

Distortions of Visual Time Induced by Motor Adaptation

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As perception of time is fundamental for action planning and execution, we investigated how action distorts the perception of visual duration. Participants adapted to tapping in midair for a few seconds, either slowly or quickly, then judged the relative duration of 2 drifting gratings, 1 spatially coincident with the tapped region and the other in the opposite field. Fast tapping decreased apparent duration in the tapping region while slow tapping increased it. The effect was spatially specific in external (not body-centered) coordinates, occurring within a 10° region centered on the tapping hand. Within this space, motor adaptation similarly distorts visual numerosity, suggesting common mechanisms for number and time. However, motor adaptation did not affect the perception of speed, a lower level visual property, suggesting that the interactions were at a high level of processing. These results reinforce studies that suggest that visual time perception is coupled with action and suggest the existence of multiple local visuomotor clocks.

Keywords: time perception, numerosity perception, perception and action, adaptation, cross modal perception

Temporal duration is a fundamental aspect of any physical event. It is particularly important for planning and executing actions, from the simplest, such as repetitive tapping, to the most complex, such as playing music, dancing, or driving. However, it is far from clear how humans encode time and how time perception interacts with the motor system.

Many investigations have addressed this issue, revealing fascinating interconnections. During saccadic eye movements, perceived duration is strongly compressed, along with spatial position and numerosity (Burr, Ross, Binda, & Morrone, 2010; Ross, Morrone, & Burr, 1997). Similarly, visual intervals are compressed during circular hand movements, more for faster than for slower actions, independently of involuntary eye movements (Yokosaka, Kuroki, Nishida, & Watanabe, 2015). Time intervals are also distorted when stimuli are displayed while performing consecutive finger taps (Tomassini, Vercillo, Torricelli, & Morrone, 2018), and during planning and execution of horizontal hand movements, overestimating for rightward motion and underestimating for leftward motion (Tomassini & Morrone, 2016). Subjective visual duration can also be selectively slowed by action. During preparation of a ballistic reaching movement, static visual stimuli are perceived as lasting longer than when no motor preparation was involved (Hagura, Kanai, Orgs, & Haggard, 2012). Tactile duration intervals are also reduced during hand movements (Tomassini, Gori, Baud-Bovy, Sandini, & Morrone, 2014), and perception of the time of voluntary actions (key press) can be shifted toward a subsequent tone with the perceived time of the tone shifted toward the action (Haggard, Clark, & Kalogeras, 2002). Even whole-body passive motion induced by a rotating chair distorts time perception, both in perceptual discrimination and time reproduction. Taken together these reports suggest that vestibular-proprioceptive information plays a key role in the calibration and regulation of

This article was published Online First December 2, 2019.

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This research was funded by the Italian Ministry of Health and Tuscany Region 'Ricerca Finalizzata', Grant GR-2013-02358262; from the European Union's Horizon 2020 research and innovation programmes ERC Advanced Grant 832813 (GenPercept); and from the Italian Ministry of Education, University, and Research PRIN2017 programme, Grants 2017XBJN4F and 2017SBPZY.

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the internal pacemaker (Binetti, Siegler, Bueti, & Doricchi, 2010, 2013).

Cross-modal training studies also point to interconnections between motor and perceptual timing. Perceptual training with an auditory duration discrimination task showed significant transfer to a motor duration reproduction task (Meegan, Aslin, & Jacobs, 2000). Training on discrimination of subsecond temporal intervals in visual stimuli produced functional and structural changes in sensory-motor networks including occipital, parietal, insular cortices and the cerebellum (Bueti, Lasaponara, Cercignani, & Macaluso, 2012).

One method to study interactions between action and perception is to look at cross-adaptation. Prolonged exposure to a specific stimulus (adaptation) can bias the perception of subsequent stimuli away from the adaptor. Adaptation effects are thought to result from changes in activity of the system encoding that perceptual feature (Barlow & Hill, 1963; Clifford et al., 2007). The strength of adaptation effects is both stimulus- and space-specific, with maximal effects for adapter and test stimuli sharing physical features and spatial position. In spatial vision, adaptation has been widely used to reveal selective perceptual channels (Webster, 2011), as well as shared or independent sensory mechanisms (Anobile et al., 2018; Arrighi, Togoli, & Burr, 2014; Schwiedrzik, Bernstein, & Melloni, 2016).

Specific adaptation effects also occur in time, consistent with the existence of duration-channels (Heron et al., 2012). For example, adaptation to moving or flickering stimuli induces strong distortions of perceived duration of visual stimuli: viewing a fast translating or flickering visual patch causes the perceived duration of subsequent stimuli to be underestimated (Johnston, Arnold, & Nishida, 2006). The temporal aftereffects are selective to the spatial region that was adapted, in spatiotopic rather than retinotopic coordinates (Burr, Tozzi, & Morrone, 2007). Subsequent investigations showed that only simple unidirectional translating motion—not circular or radial motion, nor motion sectors moving in opposing or orthogonal directions—was effective in inducing duration adaptation (Fornaciai, Arrighi, & Burr, 2016). Interestingly, duration aftereffects induced by visual motion and flicker are asymmetric, showing stronger temporal compression than expansion (Ayhan, Bruno, Nishida, & Johnston, 2009; Johnston et al., 2006). Adaptation to duration also occurs in the haptic system: sustained stimulation of tactile motion compresses perceived tactile duration (Tomassini, Gori, Burr, Sandini, & Morrone, 2012). Interestingly, a voluntary hand motion performed between the adaptation and test phase completely abolishes the aftereffect.

In a recent study (Anobile, Arrighi, Togoli, & Burr, 2016), we reported a strong interaction between motor adaptation and visual perception of numerosity. Sustained voluntary action (hand-tapping in midair) changed robustly apparent numerosity of both temporal sequences and spatial arrays: fast tapping reduced apparent numerosity and slow tapping increased it. Here we apply a similar method to study the link between action and perception in visual event duration. We replicate the effects of tapping on numerosity, and further show that fast and slow tapping adaptation robustly reduces or increases apparent duration of visual stimuli. Importantly, aftereffects are spatially specific and do not generalize to low-level visual properties (such as motion speed), showing that they are perceptual rather than cognitive in nature.

General Method and Procedure

A total of 29 adults (25 naïve and four authors, $M_{\text{age}} = 26.62$, $SD = 4.06$; all right-handed with normal or corrected-to-normal vision) participated across all the experiments. Each of them participated in a subset of the experimental conditions (details given below), with the exception of Nicola Domenici, who took part in all experiments. We did not set any inclusion criteria for subject selection: all data, for all experimental conditions, were analyzed and reported. All participants gave written informed consent. The experimental procedures were approved by the local ethic committee (Comitato Etico Pediatrico Regionale—Azienda Ospedaliero-Universitaria Meyer—Firenze FI). As the main goal of the study was to investigate whether motor adaptation affected perceived duration, we computed a power analysis to estimate sample size necessary to reach statistical significance. The analysis revealed that a sample size of 6 was needed to obtain a power of 0.97 with an alpha level of 0.05 (one-tailed). Therefore, in the main experiments dedicated to assess the effect of motor adaptation on visual time, we tested up to eight participants. Data were analyzed by Matlab_R2017B and JASP software (Version 0.8.6).

Stimuli were created with Psychophysics Toolbox for Matlab (Kleiner, Brainard, & Pelli, 2007) and displayed on a 60 Hz, 17" touch screen monitor (LG-FLATRON L1730SF) placed horizontally at viewing distance of 57 cm. For the visual adaptation experiments we displayed stimuli on a CRT screen monitor (rate 100 Hz, 17"). To test adaptation aftereffects at the most extreme distances between the visual adapter and test (20° and 30°), we reduced the viewing distance to 28.5 cm.

When required, hand movements were monitored by an infrared motion sensor device (Leap Motion controller, Leap Motion, San Francisco, CA; <https://www.leapmotion.com/>) running at 60 Hz. Subjects were tested in an anechoic, dark room, to minimize visual and auditory feedback.

Performance was measured with a two-interval-alternative-forced choice method, with order of presentation of test and reference randomized across trials, and stimuli magnitudes defined by the adaptive QUEST algorithm (Watson & Pelli, 1983) algorithm (parameters were range = 0.2, tGuessSd = 1.2, pThreshold = 0.5, $\beta = 3.5$, $\epsilon = 0.01$, $\gamma = 0$). The QUEST algorithm homes in efficiently on the point of subjective equality (PSE) by calculating on each trial as the maximum likelihood estimate of the PSE (jittered with 0.15 log units to avoid the staircase to get stuck in local minima). Each psychometric function was tested at least 40 trials. To ensure that the QUEST converged and that parameters were well estimated, we carefully visually inspected each psychometric function, and added data if it had not converged. The order of tasks and conditions was pseudorandomized between subjects. All trials of a certain condition (e.g., fast, slow or no adaptation) were blocked together.

Experiment 1A–1B: Visual and Motor Adaptation on Duration and Speed Discrimination

In the first experiment, we asked subjects to indicate which of two peripheral drifting gratings lasted longer or moved faster. For both duration and speed judgments, the stimuli were drifting gratings (spatial frequency: 1 cpd; 90% Michelson contrast; square aperture of 8°), with the direction of motion of both reference and

test randomly and independently decided trial-by-trial. Test stimuli were centered 10° to the right and reference 10° to the left of a central fixation point and were sequentially presented with an ISI of 500 ms with the temporal order randomized across trials.

In the speed discrimination task, the speed of the reference was fixed at 10 Hz, whereas the speed of the test varied following a QUEST algorithm to which was added a random jitter (following a Gaussian of standard deviation 25% of the reference interval). Both test and reference presentation times were fixed at 600 ms. In the duration discrimination task, the duration of the test followed the QUEST algorithm, whereas the duration of the reference was fixed at 600 ms. Subjects were required to compare the speed or the duration the stimuli and indicate which lasted longer or moved faster.

In separate sessions, the presentation of test and reference stimuli was preceded by an adaption phase, either visual (Experiment 1 A) or motor (Experiment 1 B). In these conditions, test and reference stimuli were presented 500 ms after the adaptation phase finished (signaled by a color change of the fixation point).

Visual adapters were vertical gratings (spatial frequency: 1 cpd; 90% Michelson contrast) drifting horizontally within a squared aperture of 8° for 6 s. In this first experiment, adapters and test stimuli were spatially coincident. To avoid a motion aftereffect, gratings motion direction inverted every 2 s. Three different levels of adaptation were tested in separate sessions: “fast” (20-Hz drift), no-adaptation, and “slow” (5-Hz drift). In the experiments concerning duration discrimination, the apparent speed of the adapted and neutral stimulus was equated to avoid duration estimates being contaminated by apparent speed differences between stimuli. This compensation (of critical importance given that stimuli apparent duration has been reported to strongly correlates with their speed; Kanai, Paffen, Hogendoorn, & Verstraten, 2006) was achieved by first measuring independently for each subject the shift in apparent speed induced by adaptation in the speed discrimination task.

The motor adaptation procedure (Experiment 1B) consisted of subjects tapping with their right (dominant) hand for 6 s behind a screen with the hand floating between the monitor and the desk, without touching any surface. Only the central fixation point was presented on the screen during the motor adaptation. The tapping movements were an “up-down” movement of one finger, with the hand concealed by a panel covering the right arm. In Experiment 1, the tapping occurred in a position that spatially overlapped the region where the test stimulus was subsequently displayed. As for visual adaption, three adaptation levels were separately tested for each stimulus condition: fast tapping, no tapping and slow tapping. Following Anobile et al. (2016), for the “fast” condition, subjects tapped as fast as possible, whereas for the “slow” they tapped at about one tap per second. A Leap Motion controller measured tapping speed and kept track of position of hand tapping: If the subject’s hand was not positioned correctly, or subjects continued to tap after the end of the adaptation phase, the trial was aborted. In the “no-tapping” condition, participants kept their hands steady, leaning on the sensor.

Five participants performed Experiment 1A (s16, s26, s27, s28, and s29), whereas eight performed Experiment 1B (s16, s17, s18, s19, s20, s21, s23, and s24). One participant (s16) participated in both experiments.

Experiment 2: Visual and Motor Adaptation Spatial Selectivity

To measure the spatial selectivity of the visual and motor adaptation effects, the adapter position relative to the test position was manipulated in separate sessions and kept constant across trials. For duration and speed judgments, both stimuli and procedure were the same as in the Experiment 1A and B (apart from the fact that the position of the adapter was manipulated in separate sessions).

For visual adaptation and duration judgments, the spatial displacements between adapter and test were 0°, 5°, 10°, and 20°. For visual adaptation and speed judgments they were 0°, 5°, 10°, 20°, and 30°. For both duration and speed judgments, five participants performed the 0° displacement condition (s16, s26, s27, s28, and s29), whereas three participants were tested in the 5°, 10°, 20°, and 30° (s16, s28, and s29). For the motor adaptation and duration judgments, the spatial displacements between adapter and test were 0° (as Experiment 1A), 10°, 15°, 20°, and 30°. For motor adaptation and speed judgments we tested only the superimposed condition, as not even this condition yielded any effect. For both duration and speed judgments eight participants performed the 0° displacing condition (s16, s17, s18, s19, s20, s21, s23, and s24). Four participants were tested in duration judgment for the 10°, 15°, 20°, and 30° conditions (s16, s19, s20, and s21).

To assess the spatial tuning of visual and motor adaptation on the perception of stimuli numerosity, we also measured visual and motor adaption to spatial and temporal numerosity. Test stimuli for spatial numerosity were clouds of nonoverlapping dots (8° diameter, dots 0.3° diameter each, half-white and half-black) presented. For sequential numerosity, the stimuli were sequences of white and black disks (diameter of 8°), each presented for 40 ms. Both dots and flashes were presented at 10° eccentricity to the left and right of the central fixation point. Dot stimuli lasted for 500 ms while flashes were presented at pseudorandom times within an interval of 3 s (40 ms duration, minimum interstimulus interval 40 ms). Reference stimuli were 16 dots or 16 flashes and test numerosity was determined by the adaptive QUEST algorithm. Subjects were required to compare the numerosity of the stimuli and indicate which was more numerous. For spatial numerosity, the visual adapter was an 8° diameter cloud of nonoverlapping dots (0.3° diameter, half-white and half-black). For sequential numerosity, the adapter was a temporal series of white and black disks (diameter of 8°), each presented for 40 ms within an interval of 6 s. The “high” numerosity adaptation stimulus comprised 48 dots/temporal events, and the “low” 8. Motor adaptation procedure was identical to that described for Experiment 1B.

To measure the spatial tuning of visual adaptation of both spatial and temporal numerosity, the displacements between adapter and test were 0° (as Experiment 1A), 5°, and 10°, with three participants (s16, s28, and s29). Conversely, the spatial spread of motor adaptation on numerosity judgment, the displacements between adapter and test were 0°, 10°, 15°, 20°, and 30°. For spatial numerosity eight participants performed the 0°, 10°, 20°, and 30° displacing condition (s1, s9, s10, s11, s12, s13, s14, and s15), whereas five were tested in the 15° (s1, s10, s13, s14, and s15). For temporal numerosity eight participants performed the 0°, 10°, 20°, and 30° displacing condition (s1, s2,

s3, s4, s5, s6, s7, and s8), whereas five were tested in the 15° condition (s1, s3, s5, s7, and s8).

On average, across displacements conditions, in the fast adapting condition (subjects required to tap as fast as possible), subjects tapped at 4.75 ± 0.11 Hz (total number of taps around 29). In the slow adaptation condition participants tapped on average at a frequency of 1.13 ± 0.13 Hz (total number 7). Importantly, for all conditions, the tapping speed did not vary with the eccentricity between the adapting hand and the test stimulus, as shown by a series of *t* tests all *p* were higher than 0.42 for temporal numerosity and 0.14 for spatial numerosity.

Experiment 3: Selectivity in External or Body Space?

In this experiment, stimuli were moving visual gratings, and we tested only the effect of motor adaptation on relative duration. In order to study the reference frame of the effect, the adapter position (tapping hand) relative to the test was manipulated (in separate sessions). Participants tapped either at the same spatial position as the test stimulus (10° to the right of the fixation point), or on the diametrically opposite side, 10° to the left of the central fixation point (reference location). Eight participants were tested in the “tapping on the right” conditions (duration: s16, s17, s18, s19, s20, s21, s23, and s24; spatial numerosity: s1, s9, s10, s11, s12, s13, s14, and s15; temporal numerosity: s1, s2, s3, s4, s5, s6, s7, and s8) while five performed the “tapping to the left” conditions (duration: s16, s20, s22, s25, and s26; spatial numerosity: s1, s10, s13, s14, and s15; temporal numerosity: s1, s3, s5, s7, and s8).

Statistical Analyses

The proportion of trials where the test appeared “faster” or “longer” or “more numerous” than the reference was plotted against the test speed, duration or numerosity (on log axis), and fitted with cumulative Gaussian error functions. The 50% point of the error functions estimates the PSE. Total adaptation magnitude was measured as the difference between the PSEs measured in the two adaptation conditions (fast and slow tapping, fast and slow visual motion, high and low numerosity) normalized by the sum of the two (see below equation 1).

$$\text{Adaptation} = \frac{PSE_{\text{lowA}} - PSE_{\text{highA}}}{PSE_{\text{lowA}} + PSE_{\text{highA}}} \quad (1)$$

where PSE_{lowA} and PSE_{highA} refer to the PSEs after adaptation to “low” and “high” intensity adapters. The separate contribution of the two adaptation levels (fast and slow tapping, fast and slow visual motion) were calculated as differences between PSEs measured in the adaptation condition normalized by baseline PSE (no adaptation).

Amplitude and width of adaptations across conditions were measured by fitting average data about the magnitude of adaptation for different spatial offset between the tapping hand and the test stimulus with Gaussian functions centered at zero (X_c)—the position in which the tapping hand and the test stimulus were superimposed—and free to vary in amplitude (A), baseline (Y_0), and width (σ), following Equation 2.

$$Y = Y_0 + Ae^{-\frac{(c - x_c)^2}{2\sigma^2}} \quad (2)$$

Results

Experiment 1A: Visual Motion Adaptation: Duration and Speed Discrimination

Participants judged which of two peripheral drifting gratings lasted longer or moved faster. In the adaptation conditions, they adapted to a fast (20 Hz) or slow (5 Hz) drifting grating before making the duration or speed judgments. Replicating previous studies, we found that visual adaptation to fast or slow visual motion triggered robust aftereffects of speed and duration of visual stimuli presented in the adapted location. Figures 1B and C show the effects on representative participants. Rightward shifts of psychometric functions relative to the no-adaptation baseline (dashed lines) indicate that the physical speed or duration of the adapted stimulus had to be significantly increased to perceptually match that of the reference, reflecting a perceptual underestimation of the adapter stimulus; leftward shifts indicate overestimations. Figure 1F (left bars) shows individual and average absolute effects (difference of PSEs after fast and slow adaptation normalized by their

Figure 1 (opposite). (A) Motor adaptation paradigm. During the motor adaptation phase, participants made a series of midair tapping movements below a screen, with the hand floating above an infrared motion-tracking device. After 6 s of tapping, a stop signal (color change of fixation point) appeared and was followed, after a further 500 ms of blank screen (fixation point only), by two visual stimuli presented sequentially: the test (variable duration) at the point of tapping and the reference (600-ms duration) at the opposite position (order randomized). Stimuli were either drifting gratings (as depicted here), clouds of dots, or series of flashes. Subjects indicated which stimulus (test or reference) appeared to last longer, move faster, or comprise more dots or more flashes (investigated in separated experiments). In additional conditions, subjects were required to perform hand tapping at a given distance from the location of the test stimulus to measure the spatial tuning of motor adaptation of visual perception. (B–F) Visual and motor adaptation effects on visual perceived speed and duration. Sample psychometric functions for representative observers for duration (“Which is longer?” C and E) and speed (“Which is faster?” B and D) discrimination judgments, with adapter and test spatially superimposed. Upper panels (B and C) show performance after adaptation to visual drifting grating while lower panels (D and E) after adaptation to midair tapping. Shifts between curves reveal adaptation, with points of subjective equality (PSE; the physical test magnitude corresponding to 0.5 proportion of “longer” or “faster” responses) moving away from the physical duration or speed. Rightward shifts show that after adaptation to fast motion or tapping (20 Hz or fast tapping) the reference stimuli (600 ms of duration or 10 Hz of speed) was perceived as lasting less or moving slower. *Adaptation effects* were defined as differences in PSEs after adaptation to fast and slow visual motion or tapping, normalized by the sum of the two (see Method). Panel F shows individual subjects (open squares symbols) and average (bars) adaptation effects for speed and duration (right dash) judgments. Although both visual and motor adaptation distort perceived duration, perceived speed was affected only by visual adaptation. See the online article for the color version of this figure.

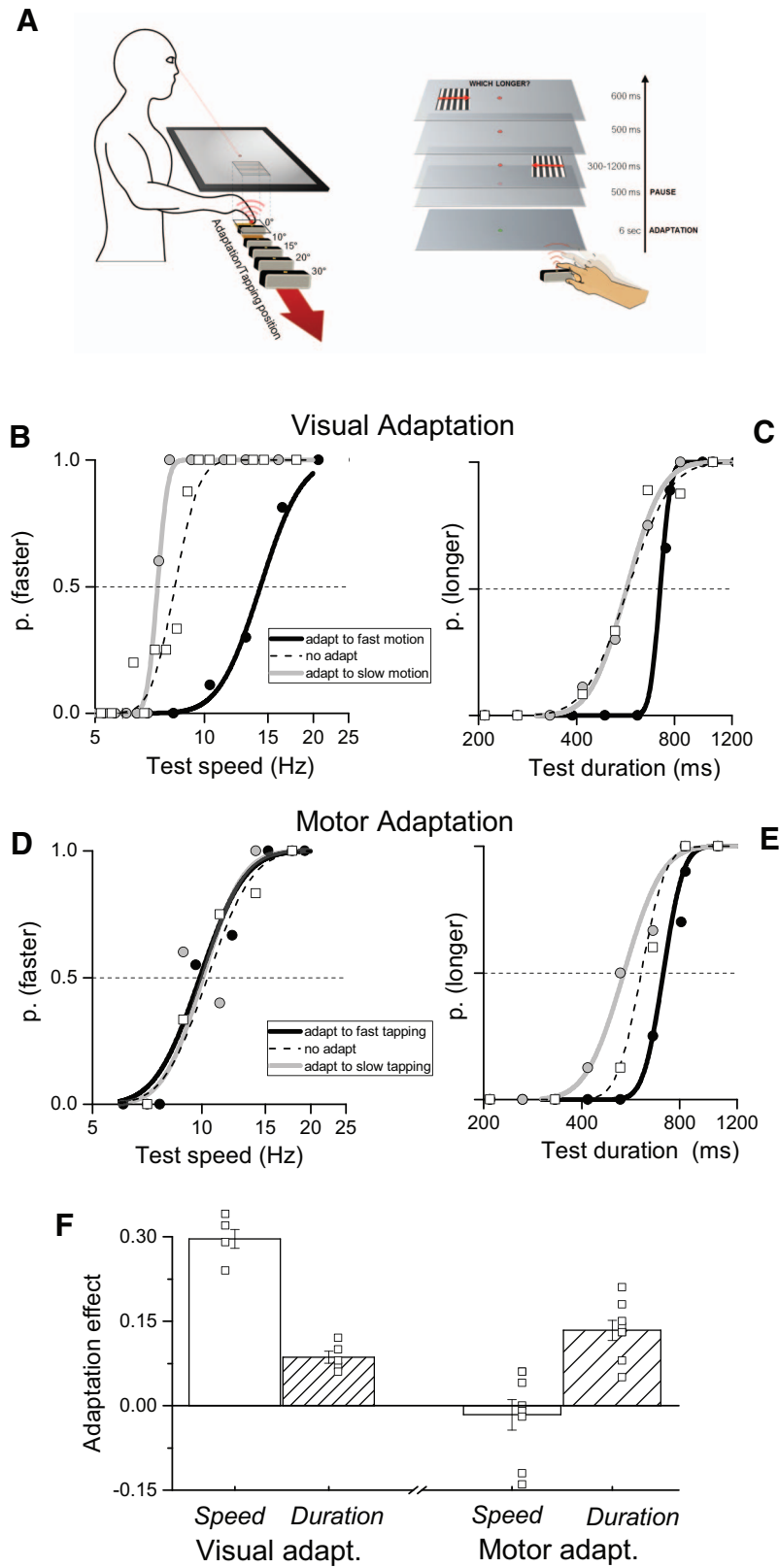


Figure 1 (opposite)

sum, eqn 1). A 2 (level of adaptation: high or low) \times 2 (task: speed or time) repeated measures analysis of variance (ANOVA) on adaptation effects (PSEs difference between adaptation and baseline normalized on baseline) revealed a statistically significant interaction, $F(1, 4) = 7.845$, $p = .049$, $\eta^2 = 0.662$, to reflect that adaptation to fast and slow visual motion differs across speed and duration judgments. A series of post hoc t tests revealed that although for speed judgments both, fast and slow motion, triggered significant (and opposite) PSEs shifts compared to baseline, $t(4) = 5.351$, $p = .006$, Cohen's $d = 2.393$; $t(4) = 4.097$, $p = .015$, Cohen's $d = 1.832$ for slow and fast; two-tailed), for duration, only adaptation to fast motion significantly shifted PSEs from baseline, $t(4) = 0.346$, $p = .747$, Cohen's $d = 0.155$; $t(4) = 3.551$, $p = .024$, Cohen's $d = 1.588$ for slow and fast; two-tailed).

Experiment 1B: Motor Adaptation: Duration and Speed Judgments

Participants made a series of fast or slow midair tapping movements below a screen (motor adaptation), then indicated which of two peripheral drifting gratings lasted longer or moved faster (see Figure 1A). Panel E of Figure 1 shows the data for perceived duration for a representative subject: relative to baseline (dashed function), fast tapping (black) caused a clear rightward shift of the psychometric function and slow tapping (gray) a similar leftward shift: fast hand tapping decreased perceived duration of stimuli presented around the tapping area and slow adaptation increased it by similar amount. Unlike visual adaptation, motor-adaptation did not affect perceived speed: the psychometric functions for adaptation to both fast and slow tapping (black and gray, respectively) were both superimposed on the baseline condition (dashed) as shown in Figure 1D. In line with that, Figure 1F (right bars) shows that motor adaptation distorted estimates for visual stimuli duration to a similar extent as visual adaptation, whereas, on the other hand, aftereffects for the estimates of perceived speed were on average nonexistent, despite high variability across subjects.

A 2 (level of adaptation: high or low) \times 2 (task: speed or time) repeated measures ANOVA on adaptation effects (PSEs difference between adaptation and baseline normalized on baseline) revealed a statistically significant interaction, $F(1, 7) = 16.681$, $p = .005$, $\eta^2 = 0.704$, to indicate that adaptation effects for fast and slow tapping differed across speed and duration judgments. Series of post hoc t tests reveals that while in case of duration judgment both fast and slow tapping triggered significant (and opposite) PSEs shifts compared to the baseline, $t(7) = 5.4$, $p < .001$, Cohen's $d = 1.9$; $t(7) = 3.5$, $p = .009$, $d = 1.3$ for slow and fast; two-tailed); for speed, neither adaptation levels caused estimates to change from baseline, $t(7) = 0.117$, $p = .910$, Cohen's $d = 0.041$; $t(7) = 0.472$, $p = .651$, Cohen's $d = 0.167$ for slow and fast; two-tailed).

The results suggest that motor and visual-motion adaptation may trigger different kinds of duration aftereffects. In line with many previous reports, adaptation to fast visual motion compressed perceived duration of the adapted stimulus, while slow motion had no effect on duration. On the other hand, adaptation to both fast and slow tapping yielded symmetric effects on visual duration, of similar magnitude. These differences in the aftereffects triggered by motor or visual motion adaptation are clearly shown in Figure 2, where adaptation effects are shown as PSEs shift from baseline. Adaptation to fast and slow tapping yielded

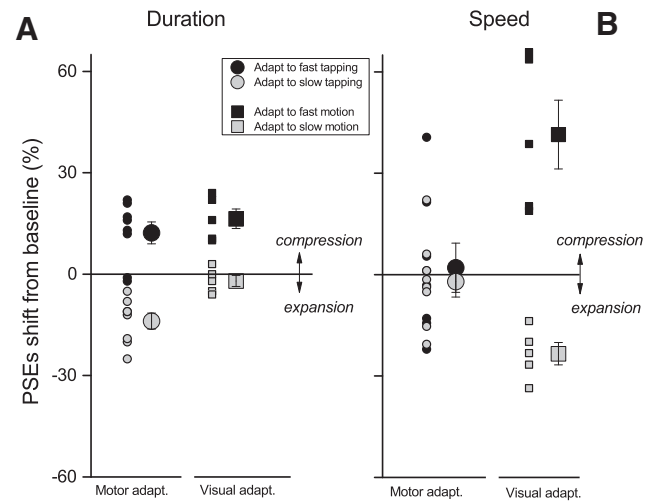


Figure 2. The effect of visual and motor adaptation on perceived duration and speed. (A) Duration distortions induced by adaptation (see methods) to slow and fast visual-motion or midair tapping (stars indicate the magnitude of adaptation averaged across participants, open circles single-subject data). Positive values indicate that test stimuli were perceived as shorter (duration compression), negative values longer (duration expansion). Adapting to fast and slow midair tapping induced symmetrical effects on perceived duration. Adapting to slow tapping caused duration expansion while fast tapping caused compression (gray and black circles). However, visual motion only induced duration compression only for high adaptation (black squares), with slow visual motion adaptation not affecting perceived duration (gray squares). (B) The effect of motor and visual adaptation on visual stimuli perceived speed. On average, motor adaptation did not affect perceived speed of visual stimuli subsequently presented in the adapted location while, as expected, adaptation to fast or slow visual motion yielded symmetrical and robust speed aftereffects for the adapted stimuli. PSE = point of subjective equality.

PSEs changes of about 15%, but neither kind of motor adaptation distorted perceived speed of the visual stimuli. On the contrary, adaptation to fast and slow visual motion dramatically distorted the perceived speed of the adapted stimuli (up to 40%) while perceived stimulus duration was affected only by adaptation to fast visual motion and not by adaptation to slow visual motion.

The results so far suggest that action and perception are intimately linked in the processing of visual time. However, it may be argued that the interaction is not perceptual but occurs at later, post-perceptual or decisional stages. The first evidence against this possibility is that subjects were required to discriminate between two stimuli, one displayed in the adapted and the other in a neutral location. If adaptation triggered a cognitive bias, it would have affected both stimuli (the test and the neutral stimulus), cancelling out all adaptation aftereffects. Another point is that the Weber fractions (width of psychometric functions normalized by PSEs) for the three experimental conditions (baseline, high and low motor adaptation) were all similar: a one-way repeated measures ANOVA with adaptation conditions as a factor and Weber Fractions as dependent variable, the Weber Fractions in the three conditions were far from being statistically significant different, $F(2, 7) = 0.599$, $p = .563$, $\eta^2 = 0.08$. This does not prove, but

does suggest, that similar perceptual and decisional strategies were used in the three conditions, unlikely if different cognitive strategies came into play after adaptation.

Lastly, the differential effect of motor adaptation on duration and speed (but also for numerosity, described below) cannot be explained by task-difficulty. Figure 3 shows that Weber Fractions measured in the baseline condition were similar across tasks (WFs: 0.29 ± 0.04 , 0.20 ± 0.03 , 0.23 ± 0.03 , 0.16 ± 0.02 for duration, speed, spatial, and temporal numerosity, see the data distribution along the abscissa). As participants overlapped only partly across tasks, Weber Fractions were analyzed by independent sample *t* tests (duration vs. speed: $t = 1.40$, $p = .178$, Cohen's $d = 0.627$; duration vs. spatial numerosity: $t = 0.829$, $p = .491$, Cohen's $d = 0.393$; duration vs. temporal numerosity: $t = 2.135$, $p = .049$, Cohen's $d = 1.01$; speed vs. spatial numerosity: $t = 0.69$, $p = .5$, $d = 0.328$; speed vs. temporal numerosity: $t = 0.882$, $p = .391$, Cohen's $d = 0.419$; temporal vs. spatial numerosity: $t = 1.836$, $p = .088$, Cohen's $d = 0.918$). Interestingly, in all experimental conditions, WFs remained similar after adaptation. Figure 3 shows WFs in the baseline condition (x-axis) plotted against WFs measured after adaptation (y-axis). As shown by the averaged data (filled symbols) all scattered along the diagonal line, precision in the discrimination task was not significantly affected by adaptation to self-produced motor patterns.

Experiment 2: Visual and Motor Adaptation Spatial Selectivity

The previous results show that motor adaptation affects perception in a spatially specific manner. In the next series of experiments, we measured the spatial tuning of both visual-motion adaptation and motor adaptation on visual speed and duration, as well as for a related parietal function, *numerosity* (spatial and temporal). We systematically varied the distance between the

position of the adapters (drifting gratings, dot clouds, flash sequences or tapping hand) relative to the test stimuli (same visual features as adapters), in separate sessions.

The results are shown in Figure 4. Panel A–D shows the magnitude of visual and motor adaptation (normalized difference of slow and fast, eqn 1) as a function of spatial separation of adapter and the test stimulus, ranging from 0 to 30°. In all cases where there was an adaptation effect it dropped off smoothly with increasing spatial distance. As observed previously, adapting to visual motion (gray curve and data points) or motor tapping (black curve and data points) affected perceived duration of visual stimuli presented to the adapted location (0° distance) by up to a factor about 0.20 and 0.30, respectively. However, for both visual and motor adaptation, duration aftereffects faded off with increasing spatial distance between the adapter and the test stimulus locations. Adaptation decreased more rapidly for visual than motor adaptation, implying tighter tuning. A similar effect was seen for adaptation of simultaneous and sequential numerosity: In both cases adaptation decreased steadily with spatial separation, again with tighter tuning functions for visual than motor adaptation. For speed, there was strong spatial tuning for visual adaptation, but as we saw before, there was no effect of motor adaptation.

To quantify the adaptation selectivity, we fitted average adaptation data with Gaussian functions centered at zero and free to vary in amplitude, baseline, and width (σ). Amplitude is an index of maximal strength, and width of the spatial tuning spread. Both indexes were significantly higher than zero for all conditions (all $p < .05$) except motor adaptation to visual speed. Motor adaptation was greater than visual adaptation for duration and temporal numerosity, while for spatial numerosity visual adaptation was higher. In all cases the selectivity to motor adaptation was generally broad, around 12°, whereas visual adaptation was sharper, around 4° for all conditions.

Experiment 3: Selectivity in External or Body Space?

The results of the previous experiment suggest that adaptation aftereffects are centered on the tapping position. However, it remains an open question whether the selectivity is in hand-centered or external space coordinates. To address this, we tested a new condition in which subjects tapped with their right (dominant) hand either 10° to the left of a central fixation point, or 10° to the right (similarly to one of the conditions investigated in Anobile et al. (2016)). In this way, the hand was positioned either at the reference (left) or test (right). If the adaptation is selective in external (rather than body) space, tapping left or right should have opposite effects on the match between reference and test: If in hand coordinates, changing the tapping position should have no effect.

Figure 5 shows that the selectivity was in external space. Tapping on the reference (left) side distorted perceived duration of the reference stimulus (increasing or decreasing perceived duration, depending on tapping speed), while tapping on the test stimulus (right) side distorted the test stimulus in a similar way (producing an opposite effect). The amount of adaptation was similar, $t(9) = 1.14$, $p = .3$, when the hand was crossed (factor of 0.11 ± 0.23) to when it was uncrossed (factor of 0.13 ± 0.17). This result confirms that like numerosity (Anobile et al., 2016), the selectivity for motor adaptation is in external, not body space.

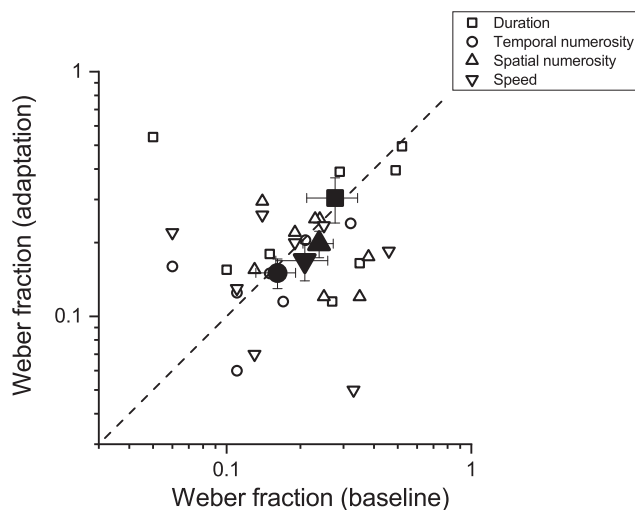


Figure 3. Discrimination thresholds across perceptual tasks. Weber Fraction (just notable difference [JND]/point of subjective equality [PSE]) measured in the baseline (abscissa) and after adaptation (ordinate) for four different perceptual tasks. Small open symbols indicate single subject data, averages across subjects by the filled symbols.

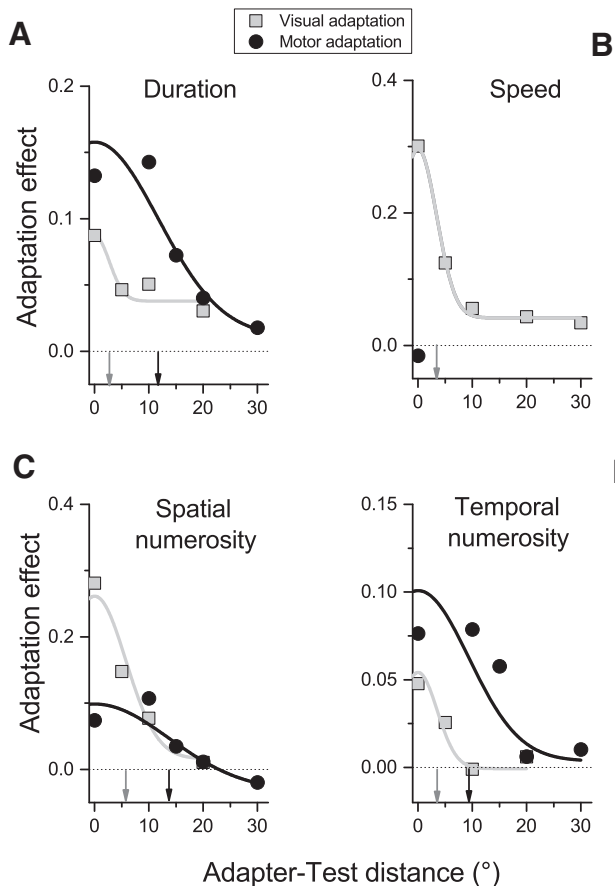


Figure 4. Spatial tuning of visual and motor adaptation. Distortions of perceived duration (A), speed (B), spatial (C), and temporal numerosity (D) induced by either visual (gray squares) or motor (black circles) adaptation as a function of spatial distance between adapter and test stimuli. Adaptation effect was measured as the normalized difference in points of subjective equality obtained after slow and fast adaptation (see Equation 1). Subject average data (symbols) were fitted with Gaussian functions (gray and black curves). The arrows on the abscissa indicate the width of the best Gaussian fit.

Discussion

This study shows that estimates of visual duration are strongly biased after adapting to repetitive finger tapping: fast midair tapping decreases apparent duration, slow tapping increases it. The effect is spatially selective, in external rather than hand-centered coordinates, and does not generalize to lower level visual properties, such as motion speed. We also replicated previous findings showing that spatial and temporal numerosity can be adapted by hand tapping and reported the spatial selectivity of these effects.

There has been a long-standing scientific interest in the connection between the motor and perceptual systems in sensing duration. Many studies (some outlined in the introduction) have described fascinating and robust cross-modal interference, with action grossly shaping subjective passage of time. The current study adds to these by showing robust transfer of sensory adaptation between the motor and the visual system, providing a strong signature of shared mechanisms in time perception.

Importantly, aftereffects were local, occurring only near the tapping region. The magnitude of motor adaptation aftereffects scaled down with the distance between the tapping hand and the test stimulus. We interpreted this result to reflect a well delimited spatial area, or receptive field, in which motor and visual signals interact. Tapping distorted perceived duration of either the right side or left side in the crossed-hand condition (see Figure 5), suggesting that the reference frame of motor adaptation is coded in external world coordinates, consistent with our previous study on numerosity perception (Anobile et al., 2016).

Previous studies show that duration (Burr et al., 2007; Fornaciai et al., 2016; Johnston et al., 2006), numerosity (Arrighi et al., 2014; Schwiedrzik et al., 2016), and spatial position (Turi & Burr, 2012) can all be locally distorted by sensory adaptation. Interestingly, all those magnitudes were distorted by visual adaptation to translating motion, showing interesting interactions between time, numerosity and motion. This fits well with other evidence for a link in these dimensions, such as the fact that all three magnitudes are similarly compressed during saccadic eye movements (Burr et al., 2010).

That adaptation occurs within a world-centered reference frame suggests that the effects are probably occurring at a fairly high level of processing (Burr, Cicchini, Arrighi, & Morrone, 2011; Burr et al., 2007; Schwiedrzik et al., 2016; Turi & Burr, 2012). Many behavioral and imaging studies in humans have shown the role of parietal areas in numerosity, time and space perception (Bueti & Walsh, 2009), areas that show a strong spatiotopic BOLD response (d'Avossa et al., 2007). In nonhuman primates, Sawamura, Shima, and Tanji (2002) has described cells in monkey parietal cortex able to keep track of the number of self-produced actions, and Leon and Shadlen (2003) reported time-tuned neurons in macaque parietal cortex.

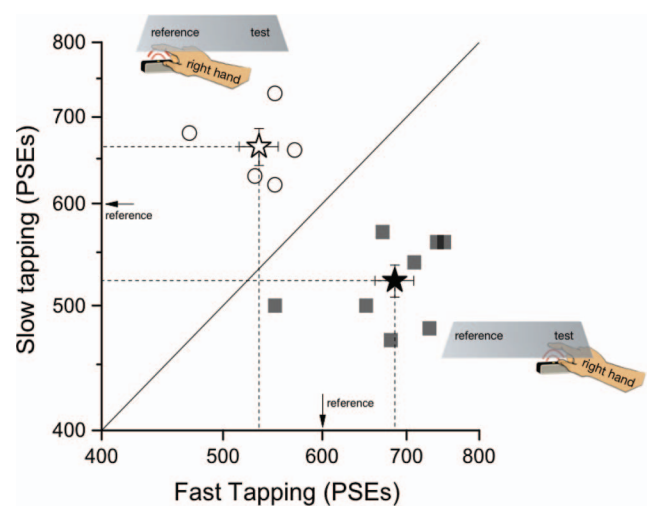


Figure 5. The effect of motor adaptation in left and right space on visual duration. Points of subjective equality (PSEs) for two separate groups of participants when tapping with the right hand on the test stimulus (right visual hemifield, constant duration [circles]) or the reference location (left visual field, variable duration [squares]). The abscissa shows PSEs after adaptation to fast tapping, the ordinate after adaptation to slow tapping. Stars indicate averaged values across participants, error bars standard errors of the mean. See the online article for the color version of this figure.

Motor adaptation might act on vision by recalibrating the activity of parietal (visual) areas. Motor and parietal regions are reciprocally interconnected, making it possible that visual parietal processing is actively calibrated by motor history (adaptation). The involvement of relatively high-level areas such as parietal cortex is also in line with the estimates of the widths of the “perceptive fields” for motor adaptation, around 12° half-width, half-height. This estimate is compatible with a previous study on visual numerosity adaptation (Zimmermann, 2018), and with receptive field sizes measured physiologically in macaque parietal cortex (Blatt, Andersen, & Stoner, 1990). This hypothesis is also interesting in the light of the lack of effect of motor adaptation on visual speed, a feature that can be encoded by earlier visual areas, including V1 (Bisti, Carmignoto, Galli, & Maffei, 1985; Foster, Gaska, Nagler, & Pollen, 1985). In this case, the visuomotor recalibration assumption predicts that the motor feedback would not propagate back to all visual brain areas. Moreover, given that the effect of motor adaptation does not generalize to all visual features (leaving motion speed unchanged) and shows a precise reference frame in “world coordinates” (aftereffects constrained around the tapping area even when subjects tapped with the hand crossed), the present data suggest that this effect is perceptual rather than cognitive in nature.

That numerosity and time can both be similarly adapted by motor tapping is highly consistent with much evidence and many theories—such as ATOM, A Theory Of Magnitude (Walsh, 2003), suggesting that the perception of time and numerosity—and space—share neural processing. Moreover, ATOM theory proposes a key role of action in linking those magnitudes; our data support this last core hypothesis. Along these lines, it would be interesting to test whether perceived visual space is also distorted by motor adaptation.

Why does fast tapping compress visual time while slow tapping expands it? At this stage, we can only speculate how the visuomotor system interprets such metrics. A speculative hypothesis is that the perceptual and the motor systems interact through a normalization process. In other words, the “weight” of the motor adaptation signals would be normalized by the “capacity of the system” a canonical principle in neural computations, thought to apply across sensory modalities and brain regions (Carandini & Heeger, 2012). In the fast adaptation condition, in which subject performed the highest number possible of repetitions of the tapping routines, this relatively high magnitude of motor signals would rebound on visual estimates to bias them toward an underestimation of the stimuli in the scene. On the other hand, in the low motor adaptation tapping movements occurred at a rate much lower than typical motor routines, so visual estimates would be biased by the low motor activity toward an overestimation. Despite we asked our subjects to tap on air to minimize tactile feedbacks arising by the contact of the finger with a rigid surface and prevent them to see their moving hand to abolish all visual feedbacks, it might still be the case that the hand motion yielded some proprioceptive signals that might have contributed to define motor adaptation aftereffects.

Taken together the present data seem to support in general the ATOM theory (Walsh, 2003), and its idea of a shared representation between time, numerosity and space, which would be used by the perceptual system to interact with actions planning and execution. Indeed, within this theoretical framework, the reported motor adaptation aftereffects on the processing of stimulus dura-

tion and numerosity are well accounted for. But what might be the rationale to combine the adapting motor signals with visual stimuli estimates? One possibility concerns reports that visual duration is influenced by the number of events. Several researchers (Brown, 1995; Gibbon, 1977; Kanai et al., 2006) reported that flickering visual stimuli are perceived to last longer than static stimuli, suggesting that the visual clock is strongly influenced by temporal frequency (number of events in time). Kanai et al. (2006) went on to show that temporal frequency is a critical element in determining visual-motion adaptation of duration, rather than motion per se. As explained above, a similar process may also apply to the motor system: “fast” tapping might be interpreted/encoded as a “long” duration, and thus induce negative visual duration aftereffects on moving stimuli (compared to “slow” or no actions). Consistent with this hypothesis, it is possible that the motor adaptation reflects cross-modal adaptation between sequential motor numerosity and visual motion duration. This idea is in line with the fact that motor adaptation had a relatively greater effect on duration and temporal numerosity than on spatial numerosity. However, the number of events might not be the only variable to play a critical role in stimuli duration estimates, as temporal dynamics may also be important. Binetti, Lecce, and Doricchi (2012) have shown that streams of auditory impulses containing exactly the same number of changes (events) were overestimated or underestimated when auditory sequences defined an accelerating or decelerating profile. A similar process could occur in vision, an idea easily testable.

Another interesting question is whether distortions of visual time induced by motor adaptation are the consequence of a change in the activity of a specific associative area (like Intraparietal Sulcus) or the result of a change in temporal processing inherited along multiple levels of the visual hierarchy (Webster, 2011, 2015). For example, Heron, Fulcher, Collins, Whitaker, and Roach (2019) have recently demonstrated that adaptation-induced changes in duration estimates spread along several stages in the visual processing hierarchy. In particular, they reported that duration encoding mechanisms at monocular, depth-selective, and depth-invariant stages all play a distinct role in defining duration aftereffects. Unfortunately, our data do not speak to this question. Motor adaptation might distort neural processing at multiple levels, and the signals available at any level might define how responses are adapted at other levels. Moreover, as motor adaptation has been reported to affect stimulus numerosity as well as duration, and these two dimensions have been reported to covary with each other, it might also be the case that motor adaptation aftereffects arise from a combination of sensitivity changes in the processing of multiple visual features. However, the fact that the amplitude of adaptation of the different perceptual dimensions varies considerably and is far from being symmetrical (i.e., motor adaptation affects temporal numerosity or duration at a greater extent than spatial numerosity) implicates a complex pattern of interactions between differently tuned areas within the processing hierarchy. It is difficult to account quantitatively to the range of aftereffects with activity changes within a single, localized brain mechanism.

To conclude, over the last few decades many studies have suggested that vision and action are linked (Arrighi, Cartocci, & Burr, 2011; Goodale & Milner, 1992), that action plays a key role in time estimation (Haggard et al., 2002; Hagura et al.,

2012; Tomassini et al., 2012, 2014, 2018; Tomassini & Morrone, 2016; Yokosaka et al., 2015), and that time, numerosity, and action share common mechanisms (Tomassini et al., 2018). Our study strongly supports all these hypotheses and, critically, adds evidence for the existence of multiple and local motor-visual clocks.

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Received February 28, 2019

Revision received July 3, 2019

Accepted October 1, 2019 ■

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