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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

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

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

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

Methods

Participants

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

Apparatus

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

Stimuli and procedure

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

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

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

Motor adaptation

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

Visual Adaptation

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

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

Statistical analysis

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

Total adaptation magnitude was measured as the difference between the PSEs measured in the adaption and baseline condition. The effects induced by visual and motor adaptation were analyzed by frequentist and Bayesians ANOVAs. Effect size was reporter as η^2 and significance by p-values and Bayes Factor. Bayes factor is the ratio of the likelihood probabilities of the two models H1/H0, where H1 is the likelihood of a difference between PSEs calculated in the baseline and in the adaptation condition, and H0 the likelihood that the difference does not exist. BF were calculated by JASP (Version 0.8.6) software and reported by transforming the BF_{10} (as provided by the software) into the Log10 of BF_{10} (LBF). By convention, a LBF > 0.5 it is considered substantial evidence in favor of the existence of the effect, and LBF < −0.5 substantial evidence in favor of it not existing.

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

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

Results

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

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

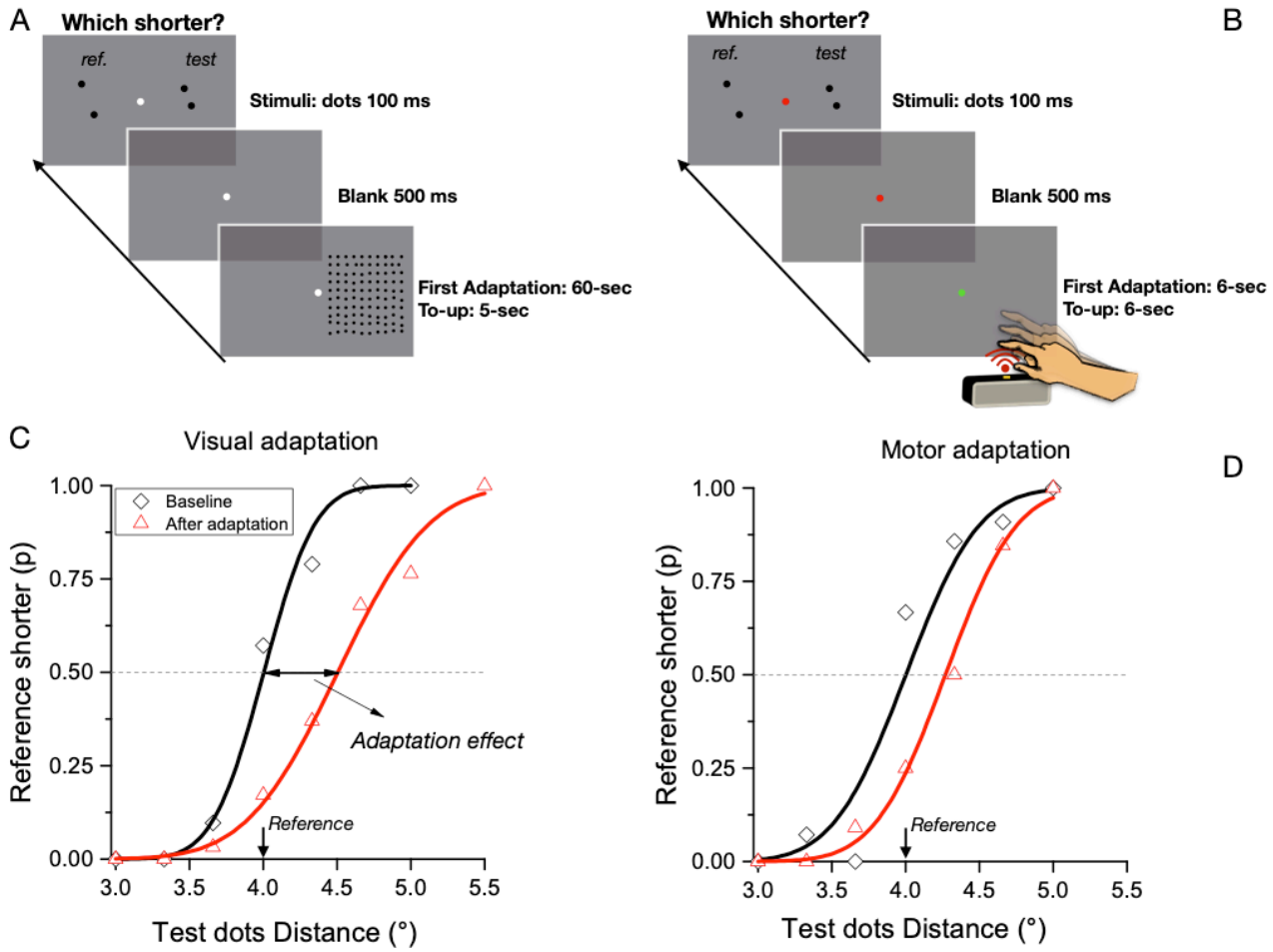

Figure 1. A. Visual adaptation paradigm. During the adaptation phase participants kept their eyes on a fixed point while they adapted to a peripheral dot-texture. Then the screen reverted to blank for 500 ms and two simultaneous dot-pairs (one on the left and the other on the right) appeared for 100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

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

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

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

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

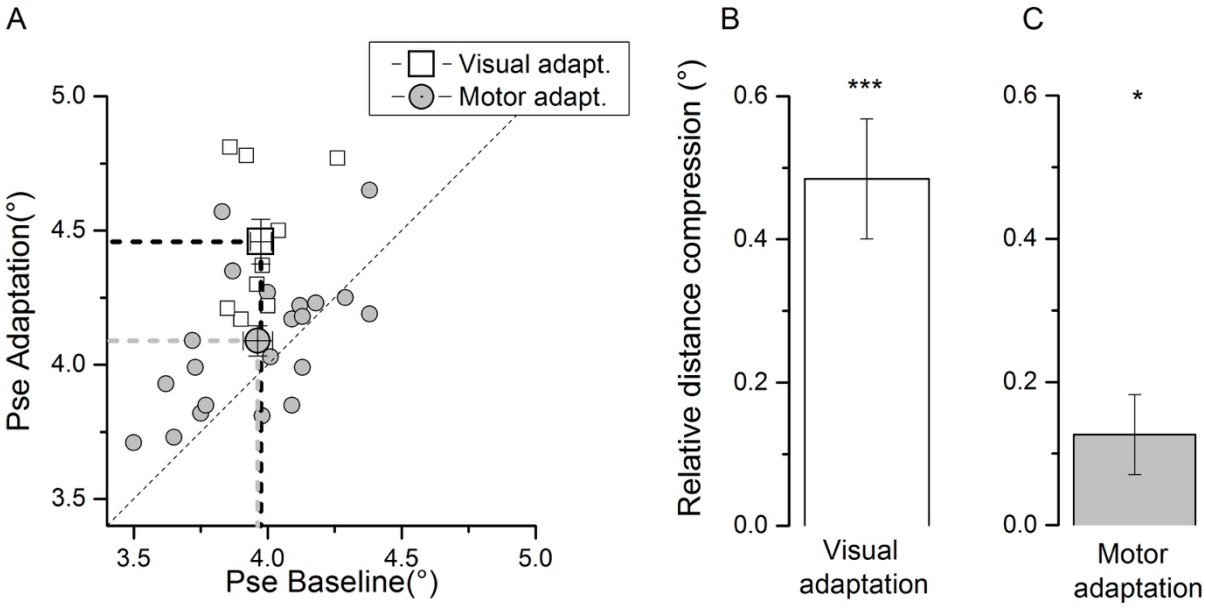

Figure 2. Visual and motor adaptation effects on visual space. A) Perceived dot-pair distance of the test stimulus to match the reference (PSEs) in the adaptation condition against those achieved in the baseline (no adaptation) condition. Open squares indicate pure visual condition whilst greys circles refer to motor adaptation. Small symbols indicate single subject data, big symbols indicate averages across participants. Data falling above the equality line indicates a perceptual compression of visual space after adaptation. **B & C)** Adaptation effect induced by visual (B) and motor (C) adaptation averaged across subjects.
* $p<0.05$, ** $p<0.01$, *** $p<0.001$. Error bars reports ±1 s.e.m.

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

Discussion

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

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

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

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

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

287 processed by a common parietal system (Bueti & 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 programing 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

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

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References

Anobile, G., Arrighi, R., Togoli, I., & Burr, D. C. (2016). A shared numerical representation for action and perception. *Elife, 5*. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/27504969. doi:10.7554/eLife.16161

Anobile, G., Domenici, N., Togoli, I., Burr, D. C., & Arrighi, R. (2019). Distortions of visual time induced by motor adaptation. *J Exp Psychol Gen*. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/31789572. doi:10.1037/xge0000709

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spat Vis, 10*(4), 433-436. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/9176952.

Bueti, D., & Walsh, V. (2009). The parietal cortex and the representation of time, space, number and other magnitudes. *Philos Trans R Soc Lond B Biol Sci, 364*(1525), 1831-1840. doi:10.1098/rstb.2009.0028

10.1098/rstb.2009.0028.

Burr, D. C., & Ross, J. (2008). A visual sense of number. *Curr Biol, 18*(6), 425-428. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/18342507. doi:10.1016/j.cub.2008.02.052

Burr, D. C., Ross, J., Binda, P., & Morrone, M. C. (2010). Saccades compress space, time and number. *Trends Cogn Sci, 14*(12), 528-533. doi:10.1016/j.tics.2010.09.005

10.1016/j.tics.2010.09.005. Epub 2010 Oct 23.

Clifford, C., Webster, M., Stanley, G., Stocker, A., Kohn, A., Sharpee, T., & Schwartz, O. (2007). Visual adaptation: Neural, psychological and computational aspects. *Vision research, 47*, 3125-3131. doi:10.1016/j.visres.2007.08.023

Freund, H.-J. (2001). The parietal lobe as a sensorimotor interface: a perspective from clinical and neuroimaging data. *Neuroimage, 14*(1), S142--S146.

Hisakata, R., Nishida, S., & Johnston, A. (2016). An Adaptable Metric Shapes Perceptual Space. *Curr Biol, 26*(14), 1911-1915. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/27426520. doi:10.1016/j.cub.2016.05.047

Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3?

Kohly, R. P., & Regan, D. (2000). Coincidence detectors: visual processing of a pair of lines and implications for shape discrimination. *Vision Res, 40*(17), 2291-2306. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/10927116. doi:10.1016/s0042-6989(00)00090-0

McKeefry, D. J., Laviers, E. G., & McGraw, P. V. (2006). The segregation and integration of colour in motion processing revealed by motion after-effects. *Proc Biol Sci, 273*(1582), 91-99. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/16519240. doi:10.1098/rspb.2005.3293

Mollon, J. (1974). After-effects and the brain. *New Scientist, 61*, 479-482.

Morgan, M. J., & Regan, D. (1987). Opponent model for line interval discrimination: interval and vernier performance compared. *Vision Res, 27*(1), 107-118. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/3617541. doi:10.1016/0042-6989(87)90147-7

Nishida, S., & Johnston, A. (1999). Influence of motion signals on the perceived position of spatial pattern. *Nature, 397*(6720), 610-612. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/10050853. doi:10.1038/17600

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat Vis, 10*(4), 437-442. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/9176953.

Snowden, R. J. (1998). Shifts in perceived position following adaptation to visual motion. *Curr Biol, 8*(24), 1343-1345. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/9843685. doi:10.1016/s0960-9822(07)00567-2

Thompson, P., & Burr, D. C. (2009). Visual aftereffects. *Curr Biol, 19*, R11-14. doi:10.1016/j.cub.2008.10.014

Turi, M., & Burr, D. C. (2012). Spatiotopic perceptual maps in humans: evidence from motion adaptation. *Proc Biol Sci, 279*(1740), 3091-3097. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/22535785. doi:10.1098/rspb.2012.0637

Walsh, V. (2003). A theory of magnitude: common cortical metrics of time, space and quantity. *Trends Cogn Sci, 7*(11), 483-488. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/14585444. doi:10.1016/j.tics.2003.09.002

Webster, M. A. (2011). Adaptation and visual coding. *Journal of vision, 11*(5), 10.1167/1111.1165.1163 1163. Retrieved from https://www.ncbi.nlm.nih.gov/pubmed/21602298 https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3245980/. doi:10.1167/11.5.3

Whitney, D., & Cavanagh, P. (2003). Motion adaptation shifts apparent position without the motion aftereffect. *Percept Psychophys, 65*(7), 1011-1018. doi:10.3758/bf03194830