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Active movement restores veridical event-timing after tactile adaptation

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Tomassini A, Gori M, Burr D, Sandini G, Morrone MC. Active movement restores veridical event-timing after tactile adaptation. *J Neurophysiol* 108: 2092–2100, 2012. First published July 25, 2012; doi:10.1152/jn.00238.2012.—Growing evidence suggests that time in the subsecond range is tightly linked to sensory processing. Event-time can be distorted by sensory adaptation, and many temporal illusions can accompany action execution. In this study, we show that adaptation to tactile motion causes a strong contraction of the apparent duration of tactile stimuli. However, when subjects make a voluntary motor act before judging the duration, it annuls the adaptation-induced temporal distortion, reestablishing veridical event-time. The movement needs to be performed actively by the subject: passive movement of similar magnitude and dynamics has no effect on adaptation, showing that it is the motor commands themselves, rather than reafferent signals from body movement, which reset the adaptation for tactile duration. No other concomitant perceptual changes were reported (such as apparent speed or enhanced temporal discrimination), ruling out a generalized effect of body movement on somatosensory processing. We suggest that active movement resets timing mechanisms in preparation for the new scenario that the movement will cause, eliminating inappropriate biases in perceived time. Our brain seems to utilize the intention-to-move signals to retune its perceptual machinery appropriately, to prepare to extract new temporal information.

time perception; touch; adaptation; action; tactile velocity

FOR A SUCCESSFUL INTERACTION with the external world, our motor system must have access to accurate information about time. How the brain encodes the temporal properties of sensory events remains much of a mystery. Over the last decade, research on time perception has highlighted its striking susceptibility to distortions (for review, see Eagleman 2008). The inherent plasticity, instability, and lack of robustness of our perceptual sense of time suggest that the underlying neural mechanisms are unlikely to be independent of the rest of the nervous system. Early theories suggesting a dedicated and centralized clock (Gibbon et al. 1997; Treisman 1963) have been challenged by evidence that timing in the subsecond range relies on multiple, distributed, modality-specific mechanisms (Johnston et al. 2006; Morrone et al. 2005). Temporal information may be extracted by local sensory processing and represented implicitly in the pattern of activity of distributed neural networks (Buonomano and Merzenich 1995; Eagleman 2008; Karmarkar and Buonomano 2007).

Several lines of evidence fit well with this suggestion. Duration judgments are highly susceptible to manipulations of low-level features of the stimulus (Kanai et al. 2006; Terao et al. 2008; Xuan et al. 2007). For example, event-time is distorted by sensory adaptation. Johnston et al. (2006) showed that adaptation to high-frequency flickering or moving stimuli decreases the perceived duration of subsequently presented visual stimuli. Interestingly, the effect is spatially confined to the previously adapted location, suggesting multiple, independent clocks within the visual system (Ayhan et al. 2009; Burr et al. 2007). Recently, vibrotactile adaptation has been shown to cause temporal compression for tactile stimuli (Watanabe et al. 2010), suggesting that similar operating principles and mechanisms may underlie the encoding of duration across different modalities.

Action also influences the perception of visual and tactile time in many different ways. Temporal dilation ("chronostasis") has been shown to occur for sensory events following many types of voluntary actions, including arm movements (Park et al. 2003; Yarrow et al. 2001; Yarrow and Rothwell 2003). Temporal delays, compression, and even perceived inversion of temporal order have been documented around the time of saccadic eye movements (Binda et al. 2009; Morrone et al. 2005), probably a consequence of a visuo-motor mechanism that mediates perceptual stability. The brain faces similar problems when it has to integrate tactile signals with action: it has to take into account the delays between tactile stimulation and the signals generating the action, as well as predicting the position of the stimulated skin in external space during the action. In addition, like visual signals during eye movements, the delays in tactile sensation and transmission can be large and variable, up to hundreds of milliseconds.

The acquisition of tactile information from the environment is an active process, governed and structured by the movement of the body in space. Time in the order of tens to hundreds of milliseconds is important for motor behavior, and it is tightly linked to sensory processing. Here, we asked whether the movement of the body can affect the processing of temporal information in the somatosensory system. To test this hypothesis, we exploited a temporal distortion induced by tactile adaptation. We adopted the paradigm previously used in vision (Burr et al. 2007), substituting drifting visual gratings with drifting tactile gratings. To investigate the role of motor commands and that of reafference signals from body movement we also tested whether active and passive movements of the body differently alter event-time adaptation.

MATERIALS AND METHODS

Approval. All participants gave written informed consent prior to testing. The study was approved by the local ethics committee (Azienda Sanitaria Locale Genovese N.3).

Apparatus and stimuli. Tactile stimuli were generated on physical wheels (diameter = 10.5 cm; width = 3 cm) etched with a corrugated

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grating (3 cycles/cm) of alternating ridges and grooves of equal widths. The two wheels were driven at specific velocities by two independent computer-controlled motors. The velocity of the wheels was calibrated by means of a visual tracking system (Optotrak Certus Motion Capture System, NDI Northern Digital), showing only minor deviation from the ideal constant velocity stimuli.

Subjects rested their fingers on the wheels with the gratings oriented perpendicular to the long axis of the finger, with direction of the motion randomized between trials. The right index finger rested on the nearest wheel, and the left index finger on the other wheel, just behind the first (Fig. 1*A*). To mask visual and acoustic cues, subjects kept their eyes closed and listened to white noise through headphones.

Motion adaptation: duration and speed judgments. Participants adapted to tactile motion by resting their right index finger on the first wheel rotating at 15 cm/s (45 Hz) for 45 s at the beginning of each experimental session, with 8 s of "top-ups" between trials. The wheel inverted rotation direction every 4 s to avoid direction-specific adaptation, with the initial direction of movement randomized between trials. Two seconds after adaption was complete, the test stimulus was presented on the same wheel for a duration that varied between trials, chosen by the adaptive QUEST algorithm (Watson and Pelli 1983). After a short pause of 500 ms, the standard stimulus was delivered to the left index finger on the second wheel for 600 ms at 7.5 cm/s (22.5 Hz). In most conditions, the speed of the test was adjusted to appear to be the same as the standard, except for one control condition where test and standard had the same physical speed (7.5 cm/s). Participants reported verbally which of the two stimuli was perceived to last longer. The direction of movement for both the test and standard was matched (along the proximal-distal axis of the finger) to the initial direction of the adapting stimulus in each trial.

Speed judgments were carried out in a preliminary phase to measure the amount of reduction in perceived speed following adaptation.

Perceived duration and speed of stimuli are known to be strongly interdependent: faster moving stimuli are perceived to last longer (Kanai et al. 2006; Kaneko and Murakami 2009; Tomassini et al. 2011). Motion adaptation causes a reduction in apparent speed (Thompson 1981), which could in turn cause temporal compression. To avoid this possibility, in most conditions we matched the apparent speed of the test and standard stimulus using the same procedure as Burr et al. (2007). To determine the matched speed, the experiment was similar to that described above, except that participants judged which of the two stimuli appeared to move faster. The speed of the test was varied from trial to trial (again using the QUEST method) to generate a psychometric function, whose median gave an estimate of matched speed. The physical speed of the test was then adjusted in the

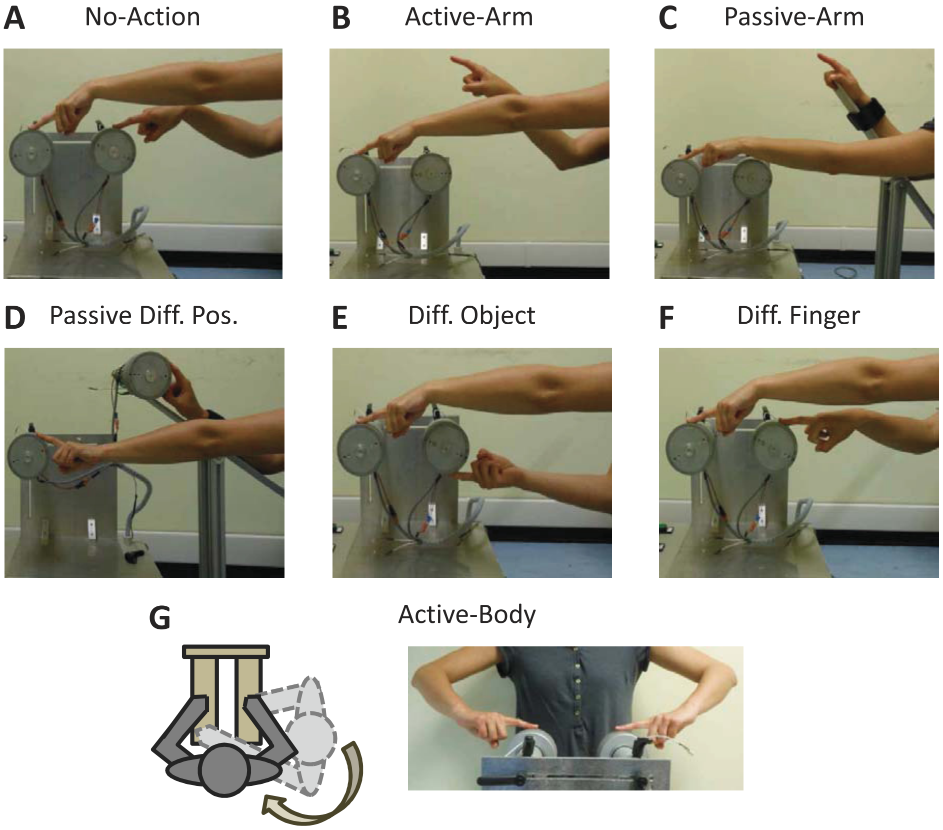

Fig. 1. Illustration of the experimental conditions. *A*: No-Action condition: the test stimulus is presented to the adapted finger (right index), held in the same position on the wheel surface (upper surface). *B*: Active-Arm condition: at the end of adaptation, the subject lifts his/her right arm and replaces it in the adapted position (upper surface of the wheel) before the test stimulus starts. *C*: Passive-Arm condition: at the end of adaptation, the arm of the subject is lifted and replaced by the experimenter with a lever. For both Active and Passive arm conditions, adapted and tested fingers (right index) and spatial positions (upper surface of the wheel) are identical. *D*: Passive Different-Position condition: after adaptation, the arm of the subject is lifted by the experimenter with a lever and maintained in this position until the end of the trial. The first wheel is fixed to the lever so that it moves jointly, and the test stimulus is presented in a different position relative to the adaptor. The arm is then replaced in the initial position and the next adaptation phase starts. *E*: Different-Object condition: the test stimulus is presented on the same finger (right index) as the adaptor, but moved to a different position on the wheel (lower surface). *F*: Different-Finger condition: the test is presented in the same position on the wheel (upper surface), but on a different finger (right middle finger). *G*: Active-Body condition: after adaptation, subjects take a step and rotate 90 degrees to face the wheels. The position of the right index fingertip on the first wheel remains unchanged; the left index finger rotates on the second wheel resulting in a mirror position relative to the right index. During the movement, both the right and left fingers are always kept in contact with the surface of the wheels. The subject's final position implies that the first and second wheels are situated on the right and left side of the body midline, respectively.

duration task, separately for each subject and condition, to match the apparent speed of the standard.

We ran seven different adaptation conditions (Fig. 1), and four baseline conditions. In the No-Action condition, nothing occurred between adaptation and test: the test stimulus was presented to the adapted finger (right index), held in the same position on the wheel surface (upper surface) (Fig. 1*A*). In two separate conditions, a movement was performed between the adaptation and test phase, keeping the starting and final positions identical. In the Active-Arm condition, the subject lifted his/her right arm at the end of adaptation and replaced it in the original position (Fig. 1*B*), whereas in the Passive-Arm condition, the arm of the subject was lifted and replaced by the experimenter with a lever (Fig. 1*C*). Movement execution was constrained by the 2-s pause between the end of the adaptor and the presentation of the test stimulus. Subjects were instructed to perform arm movements of ~30 cm in amplitude at the correct speed that allowed them to replace their finger on the wheel before the beginning of the test stimulation. We measured the dynamics of the movement in the active and passive conditions with motion tracking cameras (Optotrak Certus Motion Capture System, NDI Northern Digital) in one subject to validate the technique (28 trials for each condition). Peak velocity and movement duration were non-significantly different in the two conditions [$t_{(54)} = 0.164$, $P = 0.870$ for peak velocity; $t_{(54)} = -1.749$, $P = 0.086$ for movement duration; independent samples *t*-test].

In the Passive Different-Position condition, a change in spatial position between adaptation and test was induced by the experimenter lifting passively the subject's arm with a lever, and maintaining it in this position until the end of the test phase (Fig. 1*D*). The arm was then replaced in the initial position and the next adaptation phase started. The first wheel was fixed to the lever and moved jointly so that the test stimulus could be presented at a different spatial location from the adaptor. The No-Action, Active-Arm, and Passive-Arm conditions were also tested with no adaptation phase to yield baseline measurements both with and without velocity match. Here the adapting stimulus was replaced by an on-off 50-ms movement of the first wheel that marked the beginning of each trial.

We tested three further conditions where an active movement was interspersed between the adaptation and test phase. In the Different-Object condition, the test stimulus was presented on the same finger (right index) as the adaptor, but moved to a different position on the wheel (lower surface) (Fig. 1*E*), while in the Different-Finger condition it was presented in the same position on the wheel (upper surface), but on a different finger (right middle finger) (Fig. 1*F*). Finally, in the Active-Body condition, subjects took a step and rotated 90 degrees to face the wheels. In this way, the relative position between the subject and the wheels varied, although the position of the right index fingertip on the first wheel remained unchanged; the left index finger rotated on the second wheel resulting in a mirror position relative to the right index (Fig. 1*G*). During the movement, however, both the right and left finger were always kept in contact with the surface of the wheels. The subject's final position implied that the first and second wheels were situated on the right and left side of the body midline, respectively. No baselines were run for these conditions. In all these conditions, the movement had to be completed within 2 s.

Psychometric functions (proportion correct as a function of time or speed) were fitted with a cumulative Gaussian function, asymptotic at 0 and 1; the point of subjective equality (PSE) and the differential threshold (SD) were given by the mean and standard deviation of the psychometric function, respectively. The standard errors were estimated by bootstrap (Efron and Tibshirani 1993).

A total of 23 healthy subjects participated in the experiment (13 females and 10 males), including two authors (A. Tomassini and M. Gori). All subjects had normal tactile perception and were right handed by a self-report. Seventeen subjects (15 naïves and the 2 authors) were tested in the No-Action and corresponding Baseline condition. Eight participants from the previous group (6 naïves and the 2 authors) completed also the Active-Arm and Passive-Arm conditions as well as the corresponding baselines. Three out of eight original subjects plus one new subject repeated the No-Action and Active-Arm conditions (and corresponding baselines) without the velocity matching, as control conditions. Four subjects out of eight (2 authors and 2 naïve) completed also the Passive Different-Position condition and the relative baseline. The Different-Finger and Different-Object conditions were performed by five naïve subjects. The two authors and two naïve subjects were tested also in the Active-Body condition.

Data were collected in separate sessions of 30 trials each. Most of the subjects completed 60 trials for the No-Action, Active-Arm, and Passive-Arm conditions and the relative baselines; a minimum of one session was run for the other subjects and conditions.

RESULTS

Participants adapted to tactile motion, then compared either the speed or the duration of a test stimulus presented to the adapted finger with a standard stimulus presented to the unadapted finger. The perceived duration of tactile stimuli was strongly reduced after adaptation: the test stimulus needed to be of duration 725 ms (± 25 ms) to match the 600-ms standard [$t_{(16)} = 4.834$, $P < 0.0001$; 1 sample *t*-test; Fig. 2*A*]. The amount of reduction varied considerably across subjects (with 5 subjects out of 17 showing no effect), but on average was ~20%.

Perceived speed was also considerably reduced after adaptation: on average, the test needs to be 11 cm/s (± 0.39) to match the 7.5 cm/s of the standard [$t_{(16)} = 9.786$, $P < 0.0001$; 1 sample *t*-test; Fig. 2*A*]. The apparent slowing of tactile motion after adaptation was more consistent across subjects, with only one exception showing no adaptation of either speed or duration. To control for temporal-order effects or other possible systematic biases, we measured baseline speed and duration judgments under the same conditions without adaptation (Fig. 2). Figure 2*A* shows that the baseline measures were not significantly different from veridical [$t_{(16)} = 1.758$, $P = 0.098$ for speed; $t_{(16)} = 0.984$, $P = 0.34$ for duration; 1 sample *t*-test], but significantly different from the adaptation conditions [$t_{(16)} = -8.265$, $P < 0.0001$ for speed; $t_{(16)} = -5.891$, $P < 0.0001$ for duration; paired samples *t*-test].

Both duration and speed discrimination were slightly (but significantly) worse in the adaptation compared with the baseline condition, as indicated by the SDs in Fig. 2*B* [$t_{(16)} = -2.326$, $P = 0.034$ for duration; $t_{(16)} = -2.066$, $P = 0.055$ for speed; paired samples *t*-test].

In the No-Action condition described above, no action intervened between adaptation and test. To examine the importance of motor action on adaptation-induced changes to perceived duration, we introduced various conditions where a motor act was interspersed between adaptor and test. First, we tested an active condition, where the subject lifted his or her right arm after adaptation and replaced it in the original position before the test stimulus started. Adapted and tested spatial positions were identical. Figure 3*A* shows that the interspersed active movement completely abolished the adaptation-induced temporal compression [the average reduction of the perceived duration relative to the physical duration is 8 ± 16 ms; $t_{(7)} = 0.518$, $P = 0.620$, 1 sample *t*-test].

To dissociate the role of motor commands from that of reafferent signals caused by the movement, we also tested a passive condition, where the experimenter moved the subject's

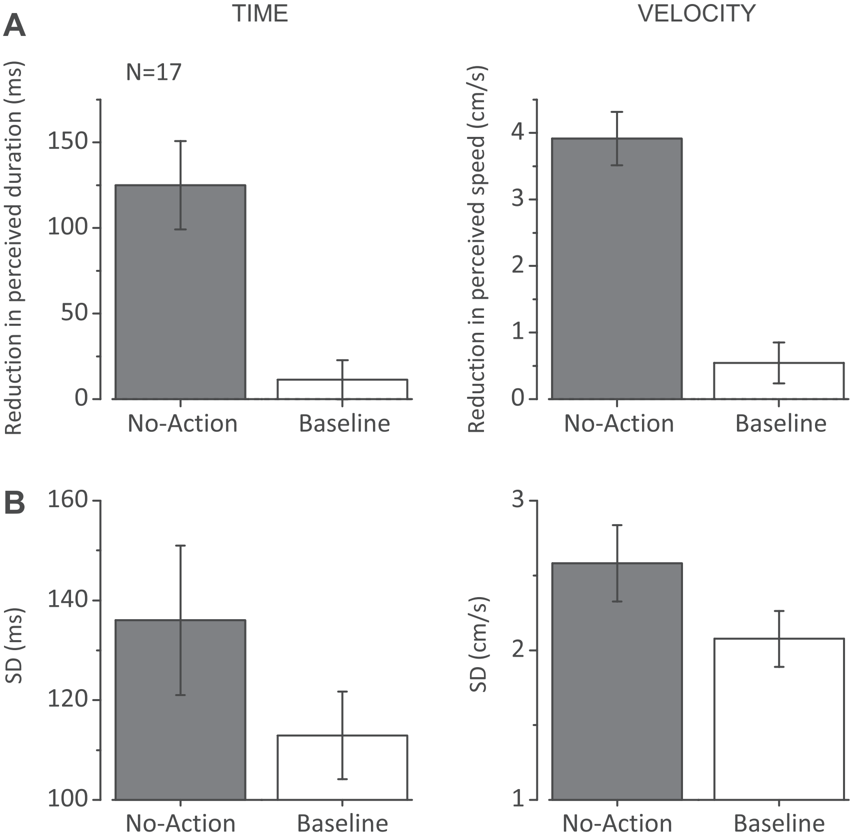

Fig. 2. *A*: average reduction in point of subjective equality (PSE), defined as the PSE of the probe minus the physical duration (*left*) or speed (*right*) in the No-Action and Baseline conditions. *B*: average standard deviations for duration (*left*) and speed (*right*) in the No-Action and Baseline conditions. Error bars represent SE.

arm (by means of a lever; see Fig. 1*C*) by the same magnitude (~30 cm) and approximate speed. The passive movement did not affect the adaptation-induced changes in apparent duration: they were as strong as they were in the no-action adaptation condition [No-Action = 192 ± 24 ms; Passive-Arm = 158 ± 24 ms; means ± SE; $t_{(7)} = 2.133$, $P = 0.07$, paired samples *t*-test; Fig. 3*A*, *left*]. Interestingly, although active movement abolished the adaption-effect on perceived duration, it did not affect apparent speed. All three adaptation conditions caused comparable changes in perceived speed [$F_{(2,14)} = 0.645$, $P = 0.54$, ANOVA for repeated measures; Fig. 3*B*, *left*]. This suggests that active movement has a specific effect on the neural mechanisms that encode the duration of tactile stimuli rather than a more general effect on somatosensory processing.

Baseline conditions were also run with both active and passive arm movements, showing no significant change of the perceived duration from the actual duration in both cases [Active-Arm = 4 ± 13 ms; Passive-Arm = 27 ± 26 ms; means ± SE; $t_{(7)} = 0.316$, $P = 0.762$; $t_{(7)} = 1.012$, $P = 0.345$; 1 sample *t*-test for the active and passive condition, respectively; Fig. 3*A*, *right*]. Speed judgments were mildly biased in the baseline conditions [Baseline = 1.05 ± 0.28 cm/s; Active-Arm = 1.21 ± 0.55 cm/s; Passive-Arm = 0.57 ± 0.49 cm/s; means ± SE; $t_{(7)} = 3.743$, $P = 0.007$; $t_{(7)} = 2.176$, $P = 0.066$; $t_{(7)} = 1.176$, $P = 0.278$; 1 sample *t*-test for the baseline, active, and passive condition, respectively; Fig. 3*B*, *right*], probably reflecting order effects. This effect tends to be greater in the active condition, but the difference across conditions was not significant [$F_{(2,14)} = 1.706$, $P = 0.21$; ANOVA for repeated measures].

Motor execution did not affect the precision of the discrimination either for duration or speed (Fig. 4). A 3 × 2 ANOVA was conducted on the SDs with Movement (no-action/active/passive) and Adaptation (adaptation/baseline) as within-subjects factors and showed no significant effect, indicating that active as well as passive movements did not either improve or deteriorate discrimination. To check if the effect of active movement on apparent duration is related to the change of apparent speed induced by adaptation, in four subjects we repeated the time duration experiment with matched physical (rather than perceived) velocity. Also, in this case the perceived duration after adaptation was significantly compressed (201 ± 75 ms; means ± SE), and an active movement restored it to almost veridical (75 ± 42 ms; means ± SE). Again, no difference between the no-action (39 ± 22 ms; means ± SE) and active condition (30 ± 23 ms; means ± SE) was reported for the baseline measures.

As passive movement did not affect adaptation, it allowed us to test whether the temporal compression is spatially selective, as has been shown in vision. After adaptation, the arm of the subject was moved passively to a different spatial location. The change in position induced by the passive movement did not alter the effect of adaptation on apparent duration, suggesting that tactile timing mechanisms are not selective in space (Passive Diff. Pos. = 216 ± 23 ms; means ± SE). Active movement per se seems to be the key determinant for the cancellation of the effect of adaptation on apparent duration.

Figure 5*A* plots the No-Action, Passive-Arm, and Passive Different-Position conditions against the Active-Arm condition, for all subjects. Data points lie well above the bisector line, indicating a much greater reduction in apparent duration

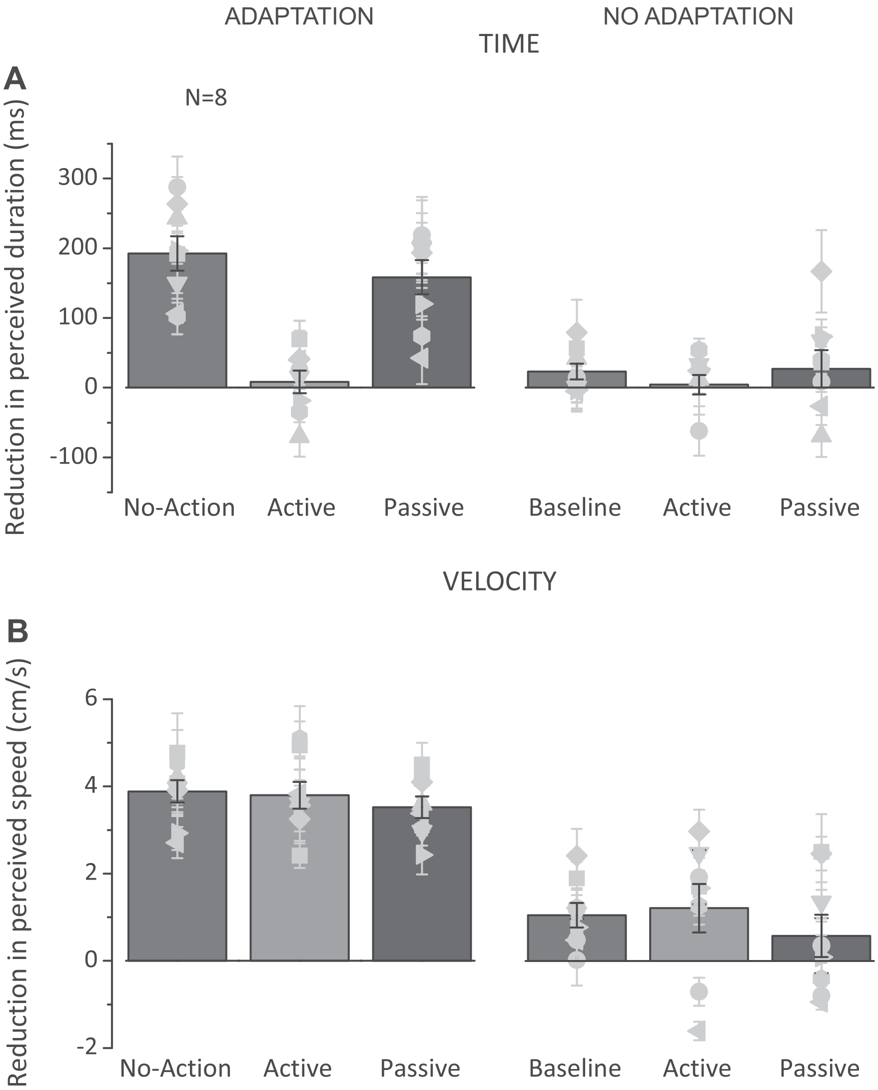

Fig. 3. Average reduction in perceived duration (*A*) and speed (*B*) for the No-Action, Active-Arm, and Passive-Arm conditions (*left*) and for the corresponding baseline conditions (*right*). The bars represent the means and the solid symbols the individual data for all subjects. Error bars represent SE.

for the no-action and passive conditions compared with the active condition. The only exception was one subject (the blue point lying on the equality line) who showed comparable effects for both passive and active movements. Overall, the data points are scattered around the dashed vertical line passing through zero, indicating that temporal judgments were almost veridical in the active condition. A very different pattern of results was observed for perceived velocity, where data points gathered around the equality line, showing equal effects across conditions (Fig. 5*B*).

To better understand whether particular aspects of the arm movement modulate the effectiveness of adaptation, we tested three other types of active movement. In one condition, subjects performed a more natural and exploratory-like movement, moving their hand to touch a different part of the object (traveling a total distance of ~10 cm). After the offset of the adapting stimulus, subjects had to touch the lower surface of the wheel with their right index finger so that the test was presented to the same finger as the adaptor but moved in a different position on the object. Again, the effect on duration was less than for the no-action condition [Different-Object = 103 ± 54 ms; No-Action = 251 ± 68 ms for the same sample; means ± SE; $t_{(4)} = 2.813$, $P = 0.048$, paired samples *t*-test; Fig. 6*A*]. In another condition, the test was presented to a different finger (middle finger) actively moved to the same spatial position on the wheel (upper surface). This active manipulation had little effect on the adaptation-induced distortion of perceived duration, being comparable to that observed in the no-action condition [Different-Finger = 181 ± 62 ms; No-Action = 251 ± 68 ms for the same sample; means ± SE; $t_{(4)} = 1.463$, $P = 0.217$, paired samples *t*-test; Fig. 6*A*]: the small, distal movement of the fingers (of ~2 cm in amplitude) had little influence on the adaptation effect. Furthermore, the effect on duration transferred from one finger to another, indicating a broad tuning in body coordinates. The third condition involved a movement of the whole body. At the end of adaptation, participants took a step and rotated their body by 90 degrees to face the wheels, so the position of the subject changed in absolute external coordinates, while the position of the right index finger on the first wheel remained unchanged. During the movement, both the right and left fingers were always kept in contact with the surface of the wheels. Like the large arm movements, this movement counteracted the adaptation-induced compression of time [Active-Body = 65 ± 27 ms; No-Action = 221 ± 57 ms for the same sample; means ± SE; $t_{(3)} = 3.753$, $P = 0.033$, paired samples *t*-test; Fig. 6*A*].

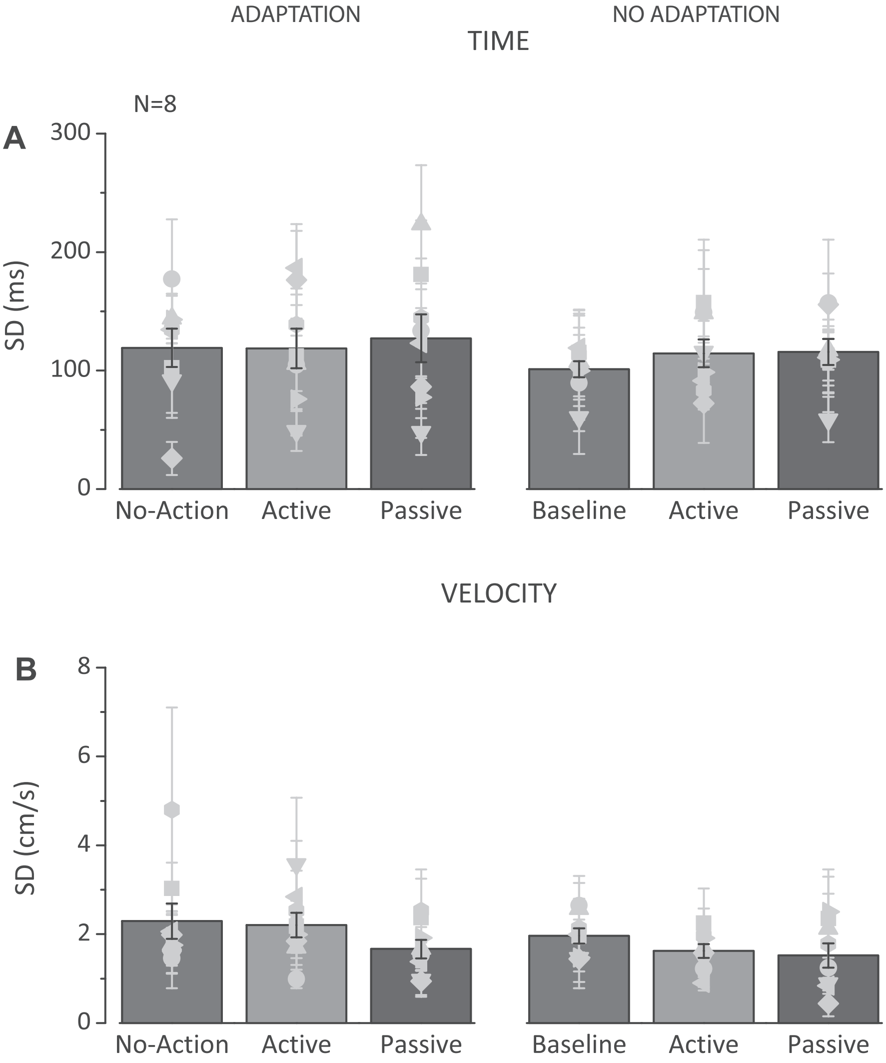

Fig. 4. Standard deviations for the duration (*A*) and velocity (*B*) judgments in the No-Action, Active-Arm, and Passive-Arm conditions (*left*) and in the corresponding baseline conditions (*right*). The bars represent the means and the solid symbols the individual data for all subjects. Error bars represent SE.

The different types of movement attenuate the time adaptation effect with different strengths: passive movements are completely ineffective; large active movements involving the adapted body part have the largest effect; smaller movements have intermediate effects.

The adaption-effect on apparent speed was unaffected by any of these experimental manipulations (Fig. 6*B*), indicating again that the effects of active movement on duration and speed are clearly dissociable.

DISCUSSION

How we time events, with a single centralized clock or multiple, distributed timing mechanisms, has become a central issue for time perception research. A growing set of evidence points to the existence of different clocks for different time scales, but it is less clear whether these are supramodal or modality specific. Recently, temporal distortions for visual stimuli localized in space have been reported after adaptation to high-frequency visual flicker or motion (Johnston et al. 2006), providing strong evidence for local, sensory timing mechanisms, at least in the subsecond range. However, the exact nature of this spatial tuning, and the underlying neural mechanisms and their cerebral locus, are currently a matter of debate (Ayhan et al. 2009; Bruno et al. 2010; Burr et al. 2011). The most important new finding reported here is that the adaptation-induced effects for touch can be completely counteracted by performing an active movement between adaptation and test. The motion needs to be actively performed by the subject; passive motion of similar magnitude and dynamics had no effect.

Several studies show that many aspects of time perception are subject to adaptation (Eagleman and Pariyadath 2009; Heron et al. 2011; van Wassenhove et al. 2008). It is still unclear why adapting to motion, either visual or in this case tactile, should interfere with duration judgments, making durations appear shorter. However, adaptation is a ubiquitous phenomenon in all perceptual systems. In many cases, adaptation confers distinct functional advantages, such as the improved luminance discrimination after light-adaptation. In other cases it can induce strong distortions, such as with adaptation to particular orientations (Gibson and Radner 1937). In the case of interval perception, it is far from clear what the mechanisms of adaptation are, or what purpose they serve. The adapting stimulus is motion, but the effect is on perceived duration. However, whatever the mechanisms or motives behind the adaptation, the effects are large and could potentially

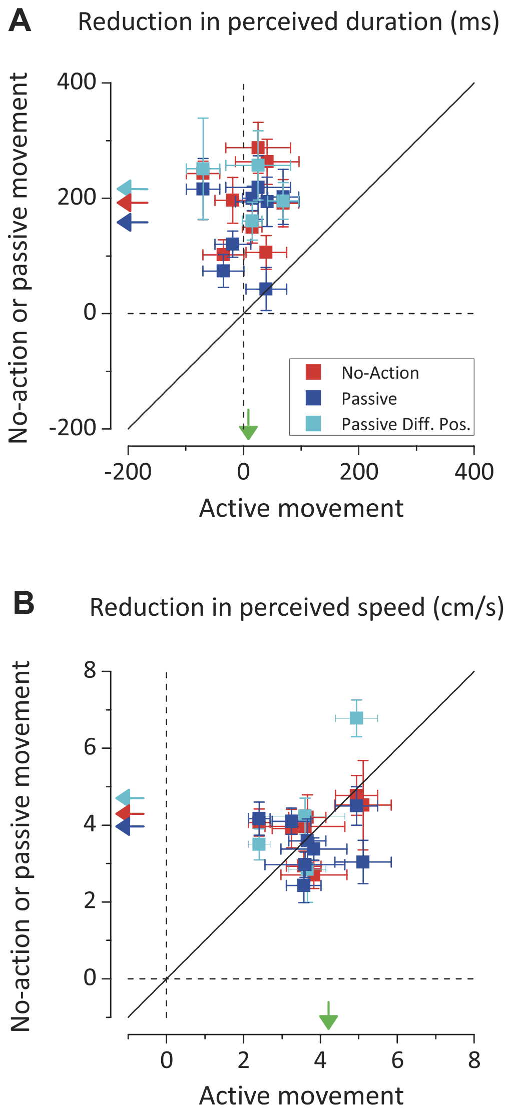

Fig. 5. Reduction in perceived duration (*A*) and speed (*B*) for the No-Action and both the Passive conditions plotted against the Active-Arm condition for all subjects. The vertical and horizontal dashed lines show zero effect; the diagonal lines show equal effect. The arrows indicate the means.

create confusion, especially when the subject needs to act on the tactile stimulus. It is therefore interesting that making an active movement annuls the adaption-induced changes in duration, as if it were resetting the clock. We did not observe statistically significant changes in perceived time after an action in the unadapted condition (baseline), but in this condition there was no time bias. Indeed, if the effect of the action were to keep veridical the estimate then it should be only present when perceived time is altered, as we find after adaptation.

Why the clock needs to be reset is an interesting question: perhaps the system needs to access timing mechanisms when programming a large movement. More surprising is why a system with the capability to endorse a calibration or reset, allows so large a perceptual alteration. One possibility is that calibration is computationally expensive, and therefore performed only when needed. Another possibility is that there exist (at least) two independent networks to measure time, one subject to adaptation and the other not, with the second coming into play only when an action is programmed.

Our data show a clear link between the amplitude of the movement and resetting: small finger movements alter duration only slightly, whereas full body swing or large arm movements severely reduce, or even eliminate, the effect. All these movements are concerned with portions of the body connected with the sensors being stimulated. We do not know if programming an action of an effector unrelated to the stimulated skin (such as the other arm) would produce a similar reset on time perception.

Our findings reinforce those of Watanabe et al. (2010), showing that the temporal compression induced by sensory adaptation is not exclusive to visual timing, but common to different sensory modalities. The effects of adaptation on

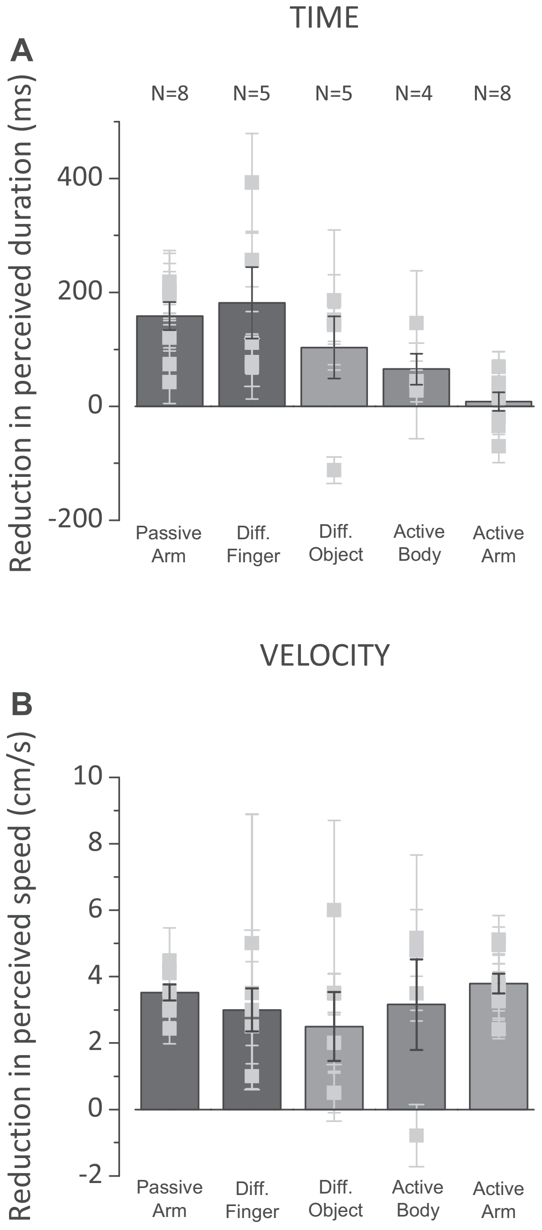

Fig. 6. Reduction in perceived duration (*A*) and speed (*B*) for all the movement conditions. The bars represent the means and the solid symbols the individual data for all subjects. Error bars represent SE.

apparent duration and on speed transferred from the adapted body part (right index finger) to another (right middle finger), indicating that they are not strictly selective in body coordinates. As both peripheral mechanoreceptive afferents and SI neurons are sensitive to the speed of tactile moving stimuli (Essick and Edin 1995; Ruiz et al. 1995), we might have expected the effect on speed to be disrupted by the change in skin location, showing a more fine-tuned somatotopy. However, the adapted index and tested middle fingers occupy adjacent positions on the somatotopic cortical map, and their functional representations may be partially overlapped at the early stages of somatosensory processing (Biermann et al. 1998; Krause et al. 2001; Simoes et al. 2001). Adaptation of the index finger might thus have spread also to central neurons involved in the encoding of somatosensory signals coming from the middle finger of the same hand. Moreover, as most of the mechanoreceptor afferents were probably substantially activated by the tactile moving stimuli that we used, we cannot exclude the potential contribution of the Pacinian afferents, whose large receptive fields may cover the entire hand or arm (Johnson 2001; Macefield 2005; Vallbo et al. 1984).

Sensory events occurring after voluntary movements are often perceived dilated in time (Haggard et al. 2002; Yarrow et al. 2001). This temporal illusion, which has been termed chronostasis, might at first sight be invoked to account for our results: temporal dilation due to action and temporal compression induced by adaptation could have canceled each other. It is also well known that attention can change our perception of time (Seifried and Ulrich 2011; Tse et al. 2004), and motor preparation is known to be tightly coupled with shifts of attention to the intended goal, leading to speeded and enhanced perceptual processing (Eimer et al. 2006; Juravle and Deubel 2009). Some accounts of the chronostasis illusion have, indeed, discounted the special role of motor acts and primarily implicated attentional modulation and arousal (Alexander et al. 2005; Georg and Lappe 2007). However, whatever the mechanism underlying chronostasis, it seems unlikely that it can explain our results, as its effect is additive in nature, corresponding to adding about the duration of the movement, at least for the saccadic eye movements. Action produced no statistically significant change in perceived time in the baseline condition (without adaptation), while chronostasis should have done so. Active movement did not in itself cause an expansion of apparent time, but rather modified the adapted state of neurons that encode duration, counteracting the adaptation-induced temporal compression. It is the motor commands themselves, rather than reafferent signals from body movement, that reset timing mechanisms for touch and restore veridical event-time. Importantly, no concomitant changes in perceived speed were reported, ruling out a generalized effect of body movement on somatosensory processing and rather pointing to a specific interconnection between timing mechanisms and action systems.

The processing of temporal information is essential for motor behavior, and several motor-related areas have been consistently identified as part of the neural network underlying time perception (Coull et al. 2004; Ivry et al. 2002; Lewis and Miall 2003; Schubotz et al. 2000). Recently, the reason for such a close link between time and action has been outlined in a more general theoretical framework. Time, space, and other magnitudes seem to be intrinsically interconnected and represented within a common metric that ultimately serves action planning (Bueti and Walsh 2009; Burr et al. 2010; Walsh 2003). The neural substrate of this unified code for action form part of the parietal cortex, where sensory cortex meets motor cortex. Not only are time and space necessary for action, but they may be structured and modified by action. Active movement may reset timing mechanisms in preparation for the new scenario that the movement will cause. Our brain seems to utilize the intention-to-move signals to appropriately retune its perceptual machinery and prepare it to extract new temporal information.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

A.T., M.G., D.C.B., and M.C.M. conception and design of research; A.T. performed experiments; A.T. analyzed data; A.T., M.G., D.C.B., G.S., and M.C.M. interpreted results of experiments; A.T. prepared figures; A.T. drafted manuscript; M.G., D.C.B., and M.C.M. edited and revised manuscript; M.G., D.C.B., G.S., and M.C.M. approved final version of manuscript.

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