for the visual and the motor conditions, we randomly resampled (with reemission) the
154 adaptation effects (differences between PSEs), computed the average effects and then counted the
155 proportion of time the motor condition provided higher values compared to the visual condition (the
156 p value).

157 Data were analyzed by JASP (Version 0.8.6) software and Matlab (R2017b).

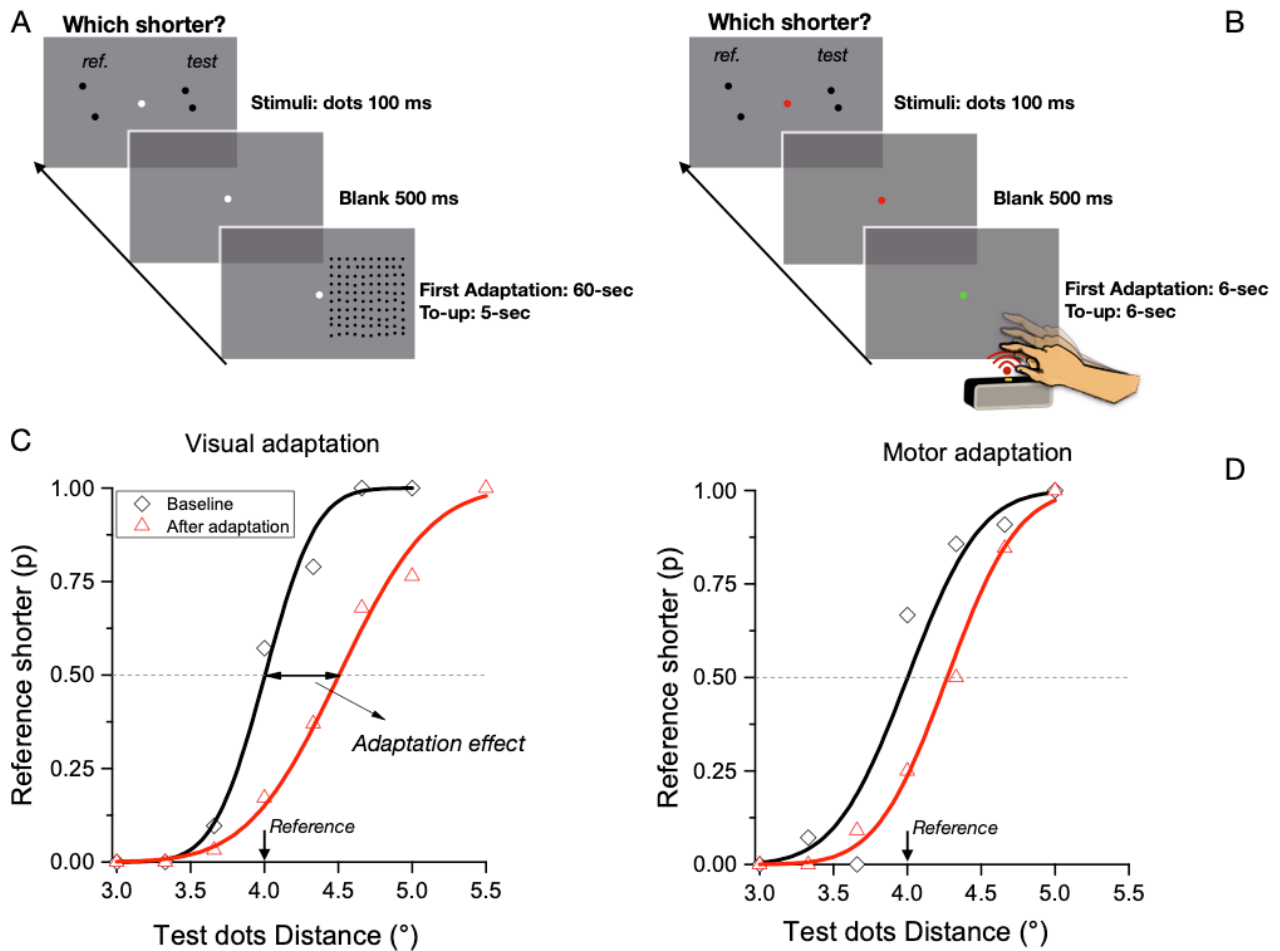
158

159 **Results**

160 We measured whether and to what extent perceived distance between dot-pairs changed after visual
161 or motor adaptation. In the baseline condition, subjects were asked to indicate which one of two
162 distances demarked by a pair of visual inputs was shorter. In the visual adaptation condition, the
163 discrimination task was preceded by a sustained exposure to a dense dot-texture (see Fig 1A). In the
164 motor adaptation condition, the presentation of the visual stimuli was preceded by 6 seconds of fast
165 mid-air tapping not involving any visual, auditory or tactile stimulation (see Fig 1B).

166 Figure 1 C and D show sample psychometric functions for a single representative subject. In the
167 baseline condition, the PSEs were around 4° (the actual dot distance of the fixed reference stimulus).
168 After both motor and visual adaptation, the PSEs shifted rightwards relative to the baseline, indicating
169 a compression of perceived distance for the adapted visual markers.

170



171

172

173 **Figure 1. A. Visual adaptation paradigm.** During the adaptation phase participants kept their eyes
 174 on a fixed point while they adapted to a peripheral dot-texture. Then the screen reverted to blank for
 175 500 ms and two simultaneous dot-pairs (one on the left and the other on the right) appeared for 100
 176 ms. Participants indicated which pair was shorter. **B. Motor adaptation paradigm.** Stimuli were
 177 identical to the visual version of the experiment with the exception of the adaptation phase. Here
 178 participants performed a series of fast mid-air tapping movements behind the screen with their hand
 179 floating above an infrared motion-tracking device. After six seconds of motor-adaptation and a 500
 180 ms of blank screen (fixation point only) the stimuli were presented and participants indicated which
 181 pair was shorter. **C & D. Sample psychometric functions for one representative observer.** The
 182 probability of judging the reference as shorter than the test was plotted against the dot separation of
 183 the test stimulus (variable). Black curves and datapoints indicate the baseline condition, whilst in red
 184 data and fitting curves for the adaptation condition (C, visual; D, motor). The rightward shift of the
 185 red curves (indicating the adaptation condition) reflects a perceived compression of the dot distance
 186 in the adapted test stimulus.

187

188

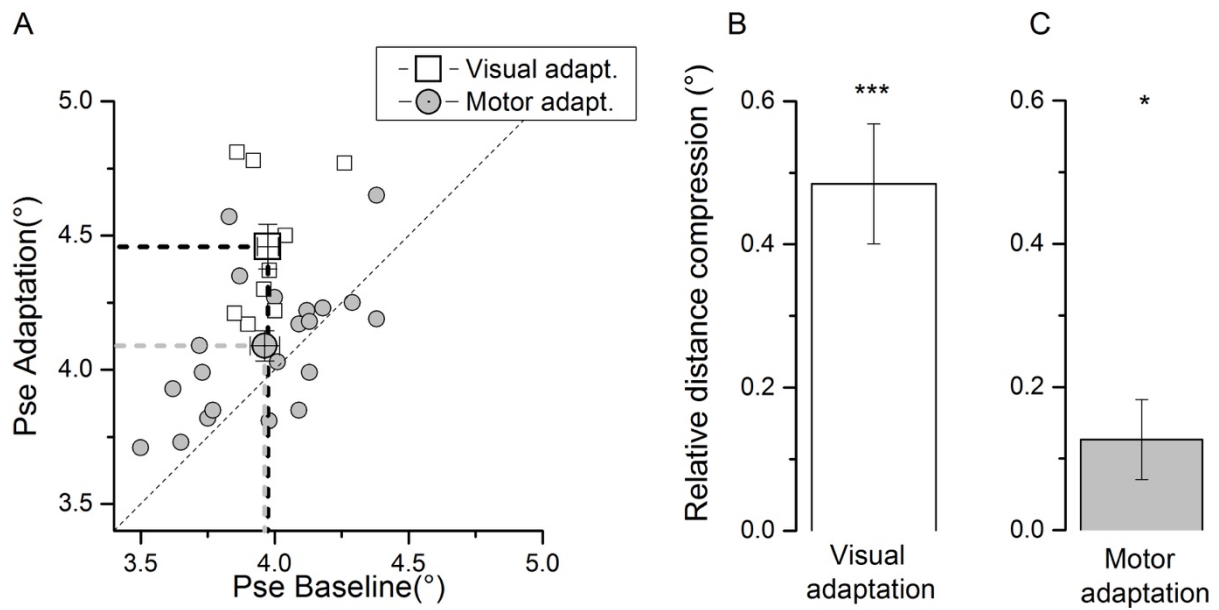
189 Perceived dots distance in the baseline and adaptation conditions were separately measured for each
 190 participant. Figure 2A shows single subject data in terms of PSEs obtained in the adaptation

191 conditions as a function of baseline PSEs for visual (open squares) and motor (filled circle)
192 adaptation. Data falling above the equality line indicate a compression of visual space after
193 adaptation. Despite a large inter-subject variability, 16 out of 21 participants (76%) experienced a
194 compression of the spatial separation of the test stimulus (displayed around the tapping region) as a
195 consequence of motor adaptation. As expected, the effect achieved in the pure visual condition was
196 even more robust, with all participants showing a perceived compression of the adapted stimulus, a
197 result in line with Hisakata et al. (2016).

198
199 To statistically test for the significance of the after-effects, we ran two separate ANOVAs, one for
200 the motor and one for the visual adaptation condition. PSEs were entered in one-way ANOVAs with
201 conditions (2 levels, baseline and adaptation) as factors. For both motor and visual adaptation
202 conditions, the analysis revealed a significant main effect of condition ($F(1,20)=6.044$, $p=0.023$,
203 $\eta^2=0.168$, $LBF=0.42$; $F(1,8)=32.481$, $p<0.001$, $\eta^2=1.056$, $LBF=2.89$, for motor and visual adaptation
204 respectively), indicating that both adaptation methods induced a significant change in the visual
205 stimuli perceived position.

206
207 Figure 2 B and C show adaptation effects averaged across subjects. The effect was indexed as the
208 difference between PSEs obtained in the baseline and adaptation conditions. The overall effect
209 induced by motor adaptation was 0.13° consisting of a change of the perceived spatial interval of
210 about 3%. The effect induced by visual adaptation was about 12%, corresponding to an average PSE
211 shift of 0.47° , a result in line with that reported by Hisakata et al. (2016) and statistically stronger
212 compared to that provided by the motor adaptation ($p<0.001$).

213



214

215 **Figure 2. Visual and motor adaptation effects on visual space.** A) Perceived dot-pair distance of
 216 the test stimulus to match the reference (PSEs) in the adaptation condition against those achieved in
 217 the baseline (no adaptation) condition. Open squares indicate pure visual condition whilst greys
 218 circles refer to motor adaptation. Small symbols indicate single subject data, big symbols indicate
 219 averages across participants. Data falling above the equality line indicates a perceptual compression
 220 of visual space after adaptation. **B & C)** Adaptation effect induced by visual (B) and motor (C)
 221 adaptation averaged across subjects.

222 * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars reports ± 1 s.e.m.

223

224

225 Finally, we looked at discrimination thresholds. In the motor experiment, the averaged baseline
 226 Weber fraction was 0.12 (SD=0.04), slightly decreasing after adaptation (M=0.10 SD=0.04,
 227 $F(1,20)=3.309$, $p=0.084$, $\eta^2=0.004$, LBF=0.15). Also in the pure visual experiment, the Weber
 228 fractions obtained in the baseline and adaptation conditions were similar (baseline 0.11, (SD=0.032),
 229 adaptation was 0.096 (SD=0.021) despite the fact that the difference turned out to be statistically
 230 significant $F(1,8)=8.177$, $p=0.02$, $\eta^2=0.001$, LBF=0.436). These results clearly indicate that the main
 231 effect of motor adaptation on stimuli perceived position mainly occurs for judgement accuracy, along
 232 with a tendency to reduce spatial discrimination thresholds.

233

234

235

236 **Discussion**

237 In this study, we reported that a period of fast mid-air tapping (not involving any visual, tactile and
238 auditory stimulations) is able to decrease the apparent distance between dot pairs subsequently
239 presented around the tapping region. Replicating previous findings (Hisakata et al., 2016), we also
240 found that the same compression is induced by adapting to a dense visual dot-array. These results
241 suggest that the visual and the motor system interact in order to compute the distance between visual
242 objects.

243 In their original paper Hisakata et al.(2016) found that the effect of adaptation on space peaked when
244 the average dot separation in the adapter matched that of the test stimulus, with the effect saturating
245 for shorter separations. This result suggested that the adapting feature was the objects' separation, an
246 index of density. Counterintuitively, adapting to the same dot array reduced the perceived density of
247 a similar dot ensemble, making the elements appear sparser (Hisakata et al., 2016). Similarly,
248 adaptation to a relatively high numerous dot array has been previously demonstrated to reduce
249 apparent numerosity (Burr & Ross, 2008). Together, these results suggest an inverse link between
250 perceived density, numerosity and spatial extent, with results differing when adapting with an array
251 of dots and testing with a similar array of dots with lower density or testing with a single pair of dots.
252 Interestingly, motor adaptation provides a similar pattern of results. Whilst being able to reduce the
253 apparent numerosity of dot arrays (Anobile et al., 2016), theoretically making the apparent stimulus
254 sparser, it also compresses the perceived spatial separation of a dot pair (theoretically making the
255 stimulus appear denser). This striking parallelism seems to suggest similar mechanisms for the visual
256 and the motor adaptation effects. However, it is worth noting that, although both kind of adaptations
257 yielded a compression of visual space revealing a visuo-motor interaction, the magnitudes of the
258 effects were very different. While visual adaptation provided a perceived compression of about 12%,
259 that induced by motor adaptation was much smaller, on average 3%. This difference could be partially
260 induced by methodological differences (as the shorter initial motor adaptation phase compared to the

261 visual condition) but it is also compatible with the idea that the two adaptations tap on different
262 mechanisms. Interestingly, we recently found that motor adaptation provided stronger after-effects
263 than visual adaptation when subjects were asked to estimate stimuli duration or numerosity of
264 sequentially presented items (temporal numerosity). On the contrary, in case participants had to
265 estimate the numerosity of objects scattered over a region of space (spatial numerosity) or
266 discriminate between the speed of moving gratings, visual adaptation outperformed motor adaptation
267 in producing perceptual distortions (Anobile et al., 2019). Notably, judgements on spatial numerosity
268 or stimuli speed share a significant amount of spatial information (as the discrimination of spatial
269 separation tested here), suggesting that the processing of visual spatial information is more easily
270 distorted by visual than motor adaptation. One possibility to account for a such difference, it is in
271 terms of "compatibility" of the adaptor and test stimuli. Primarily temporal and sequential routine
272 like motor adaptation might affect to a larger extent sequential/temporal stimuli whilst visual
273 adaptation with a prominent spatial component would be more efficient to distort the processing of
274 spatial/numerical information.

275 What is the visual spatial mechanism that is distorted by motor adaptation? In the visual domain, it
276 has been suggested that the discrimination of visual spatial intervals can be achieved by the use of
277 pairs of coincidence detectors receiving inputs from separated and spatially localized regions of the
278 visual space (Morgan & Regan, 1987). A distributed mechanism characterized by a population of
279 such coincidence detectors, preferring different separations, could thus sustain distance perception
280 (Kohly & Regan, 2000; Morgan & Regan, 1987). Though it is conceivable that visual adaptation
281 aftereffects arise by a perturbation of the activity of such mechanisms, how motor adaptation might
282 interact with such a mechanism is still unknown. A speculative hypothesis is that the output of the
283 visual coincidence detectors is somehow normalized by the previous overall motor activity but,
284 clearly, future studies are needed to test this idea.

285 That visual perception of magnitudes is linked with the motor systems is highly consistent with the
286 influential ATOM (A theory of magnitude) theory according to which space, time and number are

287 processed by a common parietal system (Buetti & Walsh, 2009; Walsh, 2003). Crucially, the key idea
288 of this theory is that action would be the linking factor across the different perceptual magnitudes,
289 meaning that space, quantity and time would be combined by a common metric for action: an “action-
290 based magnitude system”. The current results, together with previous reports, clearly demonstrate
291 that a sustained activity of the motor system is able to distort all these magnitudes, suggesting that
292 the link between the visual and the motor system in magnitude encoding is likely to occur in parietal
293 cortex. In line with this, it has been reported that duration, numerosity and space are also similarly
294 affected by saccadic eye movements (Burr, Ross, Binda, & Morrone, 2010). Even if saccades are
295 quite different from tapping movements, they also strongly engage parietal areas, suggesting that the
296 interaction between the motor and the visual system might not be effector dependent (i.e. upper limbs)
297 but generalizes to the programming and execution of very different motor routines. The close link
298 between action and perception in the parietal cortex is well documented by both clinical and
299 neuroimaging data: it is known from lesions studies that a wide range of sensorimotor functions can
300 be selectively affected in patients with parietal lobe damage, including motor planning and execution
301 (Freund, 2001).

302 In conclusion, with the current set of behavioral data, we cannot definitively explain why motor
303 adaptation shapes visual perception of distances, as we cannot definitively conclude that the visual
304 and motor adaptation are mediated by the same neural mechanisms. However, in light of the present
305 data, we find it reasonable to frame the results within the well-established ATOM theory (Walsh,
306 2003) by suggesting that the mechanism linking motor adaptation to visual perception of space is a
307 shared parietal metric for magnitude perception. Even if still speculative, the after-effects induced by
308 motor adaptation would reflect a cross-modal calibration of this shared metric. As the visual
309 environment continuously changes as a function of contextual effects, the adaptive nature of such a
310 flexible mechanism could reside in linking goal-directed actions within the visual environment. It
311 seems plausible to think that the functional role of the visual-motor adaptation is to maximize the

312 efficiency of the motor interaction with the environment, by a continuous cross-calibration
313 mechanism.

314

315

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321 perception: serial dependence and rhythmic oscillations’).

322

323

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