

Short-term global motion adaptation induces a compression in the subjective duration of dynamic visual events

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Apparent duration can be manipulated in a local region of visual field by long-term adaptation to motion or flicker (Johnston, Arnold, & Nishida, 2006). These effects show narrow spatial tuning (Ayhan, Bruno, Nishida, & Johnston, 2009), as well as retinotopic position dependency (Bruno, Ayhan, & Johnston, 2010), supporting early locus in the visual pathway. Here, we introduce a new effect using RDK as a short-term visual adaptor and demonstrate that a brief, subsecond range adaptation induces a significant subjective duration compression (~10%) on a subsequently presented test stimulus (RDK pattern) only for global motion patterns drifting at 50% motion coherence but not for those drifting at 0% coherence, suggesting a higher level area as a source of origin. In another set of experiments using a plaid stimulus as the adaptor and gratings as the tests, we report again a significant duration compression following a brief motion adaptation, although the effect does not seem to be consistently selective for a particular direction of the standard test relative to that of the plaid adaptor (two-dimensional motion) or its components (one-dimensional motion). Finally, we conduct an experiment using shutter glasses and find that the effects of a short-term adaptor presented monocularly to one eye transfer to the nonadapted eye, providing evidence for the interocular transfer. In a series of control experiments, we also show that the duration effects cannot be explained by adaptation-induced changes in perceived speed, perceived onset-and-offset, and attentional resource allocation. Overall, the duration compression effect requiring motion coherence in RDK, persisting in plaid stimulus, and showing interocular transfer imply explicit genuine mechanisms mediating duration effects in the higher level motion areas.

Introduction

All forms of sensory signal extend both in space and time. One of the unique challenges of time perception in comparison to the perception of spatial attributes is that there is not a direct coding system dedicated to process temporal information like the one in the spatial domain, where the spatial arrangement of active neurons can discriminate the spatial position extent. Although there is a deeper understanding of spatial vision in the literature, what is derived as temporal information in various contexts is still an open question yet to be answered. In the past century temporal processing in our brain has revealed itself to be a complex issue, involving a range of interrelated phenomena (e.g., Gorea, 2011), some of which are (a) temporal order or judging the simultaneity of events (Battelli, Pascual-Leone, & Cavanagh, 2007; Moutoussis & Zeki, 1997; Nishida & Johnston, 2002; Verstraten, Cavanagh, & Labianca, 2000); (b) cognitive factors such as memory (Blake, Cepeda, & Hiris, 1997) and decision-making involved in timing judgments (Gibbon, 1977; Gibbon, Malapani, Dale, & Gallistel, 1997; Wittmann, Leland, & Paulus, 2007); (c) the effect of interval structure (i.e., empty vs. filled intervals, stimulus intensity, visual vs. auditory) on apparent duration (Goldstone, Lhamon, & Secher, 1978; Grondin, Meilleur-Wells, Ouellette, & Macar, 1998; Rammsayer & Lima, 1991; Wearden, Edwards, Fakhri, & Percival, 1998); (d) attention and arousal as potential modulators of subjective time (Thomas & Weaver, 1975; Treisman, 1963; Treisman, Faulkner, Naish, & Brogan, 1990; Tse, Intriligator, Rivest, & Cavanagh, 2004; Ulrich, Nitschke, & Rammsayer, 2006; Wearden, Denovan, Fakhri, & Haworth, 1997); and (e) distortions of event time induced by the adaptation,

Citation: Gulhan, D., & Ayhan, I. (2019). Short-term global motion adaptation induces a compression in the subjective duration of dynamic visual events. *Journal of Vision*, 19(5):19, 1–22, <https://doi.org/10.1167/19.5.19>.

<https://doi.org/10.1167/19.5.19>

Received July 19, 2018; published May 21, 2019

ISSN 1534-7362 Copyright 2019 The Authors



suppression, or interruption of transient signals (Burr, Tozzi, & Morrone, 2007; Johnston, Arnold, & Nishida, 2006; Morrone, Ross, & Burr, 2005; Terao, Watanabe, Yagi, & Nishida, 2008). Our current study is mainly concerned with the last of these issues with a specific focus on the mechanisms underlying the adaptation-induced temporal distortions within the perceptual milliseconds range.

One classical perspective with regard to time perception is the idea of a single, centralized timing mechanism dedicated to decoding temporal information (Treisman, 1963). The main hypothesis postulates a single (i.e., independent across sensory modalities), internal mechanism of subjective interval timing. In this account, there is a pacemaker responsible for producing periodic “tics” at a fixed rate, and an accumulator that either stores or sometimes (i.e., at times of deprived attention to temporal events) fails to store the products of the pacemaker. At the end of an interval, once the gate of the accumulator is shut, a counter detects the tics generated by the pacemaker. Distortions of perceived time are then explained by an alteration in the pacemaker rate as a result of a change in the level of arousal (Droit-Volet & Wearden, 2002; Treisman et al., 1990; Wearden, Philpott, & Win, 1999). One critical aspect with regard to these types of internal clock models is that they hold an abstract concept of time dissociated from the low-level sensory processing, which is inconsistent with what is known about the physiology underlying the perception of other visual attributes such as motion or color (for a discussion, please see Nishida & Johnston, 2002). In a seminal study in 2006, Johnston et al. demonstrated that adapting a particular region of visual space to 20-Hz oscillatory motion or flicker reduces the apparent duration of a 10-Hz dynamic test stimulus, while 5-Hz adaptation has very little influence on apparent duration, implying modality-specific, sensory-based mechanisms of event time perception. Thus, timing is not only modality-specific, but also has a spatial component. In fact, a growing body of evidence now suggests that the temporal and spatial factors are not processed independently, and that timing has a spatial component. Saccadic eye movements, for example, are known to induce distortions of time, as well as space, implying that time and space are not processed separately in the brain (Bruno & Cicchini, 2016; Morrone et al., 2005). Moreover, duration judgments change according to which visual hemisphere the stimulus is presented to (Vicario et al., 2008), suggesting spatial anisotropies in time perception.

Following Johnston et al.’s (2006) original report on the spatially specific adaptation effects on perceived time, with the aim of conducting a more detailed investigation on the spatiotemporal interactions in interval timing, we conducted a series of studies that

demonstrated that the local sensory-based mechanisms (Ayhan, Bruno, Nishida, & Johnston, 2009, 2011) encode the duration of visual events in a retinotopic frame of reference (Bruno, Ayhan, & Johnston, 2010) and that the judgments in the millisecond range are dependent upon low-level mechanisms. Importantly, we also showed that changes in apparent duration are dissociable from changes in perceived temporal frequency or speed, suggesting a common component but separate neural mechanisms for the processing of motion and duration. The link between the temporal change or motion and the duration is a well-established one in the literature. It is known that moving objects appear to last longer than static objects of the same duration (Brown, 1995), a phenomenon referred to as *subjective time dilation*. Whereas Kanai, Paffen, Hogendoorn, and Verstraten (2006) have demonstrated that it is the temporal frequency (rather than speed) that determines the magnitude of time expansion observed in dynamic displays, Kaneko and Murakami (2009) separated out the effects of trajectory length and speed with the use of a Gabor patch and pointed to the importance of stimulus speed in inducing time dilation in dynamic displays. In this context, it is important to note that in the Johnston et al. (2006) study, the duration bias was induced by a temporal frequency rather than a duration interval adaptation, providing evidence against time models framed around the idea of duration channels or templates (such as Miall’s neural oscillator model [1989], where some pacemaker cells with varying [but still similar] oscillation frequencies are suggested to encode a broad range of time intervals and recall the intervals at a later time)—and rather link duration processing to early-level stages of motion pathway (i.e., magnocellular layers of lateral geniculate nucleus), where neurons process change in luminance contrast as a function of time.

It is known that early visual areas have strong retinotopy that is unaffected by eye position, while higher order areas seem to encode information in spatiotopic coordinates. That the locus of temporal frequency adaptation is early in the visual pathway, as claimed by Johnston et al. (2006) and our later follow-up studies (Ayhan et al. 2009, 2011; Bruno et al., 2010), was in controversy with the results of Burr et al. (2007), where the researchers used a saccadic paradigm to show that adaptation-based temporal compression occurs within the real world, rather than retinotopic coordinates. More recently, using drifting plaids, known to target global-motion mechanisms in MT as adapting stimuli and random dot kinematograms (RDKs) as tests, Latimer and Curran (2016) provided further support for both the spatiotopic, as well as the retinotopic, encoding in the long-term adaptation-induced duration compression. As a further support for the involvement of higher level areas in interval timing,

Curran and Benton (2011) also showed that at low drift rates ($3^\circ/\text{s}$), long-term (approximately 30 s) adaptation-based temporal compression is only significant if the adaptor and the test stimulus have the same motion direction, implying a rather cortical origin for the direction-specific duration effects. Similarly, Yamamoto and Miura (2016) demonstrated that the relative distortions of the perceived duration of line segments moving either coherently or incoherently in reference to the global motion of an occluded diamond stimulus were comparable to the size of distortions in the perceived speed, indicating that motion coherence has an influence on perceived duration and that these effects might be mediated by changes in perceived speed. We suggest that taken together, these findings might indicate that time and speed processing share a common neural component, originating from lower levels and proceeding up in the higher level visual areas and that the mechanisms underlying the spatiotemporal interactions at each level of visual hierarchy are in a complex relationship so as to lead to controversial results in the timing literature.

After the transient signal is processed at the magnocellular neurons, later at the hierarchical motion processing system, visual motion categories are known to be formed based on whether the signal is composed of a single vector or a sum of vectors, denoted as local and global motion, respectively (see Cropper, 2001). Larger receptive fields of the higher visual areas, such as area MT+, as well as V3/V3A (Braddick et al., 2001) allow the system to achieve the integration of local motion signals to give a coherent percept in global motion patterns embedded in noise. Using stimuli set known to target higher level motion processing areas in the brain (i.e., RDKs), here we introduce a novel duration effect, where unlike the long-term temporal frequency adaptation as demonstrated by Johnston et al. (2006), a rather brief (~ 700 ms) adaptor induces a significant subjective duration compression on a subsequently presented test stimulus only for global motion patterns drifting at 50% motion coherence but not for those at 0% coherence, suggesting that sensory interval timing effects are not only modulated at low-level loci but also extend to higher level areas in the temporal processing pathway.

We have previously linked the long-term temporal-adaptation-induced perceived duration effects to the changes in the temporal tuning curve of M cells (Ayhan et al., 2009; Johnston et al., 2006). The temporal impulse response function provides a description of the temporal response of the visual system to a range of stimuli and is directly related to the temporal frequency tuning function by means of a Fourier transform. Physiological evidence has shown that a fast adaptation phase called *contrast-gain control* induces a reduction in the contrast gain of cat ganglion (Shapley & Victor,

1978) and LGN cells (Mante, Bonin, & Carandini, 2008) at low temporal frequencies, delivering a more bandpass temporal frequency response. There is also evidence that high temporal frequency adaptation induces changes in the temporal frequency tuning of the band-pass cells of the nucleus of the optic tract in wallaby, decreasing relative sensitivity to low temporal frequencies and sharpening the temporal impulse response (Clifford, Ibbotson, & Langley, 1997; Ibbotson, 2005; Ibbotson, Clifford, & Mark, 1998). In order to establish a link between the changes in the shape of temporal impulse response to the changes in perceived duration, in a psychophysical setup, Bruno and Johnston (2010) demonstrated a reduction in the perceived duration for intervals following a high-contrast context relative to a low-contrast context, implying that reductions in perceived duration may be mediated by a change in the phase of the temporal impulse response in the magnocellular cells of LGN, in this case following contrast gain. In order to explain the fast and long-term adaptation effects on perceived duration, Johnston (2010) proposed a content-dependent clock model, where a forward model of the visual signal is generated from the visual input, which is continuously compared with the current sensory signal. A match between the prediction and the incoming sensory data results in a clock tick, the end-count of which is used as a measure of the duration of the interval. In this model, the forward prediction needs to know the rate of change of image brightness and therefore relies on band pass differentiating temporal filters (magnocellular neurons), whereas the current brightness signal can be provided by a low pass channel, which does not adapt to the same degree (parvocellular neurons). After adaptation, the phase advance in the magnocellular signal shifts the prediction forward in time, increasing the time to reset and thereby producing the psychophysically observed time compression. Whereas changes in the responsiveness of M cells relative to P cells explain changes in apparent temporal frequency (or speed), sharpening of the M cell temporal impulse response explains apparent time compression (Johnston et al., 2006), dissociating the effects of temporal adaptation on perceived speed and time.

Early source contrast gain effects are known to be manifested in the response of higher level motion areas such as area MT+ (Kohn & Movshon, 2003). In their single-cell recording study, Kohn and Movshon (2003) showed that adaptation to their preferred direction of motion decreases MT+ cell responses via a contrast gain mechanism. It has also provided evidence for a short-term motion adaptation effect with a locus distinctly in the area MT+, independent of the feedforward connections from the early-level visual motion areas (Priebe & Lisberger, 2002). Priebe and

Lisberger (2002) showed that short adaptor drifts in opposite directions cause not only an enhancement of the response to subsequent test motion, but also a change in the latency of response in neurons of macaque area MT. If contrast-gain were a mediator in duration distortion effects, as Bruno and Johnston (2010) and Johnston (2010) have suggested, then one could expect to observe subjective duration changes as a result of manipulations known to change the temporal tuning of neurons in higher level motion areas, too. To test this hypothesis, in this study, we use a brief motion adaptation, which was previously shown to affect the temporal impulse response properties of the macaque area MT+ cells, and show, for the first time, a reduction in the perceived duration of dynamic stimuli following an adaptation to a short-term coherent global motion. We also demonstrate that adaptation-based changes in perceived speed are negligible, implying a dissociation between the mechanisms modulating changes in duration and speed in the motion-detecting units. By manipulating various parameters of RDKs, as well as grating and plaid stimuli, we provide a detailed psychophysical investigation as to the locus of this effect, either precortical, or cortical.

Experiments: Methods and results

General methods: Participants

Number of participants corresponding to the various sets of experiments were 11, four, two, 20, 10, and eight for the Experiments 1A through C, 1D, 1S, 2A and B, 2C and D (as follow-ups of 2A and B), and 3A and B, respectively. Participants had normal or corrected-to-normal vision via glasses or lenses. All experiments were compliant with the Bogazici University research ethics requirements, as well as the Declaration of Helsinki. All participants gave their consent prior to the experiments. Written and oral information regarding the nature of the study were given them prior to the experiments.

General methods: Stimuli

Stimuli were coded and displayed by using MATLAB (MathWorks, Natick, MA) with Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). A 17-in. CRT monitor (Samsung SyncMaster 753DF, 100 Hz) was used for all the experiments except for the experiments in which shutter glasses (Nvidia 3D Vision 2) were used. In those experiments (Experiments 3A and B), participants were presented stimuli using a

21.5-in. LED monitor (Eizo FG2421) with a refresh rate of 120 Hz. All displays were calibrated using a colorimeter (Datacolor Spyder4Elite). For both displays, maximum and minimum luminance were set to 60 and 0.01 cd/m², respectively. Experiment-specific stimuli properties were further explained in their corresponding method sections individually.

General methods: Procedure

In a typical psychophysical setup, visual stimuli were presented on a computer screen (and sometimes with an accompanying audio through headphones) and responses were collected via a common computer keyboard. A typical session lasted about 45 min. Experiments were run in a dark, quiet cubicle at the Bogazici University Vision Laboratory (<https://visionlab.boun.edu.tr/en>), using a chinrest for preserving the viewing distance to the monitor at approximately 57 cm. At this viewing distance, 1 cm on the screen corresponded to 1 degree of visual angle (dva). The main technique used in the experiments was two-alternative forced-choice (2AFC) based on method of constants, except for Experiment 1S, where QUEST (Watson & Pelli, 1983) was used as the experimental methodology.

General methods: Data analysis

Since the main experimental technique was 2AFC based on method of constants, individual data coming from participants per experimental condition were the responses as indexed by “percent-correct” values in reference to the physical values such as the speed or duration of stimuli for each level of constants (i.e., seven). For each participant, n number of trials in a condition resulted as $n/7$ data points corresponding to levels of constants on a (semi-) logarithmic scale. In order to assign a duration value in which the test stimulus was perceived equally long to the standard stimulus, point of subjective equality (PSE) was estimated individually. The PSE values were estimated using a maximum-likelihood Weibull fit to the dataset, a method adapted from Watson (1979). Parametric statistical testing such as analysis of variance (ANOVA) and the relevant planned comparisons were implemented using these PSE values.

Experiment 1A: Perceived time changes following a short-term global motion adaptation

Johnston et al. (2006) previously linked duration distortions induced by the temporal frequency adap-

tation to the changes in the temporal impulse response of early visual neurons via a contrast gain mechanism (Bruno & Johnston, 2010). Early-source contrast gain effects are known to be manifested in the response of higher level motion areas such as area MT+ (Kohn & Movshon, 2003). Evidence has also been provided for a short-term motion adaptation effect with a locus distinctly in the area MT+, independent of the feedforward connections from the early-level visual motion areas (Priebe & Lisberger, 2002). Thus, if contrast-gain effects were a mediator in duration distortion effects, as Johnston et al. (2006) have suggested, then we thought we could also expect to observe subjective duration changes as a result of manipulations changing the temporal tuning of neurons in the higher level motion areas (i.e., area MT+). In order to test that, we used a 2AFC paradigm, where an adaptor and a standard test stimulus were presented sequentially on the same spatial position on either the left or right side of a central fixation spot. Subsequent to the disappearance of the standard stimulus, a comparison test was presented on the opposite side of the fixation and participants were asked to make duration judgments between the two consecutive tests. In blocked trials, the extend of temporal change following a brief presentation (700 ms) of a random dot array was examined as a function of different (a) global motion coherence levels, (b) motion speeds, and (c) relative motion directions of the standard and the adaptor stimuli. The manipulation of the global coherence level of the stimuli allowed us to evaluate the locus of the temporal effect we expected to observe here: If the local temporal signals (i.e., 0% global motion coherence) would have been enough to induce any changes in subjective duration in our current paradigm, then this would point out to an early source of origin, whereas if the global motion signal (i.e., 50% global motion coherence) were critical in modulating the changes in subjective duration as we expected, then this would imply rather higher level mechanisms underlying the changes in subjective interval timing.

Methods

Stimuli consisted of 200 white dots with individual Gaussian blur masks, which were used to prevent motion smear on the trailing ends. The diameter of individual dots was set to 0.25 dva and rounded to the nearest odd number of pixels on display, and the standard deviation (σ) of applied Gaussian blur mask was one-sixth of the dot radius in pixels – 1; for example, for a 13×13 pixel drawing area for a dot, $n_{\text{kernel-size}} = 13$, and $\sigma_{\text{blur}} = 2$. Discrete kernel values per pixels were then calculated such that the center pixel of dot was white (i.e., had maximum luminance level), pixels on circumference were just above midgray, and

any in-between pixel had a corresponding level of luminance. The dot array was presented within a square aperture of 10 dva (Figure 1). If Weber contrast (i.e., $C_W = [L_{\text{feature}} - L_{\text{background}}]/L_{\text{background}}$, or difference between luminance of features and background divided by luminance of background) is used as a metric of contrast for RDKs, then $L_{\text{feature}} \approx 0.6$ as indexed by average luminance value of a single dot and $L_{\text{background}} = 0.5$ luminance value of midgray background results as a $C_W \approx 0.20$ for the standard and test stimuli, and $C_W \approx 0.10$ the for adaptor stimulus (Figure 1).

In blocked trials, dots in the RDKs were moving either in random directions (i.e., 0% coherence), or at a 50% of motion coherence level (that is, half of the dots were moving in random directions, whereas the other half were consistently moving either leftwards or rightwards). In both conditions, the vectoral sum of the random trajectories (i.e., Speed \times Distance) was fixed at zero in order to obstruct any potential direction-dependent bias. Participants' use of local luminance changes as cues was prevented by keeping the individual dot-lifetime at 150 ms. Limiting the dot lifetime, however, together with the use of Gaussian envelopes reduced visibility. In order to make sure that we generated a suprathreshold, coherent global motion stimuli across all different conditions with various parameters, we conducted a control threshold experiment, the details of which may be found in Supplementary File S1, Experiment 1S.

The time course of the experiment can be seen in Figure 1. At the beginning of each trial, there was a brief (500 ms) prestimulus interval with a midgray screen and a central fixation spot, which were kept fixed throughout the whole experiment as a background. Then, a short adaptor (700 ms) drifting at a speed of either 2.5°/s or 9°/s (in blocked trials) appeared on a peripheral region (e.g., left) of the screen such that the center of the adaptor dot array was 10° away from the central fixation. Following the adaptor and a 500 ms of interstimulus interval (ISI) was a standard stimulus, which was presented for 700 ms at the same position as the adaptor. A comparison stimulus was generated consecutively at the opposite side of the fixation on a nonadapted position. Whereas the duration of the standard was kept at 700 ms across trials, the comparison stimulus took one of the seven durations defined on a semilogarithmic scale, from 400 to 1300 ms (i.e., method of constants) to generate a psychometric function. The standard and the comparison stimuli were displayed at full luminance contrast (i.e., centers of the Gaussian dots had luminance values corresponding to the maximum white point of the calibrated display, $\sim 60 \text{ cd/m}^2$), while the contrast of the adaptor was kept at half at 50% to avoid any potential contrast adaptation effects on the standard.

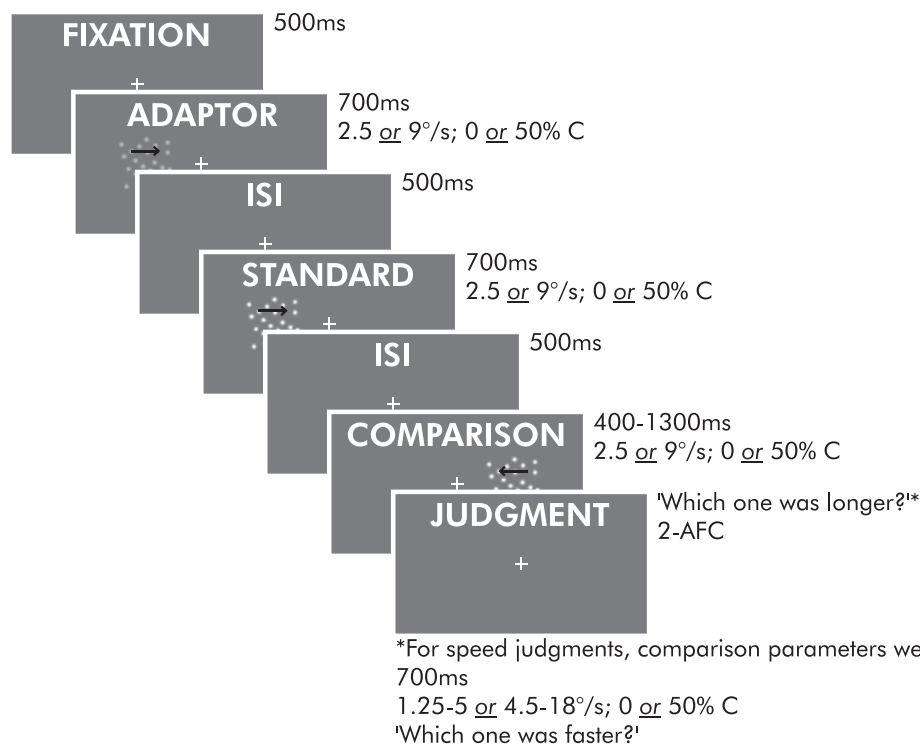


Figure 1. Time-course of the Experiment 1A through 1C (i.e., perceived time changes following a short-term global motion adaptation). In this psychophysical paradigm using method of constant stimuli, participants were asked to judge the duration (in Experiment 1A and C) or the speed (in Experiment 1B) of the two RDK stimuli following a brief adaptation phase within a 2AFC design (see Supplementary Movies S1 and S2). Adaptor type as the first IV had three levels (i.e., 0% coherent motion, 50% coherent motion where standard and test stimulus drift opposite direction, and 50% coherent with same direction) and speed as the second IV had two levels (i.e., 2.5°/s and 9°/s). The contrast of the adaptor was always kept at half of that of both standard and comparison stimuli to avoid any contrast adaptation, where if Weber contrast (C_W) was used as a metric, then $C_{W(\text{adaptor})} \approx 0.10$, $C_{W(\text{standard})} \approx 0.20$, and $C_{W(\text{comparison})} \approx 0.20$. The “perceived duration effect” in Experiment 1A and C, or “perceived speed effect” in Experiment 1B, was defined by the PSE differences of a participant in conditions with and without the adaptor across the same levels of variables. In the baseline conditions, the adaptor was not present, yet the time course of the trial was the same. In Experiment 1C, the physical speed of the comparison was matched individually and condition-based to the perceived speed of the standard, as revealed in Experiment 1B. Note that size and number of dots relative to display were modified to enhance readability of diagram.

At the onset (first 25% of the total duration) and offset (last 25% of the total duration) of all RDK stimuli, dots appeared or disappeared at different time frames to generate a “softened” temporal stimulus boundaries. This type of temporal jitter was introduced to avoid participants’ use of abrupt transients as cues. In a 2AFC duration-judgment task, participants were asked to indicate which test remained longer on the screen by making a binary choice using the left- or right-keypresses on a keyboard (For the experimental time-course, please see Supplementary Movies S1 and S2). In all experiments, the correct choice was counterbalanced. In an additional baseline condition, participants did the same task, but this time they were presented with the test stimuli without an adaptation phase.

In order to avoid any “wash-out effect” (i.e., a potential fading of the adaptor-dependent duration effects after a certain time window), the standard stimulus, which was presented on the adapted position,

came always as the first test stimulus following the adaptation phase in our paradigm. Temporal order in a sequence, however, is well-known to be influential in perceived duration experiments (e.g., Jamieson & Petrusic, 1975). Thus, in order to control for the temporal order effects, we presented the standard as the first test stimulus in the baseline control blocks, too, so that any effect caused by the temporal order would cancel each other out. Each experimental block was consisted of 140 trials (20 trials \times 7 levels of comparison), and the experiment had six blocks in total.

Results

A 3×2 repeated-measures ANOVA was conducted to compare the effects of two independent variables (IVs) as the adaptor type (0% coherent motion, 50% coherent motion, where adaptor and standard stimuli

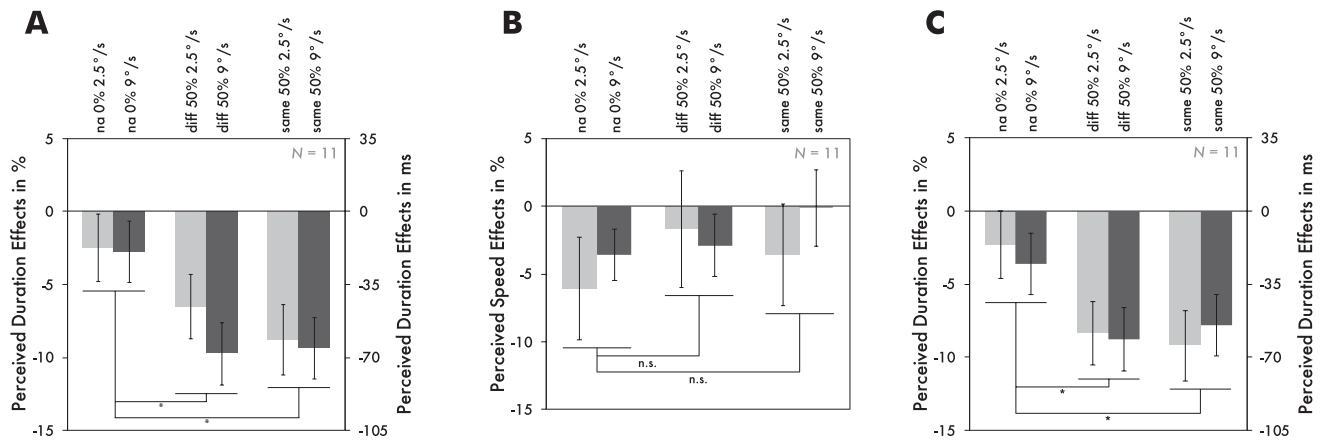


Figure 2. Results of Experiment 1A through C (i.e., perceived duration and speed using RDK). The main results on perceived duration from Experiment 1A (Figure 2A, left panel), perceived speed from Experiment 1B (Figure 2B, middle panel), and perceived duration with matched speed corrections from Experiment 1C (Figure 2C, right panel) following the short-term motion adaptation in the RDK paradigm were visualized as bar graphs. In all graphs, labels above the x-axis indicate experimental conditions using three levels of adaptor type (where labels as na 0%, diff 50%, and same 50% denote 0% coherent motion, 50% coherent motion with opposite drift direction, and 50% coherent motion with same drift direction, respectively) and two levels of speed (where labels as 2.5°/s and 9°/s refer to dot speed). To better illustrate the experimental condition, adaptor type levels were widely spaced in the x-axis, and speed levels were color-coded. Y-axes indicate either effects of perceived duration or speed. Bar values were calculated as the difference of means between and control and testing conditions. Error bars indicate the standard error of the means (SEMs) of these difference scores. Whenever available, *n.s.* indicates a nonsignificant and * indicates a significant result, in this case using contrasts after a repeated-measures ANOVA. The perceived duration effects showed significant results between incoherent and coherent motion conditions for both duration experiments (i.e., in Experiment 1A and C), whereas the perceived speed effects were nonsignificant in Experiment 1B.

drift in the opposite direction, and 50% coherent motion, where adaptor and standard stimuli drift in the same direction) and the speed of dots (2.5°/s and 9°/s) on perceived duration as indexed by individual PSE values. Note that the reasoning behind not conducting a $2 \times 2 \times 2$ ANOVA with three IVs as coherence level, direction, and speed is the following: Since at 0% coherence (i.e., incoherent motion) dots in all stimuli move in random directions, the concept of “relative direction between adaptor and standard” becomes redundant. Therefore, in this 3×2 design and for the first IV as the adaptor type, the difference between the first (i.e., 0% coherence) and the latter levels (i.e., 50% coherence) indicates the effect of coherence, whereas the difference between the second (i.e., 50% coherence with same drifting direction) and the third level (i.e., 50% coherence with opposite drifting direction) indicates the effect of direction. The same logic applies to all analyses in our RDK experiments.

As shown in Figure 2A, the analysis revealed that whereas the main effect of the adaptor type was significant, $F(1, 171, 11.706) = 6.251$, $p = 0.025$, $\eta_p^2 = 0.385$, neither the main speed effect, $F(1, 10) = 0.751$, $p = 0.406$, $\eta_p^2 = 0.070$, nor the interaction, $F(2, 20) = 0.673$, $p = 0.521$, $\eta_p^2 = 0.063$, reached into the statistical significance. Because our hypotheses were directional, the main effect of the adaptor type was further broken down using ANOVA contrasts. Two significant results

after planned contrasts revealed that the duration compression was higher in both 50% coherent motion conditions, where the adaptor’s drift direction was either opposite to that of the test ($M = -56.86$, $SEM = 14.95$) or the same ($M = -63.57$, $SEM = 9.75$) in comparison to that in the 0% coherent (i.e., incoherent) motion condition ($M = -18.21$, $SEM = 15.96$), $F(1, 10) = 4.954$, $p = 0.050$, $\eta_p^2 = 0.331$, and $F(1, 10) = 8.593$, $p = 0.015$, $\eta_p^2 = 0.462$, respectively. However, the relative direction between the adaptor and the test, either different ($M = -56.86$, $SEM = 14.95$) or the same ($M = -63.57$, $SEM = 9.75$), did not make a significant change in the perceived duration, $F(1, 10) = 1.310$, $p = 0.279$, $\eta_p^2 = 0.116$. Note that the means were indexed as the cumulative average across all participants, after having calculated the differences between the individual PSE values from each testing condition (i.e., any condition with adaptor stimulus) and the baseline (i.e., conditions without adaptor stimulus). Figure 2A shows that there is a consistent perceived duration compression for the standard stimulus in 50% coherent motion conditions (see Supplementary Movie S2), irrespective of dot speeds (i.e., 2.5°/s or 9°/s), whereas 0% coherent global motion conditions yield results similar to those in the baseline conditions (see Supplementary Movie S1).

Observing the short-term adaptation-induced duration compression only in conditions where there was a coherent global motion signal indicates that this effect

might have been mediated at higher level motion areas such as area MT+, where cells are known to make a spatiotemporal integration on the incoming signals over their large receptive fields (Pasternak & Merigan, 1994). Because the integration of local signals in 0% motion coherence condition would yield a zero global motion, yet in each local region was a meaningful temporal signal, perceived duration reaching baseline values in this condition might provide evidence that the effect cannot be fully linked to the lower level temporal information processing areas such as primary visual cortex (V1) or the magnocellular layers of lateral geniculate nucleus (LGN).

Here, because we demonstrate the effect of a brief adaptation in a paradigm, where the features (i.e., duration, speed, dot lifetime etc) of the adaptor and the standard test stimulus are similar (except for the contrast), one might argue that the standard, which is always presented as the first test stimulus, might have an influence on the perceived duration of the subsequently presented comparison test. It is important to remember, though, that the analyses were conducted on the differences between the data obtained from the experimental adaptation conditions and the baseline runs (where no adaptor was presented, yet the standard still came first). Thus, our baseline values control for any duration effects that the temporal order might have introduced. In fact, when we looked at the mean data from our control blocks, the perceived duration of the standard (with a physical duration of 700 ms) was found to be around 657 ms, a typical temporal order effect that had been reported previously (Bruno, Ayhan, & Johnston, 2012). Here, the significant duration compression relative to the control data, therefore, seems to be induced rather by the preadaptation that took place on the same spatial position as the standard.

Experiment 1B: The effect of short-term motion adaptation on perceived speed

It is known that the physical (and perceived) speed can change the perceived duration of a stimulus such that stimuli with faster speeds tend to be perceived longer in duration (Kaneko & Murakami, 2009). Although the main experiment was initially designed using the same stimulus speeds, participants may have perceived the speed of the standard stimulus as slower following the same-speed motion adaptation. In order to overcome a potential effect of apparent speed on subjective duration, participants' perceived speeds were identified individually for each condition using the method of constants in a 2AFC task. The matched speeds in relation to the subjective speed bias were then used in the following perceived duration experiment

(Experiment 1C) to overcome any speed-dependent duration judgment bias at the individual level. Implementing individual speed corrections irrespective of the overall statistical findings was crucial, since potentially, perceived speed bias at the individual level could still result in a nonsignificant overall finding across means.

Stimuli and procedure

Stimuli were almost the same as those in the main Experiment 1A (Figure 1). The only main difference was that it was the speed, rather than the duration of the comparison stimulus, which was varied in the method of constants. Whereas the speed of the adaptor and the standard were fixed at 2.5°/s or 9°/s in different conditions, the speed of the comparison was varied in seven logarithmic levels either from 1.25°/s–5°/s (for the blocks, where the standard speed was 2.5°/s), or from 6°/s–12°/s (for the blocks, where the standard speed was 9°/s), respectively. The duration of the stimuli, both the adaptor and the tests, were fixed at 700 ms. The task of participants was to report which of the two test stimuli moved “faster” on the screen, either the standard or the comparison stimulus in a 2AFC paradigm.

Results

In order to see whether there is any underestimation in the perceived speed of the standard following the adaptation phase, we conducted again a 3×2 repeated-measures ANOVA with the same independent variables as in Experiment 1A. The main results revealed that neither the adaptor type, $F(2, 20) = 1.199$, $p = 0.322$, $\eta_p^2 = 0.107$, nor the speed $F(1, 10) = 0.256$, $p = 0.624$, $\eta_p^2 = 0.025$, and the interaction $F(2, 20) = 0.744$, $p = 0.488$, $\eta_p^2 = 0.069$ were significant (Figure 2B). Similar to Experiment 1A, perceived speed values were obtained from the PSEs of the psychometric functions, where “% comparison perceived as faster” was plotted as a function of the seven constant speed levels. Even though there wasn't an overall significant change in perceived speeds, after having obtained the results here, PSEs were then used to make individual, condition-based corrections in the same duration paradigm we used in Experiment 1A in order to match the perceived speed of the comparison to that of the standard stimulus in the following experiment.

Experiment 1C: Short-term motion adaptation in global motion using RDKs with corrected test speed

Having the same motivation as in Experiment 1A, duration compression effects were investigated using

the same paradigm (Figure 1), but this time with test stimuli generating equal speed percepts.

Stimuli and procedure

The main stimuli and procedure were similar to those in Experiment 1A, with the exception that we made a perceived speed correction here: Instead of displaying physically equal speeds for each test stimuli, the speed of the comparison stimulus (on the non-adapted side) was equated to the perceived speed of the standard using the values found in Experiment 1B for each individual and condition, separately (Figure 1).

Results

A 3×2 ANOVA showed that the main effect for the adaptor type was still significant, $F(1, 222, 12.224) = 6.609$, $p = 0.020$, $\eta_p^2 = 0.398$, in such a strength that is comparable to the effect observed in Experiment 1A. Consistent with the results of Experiment 1A, the main effect of the dot speed and the interaction were found to be statistically insignificant, $F(1, 10) = 0.003$, $p = 0.960$, $\eta_p^2 < 0.001$, and $F(2, 20) = 0.501$, $p = 0.614$, $\eta_p^2 = 0.048$, respectively. As shown in Figure 2C, the main trends did not radically change in comparison to Experiment 1A, indicating a strong duration compression in 50% motion coherence conditions even after having matched the two test stimuli on their perceived speed.

Experiment 1D: Control for the perceived onsets and offsets using an audio cue

In Experiments 1A through C, we introduced temporal jitters to the RDK stimuli, lasting for 25% of the overall interval, both at the starting and ending periods to prevent participants' use of abrupt transients as cues for the interval length. This, however, might have also been argued to cause *event boundaries* to be encoded erroneously. Following the adaptation, if either the starting or the ending point were perceptually shifted on the timeline to introduce bias, then the factor underlying the duration compression effect would be a failure to judge the time point of the transients, rather than a genuine interval timing mechanism. In order to control for this possible third factor, in blocked trials, participants compared the timing of an audio stimulus to either the onset or offset of the standard.

Stimuli and procedure

As shown in Figure 3A, the stimuli were similar to those in the main experiment with one exception that around the onset or the offset of the standard stimulus was presented a very brief audio cue of 10 ms to give a time point reference to be compared to the transient

visual stimulus boundaries in a temporal order judgment task. Across different trials, the audio cue was presented either before or after, and in some trials at the same time as the onset or offset of the standard stimulus. Using the method of constants, the temporal shifts were determined as 0, ± 50 , ± 100 , or ± 150 ms relative to the onset or offset points of the standard. The task of participants was to make a binary choice as to whether it was the audio or the onset or offset of the visual stimulus that appeared first in the timeline.

Note that the ISI range we used in this study was larger than those used in similar studies in the literature to judge the temporal order of an audio and a visual stimulus. A preliminary study, however, using smaller range of stimuli were not completed successfully by our participants, potentially as a result of the relatively long temporal jitter phase used in our paradigm.

Results

In line with the previous experiments, a 3×2 repeated-measures ANOVA was conducted using two IVs as the adaptor type (with three levels as 0% coherence, 50% coherence with different drifting directions, and 50% coherence with same direction) and the dot speed (2.5°/s and 9°/s). The dependent variable was calculated by subtracting the perceived onset shift from the perceived offset shift to indicate, in each condition, the duration effect introduced by the bias in representing the temporal boundaries of the standard stimulus. If, for example, the onset of a standard stimulus was perceived as delayed for 30 ms, and the offset for 10 ms, then the duration bias would be calculated as being $10 - 30 = -20$ ms.

Analyses revealed that both the main adaptor type and the speed effects, and their overall interaction are insignificant, $F(2, 6) = 1.413$, $p = 0.314$, $\eta_p^2 = 0.320$; $F(1, 3) = 0.003$, $p = 0.958$, $\eta_p^2 = 0.001$; and $F(2, 6) = 0.069$, $p = 0.934$, $\eta_p^2 = 0.022$, respectively, as shown in Figure 3B. The nonsignificant findings imply that the levels of motion coherence, the relative direction of the standard in comparison to that of the adaptor, or the speed are not generating any consistent bias on the temporal detection of the event boundaries (i.e., onset or offset). Since there was a substantial jitter at the onset and offset of the stimuli, together with an asynchrony between the visual and the audio transients, inconsistent biases on the timing of both the onset and the offset of the standard were in fact expected at the individual level. Some participants indeed showed biases specific to some conditions, yet an overall and robust bias creating a significant, systematic change in the perceived duration of the interval was not visible.

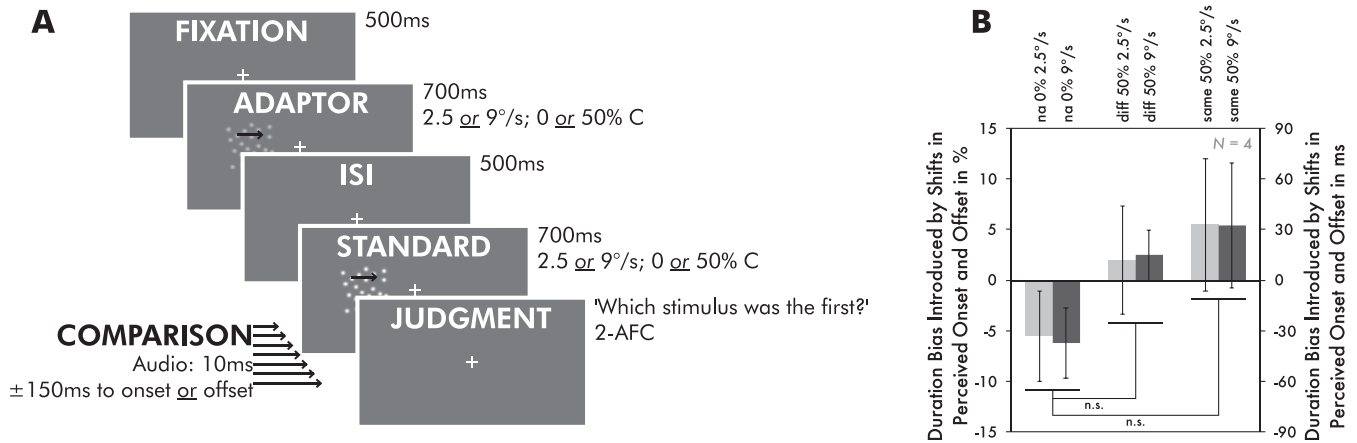


Figure 3. Time course and results of Experiment 1D (i.e., control for the perceived onsets and offsets using an audio cue). (A) In this psychophysical paradigm using method of constant stimuli, participants made a binary choice as to whether it was the audio or the onset (or offset, depending on experimental condition) of the visual stimulus that appeared first in the timeline. Similar to Experiment 1A through C, in the baseline conditions, the adaptor was not present, yet the whole course was the same. The “duration bias” was defined by the differences in point of subjective simultaneity (PSS) of a participant in conditions, where the adaptor was present (experimental) and absent (baseline) across the same variables. IVs were the same as the previous experiments as well. (B) The main results on duration bias introduced by perceived onset and offset were visualized as bar graphs. In all graphs, labels above the x-axis indicate experimental conditions using three levels of adaptor type (where labels as na 0%, diff 50%, and same 50% denote 0% coherent motion, 50% coherent motion with opposite drift direction, and 50% coherent motion with same drift direction, respectively) and two levels of speed (where labels as 2.5°/s and 9°/s refer to dot speed). To better illustrate the experimental condition, adaptor type levels were widely spaced in the x-axis, and speed levels were color-coded. Leftward y-axis indicates the duration bias in percentage (%), while rightward y-axis indicates the same effects in milliseconds (ms). Bar values were calculated in two steps: First, the PSS differences of a condition with and without adaptation for both onset and offset tasks were estimated, and then, the offset-PSS was subtracted by onset-PSS. Error bars indicate the standard error of the means (SEMs) of these difference scores. Whenever available, n.s. indicates a nonsignificant and * indicates a significant result, in this case using contrasts after a repeated-measures ANOVA. The duration bias showed nonsignificant results between nonadapting and adapting conditions.

Experiment 2A: Short-term motion adaptation in gratings and plaids

The results of Experiment 1A and C provided evidence that the brief adaptation-induced duration compression is contingent upon adaptors with a coherent global-motion direction signal. There seemed to be no selectivity, though, with respect to the relative direction of the adaptor to that of the subsequent test. RDKs consisting of both signal and noise dots as we used here, however, require the integration of motion integration across different orientation pattern motions (i.e., two-dimensional [2-D] motion analysis at area MT). In the primate visual system, though, cells in the primary visual cortex (V1) are responsive to local motion components only and do not combine across orientations scattered through a large visual field (Movshon, Adelson, Gizzi, & Newsome, 1985). Thus, in order to study the direction selectivity for the brief motion adaptation at the level of V1, we conducted a second experiment, where we rather used plaids as adaptor and drifting gratings as tests. Although it is still obscure how the 2-D texture (i.e., plaid) selectivity of single MT+ cells is related to the selectivity within

the context of random dots that contain multiple orientation and spatiotemporal frequency information, the second experiment also allowed us to make a further investigation with regard to the direction selectivity at the level of global-motion processing if there is any.

Neurophysiology studies have shown that the computation of early visual areas such as V1 could derive both the direction and the speed information of a linearly moving grating. Superposing two drifting gratings at different orientations, however, creates a relatively more complex pattern, called a drifting plaid stimulus. The combined direction and velocity in a plaid stimulus are defined as the scalar combination of these two gratings, and thus is classified as a moving 2-D texture or a 2-D motion. High-level motion areas (e.g., area MT+) are known to have cells responsive to the integrated motion of the plaid stimuli, although low-level areas such as V1 process information carried in the component gratings, separately (Movshon et al., 1985). Here, by using a plaid adaptor and drifting grating test stimuli, our main aim was to investigate direction-specific effects. If the motion direction of the standard relative to that of the adaptor had an effect on

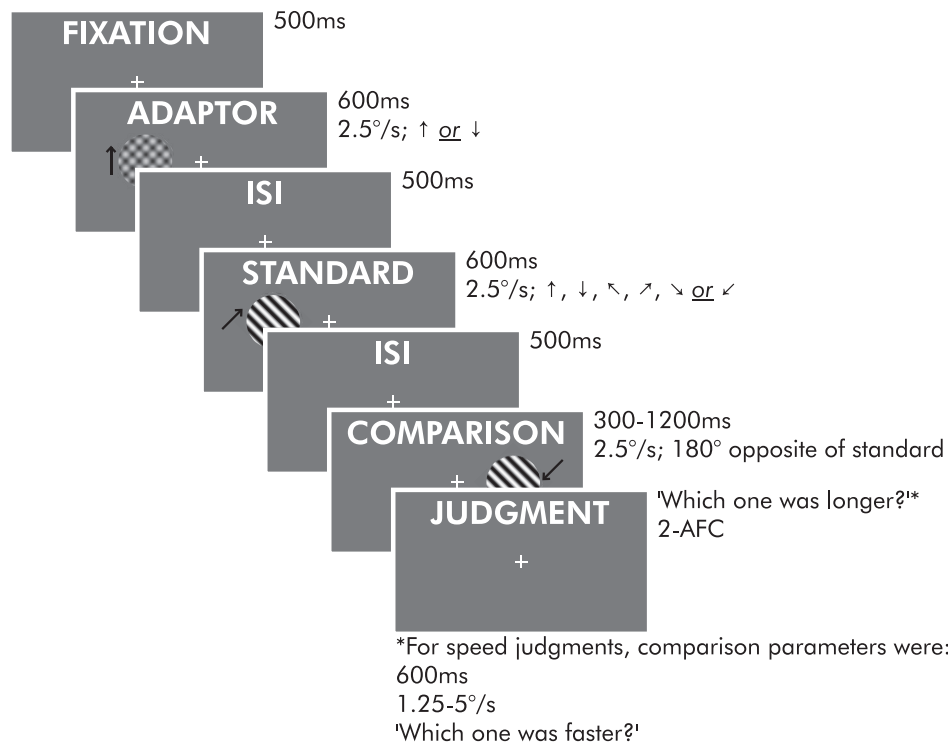


Figure 4. Time course of Experiment 2A and B and follow-ups as Experiment 2C and D (i.e., short-term motion adaptation in gratings and plaids). In this psychophysical paradigm using method of constant stimuli, participants were asked to judge either the duration (Experiment 2A and C) or the speed (Experiment 2B and D) of the two drifting grating stimuli (having 100% Michelson contrast, C_M) following a brief adaptation (having 50% Michelson contrast, C_M) to a plaid stimulus within a 2AFC design (see Supplementary Movies S3 and S4). Adaptor type as the IV had five levels: The first level was the absence of adaptor (i.e., control blocks), and all the others were the four possible relative direction of standard to that of the adaptor (i.e., opposite to plaid, opposite to grating, same to plaid, and same to grating directions). In this example, the standard has a “same to grating” direction, meaning that it has the same motion direction with that of the component gratings of the plaid adaptor drifting upward. The “perceived duration effect” was defined by the PSE differences of a participant in conditions with and without the adaptor across the same variables. The diagram indicates a generic baseline speed of 2.5°/s (instead of having an adjusted level per participant and per condition). Note that in the follow-ups referred as Experiment 2C and D, the speed of standard was set to $\sim 1.581^\circ/\text{s}$ instead of 2.5°/s, and the seven speed levels of comparison were adjusted accordingly (i.e., ranging from $\sim 0.79^\circ/\text{s}$ to $\sim 3.16^\circ/\text{s}$).

the duration compression, then it would be interesting to see whether the strength of this effect would depend on the pattern direction or the component motion directions in the adaptor.

Stimuli and procedure

As shown in Figure 4, stimuli were consisted of luminance-modulated sinusoidal gratings having a spatial frequency of $1\text{c}/^\circ$, presented within a round aperture of 6° , and having 100% Michelson contrast (C_M , as indexed by luminance differences: $(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$). Whereas the test gratings were kept at 100% luminance contrast, the adaptor stimulus had a contrast of 50% C_M in order to avoid fast contrast adaptation.

Changes in the perceived duration of the standard drifting grating stimulus with respect to that of the comparison stimulus was investigated using a plaid

adaptor consisting of two overlapping perpendicular gratings drifting upwards or downwards (see Supplementary Movies S3 and S4). For the adaptor stimulus, the speed of individual overlapping perpendicular gratings were $\sqrt{2.5^\circ/\text{s}}$ ($\sim 1.581^\circ/\text{s}$), resulting in a plaid speed of 2.5°/s. Whereas the speed of the standard test grating was 2.5°/s, the speed of the comparison grating was matched individually for each condition to the perceived speed of the standard according to the values obtained on a prior speed control experiment (for details, please see Experiment 2B). Thus, any effect observed in the apparent duration of the standard test could not be explained by the changes in its perceived speed following a position-specific motion adaptation. The matched speed values varied within a range of $\pm 20\%$ from the baseline speed of 2.5°/s. The extend of the effects were examined as a function of the direction of the comparison, as well as the relative direction of the adaptor with respect to the standard.

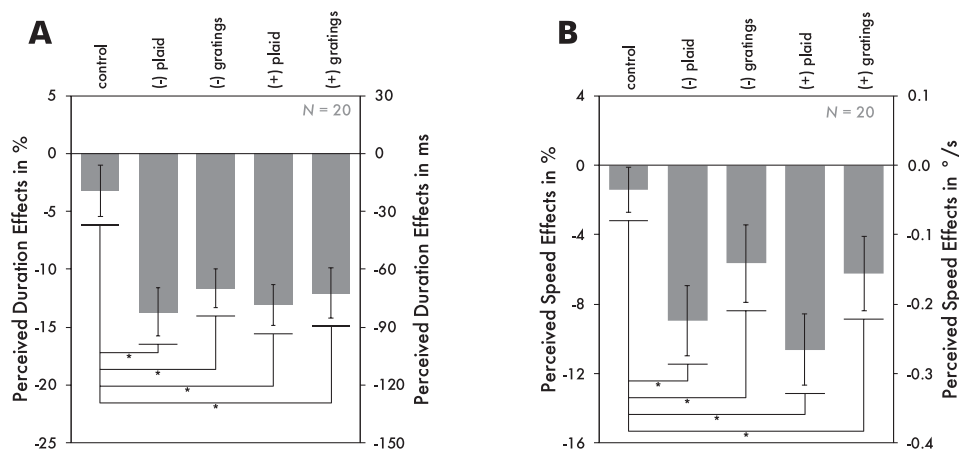


Figure 5. Results of Experiment 2A and B (i.e., short-term motion adaptation in gratings and plaids). The main results on the perceived duration from Experiment 2A (Figure 5A, left panel), and the perceived speed from Experiment 2B (Figure 5B, right panel) following the short-term motion adaptation in the plaid paradigm were visualized as bar graphs. In all graphs, labels above the x-axis indicate experimental conditions using five levels of adaptor type, where labels as control, (–)plaid, (–)grating, (+)plaid, and (+)grating denote control blocks without adaptor and all four possible relative direction of standard to that of the adaptor (i.e., opposite to plaid, opposite to grating, same to plaid, and same to grating directions, respectively). Note that the physical speed of the comparison was matched individually to the perceived speed of the standard in the duration judgment experiment. Y-axes indicate either effects of perceived duration or speed. Bar values were calculated as the difference of means between and control and testing conditions. Error bars indicate the standard error of the means (*SEMs*) of these difference scores. Whenever available, n.s. indicates a nonsignificant and * indicates a significant result, in this case using contrasts after a repeated-measures ANOVA. The perceived duration effects showed significant results across all four experimental condition in comparison to control, as well as the perceived speed effects were significant.

Each trial of the experimental conditions began with a brief prestimulus gray interval of 500 ms. Following the gray screen was the adaptation phase, where participants were presented with a plaid stimulus ($2.5^\circ/\text{s}$, 600 ms) peripherally on one side of the screen centre (e.g., left). In this position, the center of the circular plaid patch was 6° away from the central fixation spot. A 500-ms ISI was then followed by the standard stimulus, which was a drifting grating having the same speed as the adaptor and presented on the same position as the adaptor for an interval of 600 ms. Finally, the comparison drifting grating, consecutive to the standard grating appeared on the nonadapted position, at the opposite side of the fixation point. Whereas the duration of the standard was fixed at 600 ms across trials, the duration of the comparison stimulus had one of the seven levels of durations defined on an equally distributed logarithmic scale, from 300 to 1,200 ms, by using the method of constants. A control condition without an adaptation phase was also included in the study. The number of trials per condition was 140, making a total of 1,120 trials per participant for eight conditions with the aforementioned factors.

In this paradigm, one might argue that any potential significant result may be due to the discrepancies in speed, since the grating components of the adaptor has a speed of $\sqrt{2.5^\circ/\text{s}}$ ($\sim 1.581^\circ/\text{s}$), whereas both the

standard and the comparison gratings have a speed of $2.5^\circ/\text{s}$. To overcome this argument, we also conducted a follow-up experiment (referred as Experiment 2C and D) in which the speed of the adaptor was the same (i.e., consisting of two perpendicular gratings each having a speed of $\sim 1.581^\circ/\text{s}$), but the speed of standard was set to $\sim 1.581^\circ/\text{s}$, and the seven speed levels of comparison were adjusted accordingly (i.e., ranging from $\sim 0.79^\circ/\text{s}$ to $\sim 3.16^\circ/\text{s}$).

Results

For the main experiment, a one-way repeated-measures ANOVA was conducted with five levels, where the first level was the absence of adaptor (i.e., control blocks), and all the others were the four possible relative direction of standard to that of the adaptor (i.e., opposite to plaid direction, opposite to grating directions, same to plaid direction, and same to grating directions). This allowed us to see whether the deviations in the perceived duration following various adaptation conditions were significantly different from the baseline condition. Following the analyses, main effect was found to be significant, $F(4, 76) = 12.699$, $p < 0.001$, $\eta_p^2 = 0.419$. Four planned simple contrasts yielded significant difference for all above-mentioned adaptor conditions ($M_{\text{opposite-to-plaid}} = 517.74$, $SEM_{\text{opposite-to-plaid}} = 12.47$, $M_{\text{opposite-to-grating}} = 530.23$,

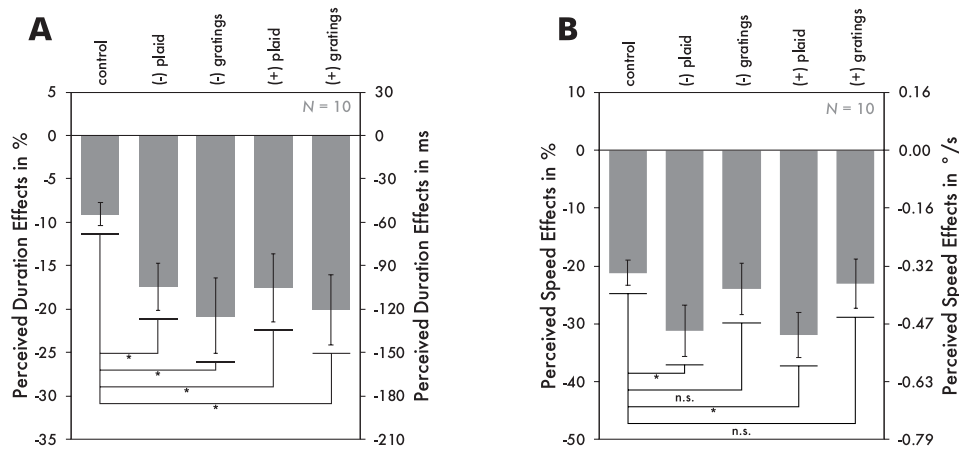


Figure 6. Results of Experiment 2C and D (i.e., follow-up experiments of short-term motion adaptation in gratings and plaids). The main results on the perceived duration from follow-up conditions as Experiment 2C (Figure 6A, left panel), and the perceived speed as Experiment 2D (Figure 6B, right panel) following the short-term motion adaptation in the plaid paradigm were visualized as bar graphs. In all graphs, labels above the x-axis indicate experimental conditions using five levels of adaptor type, where labels as control, (–)plaid, (–)grating, (+)plaid, and (+)grating denote control blocks without adaptor and all four possible relative direction of standard to that of the adaptor (i.e., opposite to plaid, opposite to grating, same to plaid, and same to grating directions, respectively). Note that the physical speed of the comparison was matched individually to the perceived speed of the standard in the duration judgment experiment. Y-axes indicate either effects of perceived duration or speed. Bar values were calculated as the difference of means between and control and testing conditions. Error bars indicate the standard error of the means (SEMs) of these difference scores. Whenever available, n.s. indicates a nonsignificant and * indicates a significant result, in this case using contrasts after a repeated-measures ANOVA. The perceived duration effects showed significant results across all four experimental condition in comparison to control, and the perceived speed effects were significant for two conditions and nonsignificant for the remaining two.

$SEM_{\text{opposite-to-grating}} = 10.16$, $M_{\text{same-to-plaid}} = 521.27$, $SEM_{\text{same-to-plaid}} = 10.65$, $M_{\text{same-to-grating}} = 527.62$, $SEM_{\text{same-to-grating}} = 13.14$) in comparison to control condition ($M_{\text{control}} = 580.61$, $SEM_{\text{control}} = 13.17$), where all F statistics were $F(1, 19) = 39.796$, $p < 0.001$, $\eta_p^2 = 0.677$; $F(1, 19) = 21.702$, $p < 0.001$, $\eta_p^2 = 0.533$; $F(1, 19) = 40.058$, $p < 0.001$, $\eta_p^2 = 0.678$; and $F(1, 19) = 17.912$, $p < 0.001$, $\eta_p^2 = 0.485$, respectively (Figure 5A).

Although the perceived durations were compressed in all adaptor conditions, a significant direction-specific effect was not visible in overall, apart from a subgroup of participants. These findings (i.e., persistence of duration compression, yet lack of direction-selectivity) imply that the brief-adaptation-induced duration compression effects are not purely mediated by the higher level motion areas (e.g., do not have a mere extra-cortical origin in the pattern cells of the area MT+) in which case we would expect to see a significant duration compression selective to the direction of the integrated plaid texture. The absence of a significant difference in the perceived duration effects in the test stimulus drifting in the same- and the opposite-to-the-adaptor motion direction conditions provide further support for the results of Experiment 1A and C, where the data indicated no good evidence of direction selectivity.

The follow-up experiment was treated as a different design due to changed parameters, thus instead of

merging data from both experiments, we rather conducted a single one-way repeated-measures ANOVA. In the follow-up experiment, the main effect was again significant, $F(4, 36) = 5.623$, $p = 0.001$, $\eta_p^2 = 0.385$, and the four planned simple contrasts yielded four significant difference for all above-mentioned adaptor conditions

($M_{\text{opposite-to-plaid}} = 495.21$, $SEM_{\text{opposite-to-plaid}} = 16.15$; $M_{\text{opposite-to-grating}} = 475.41$, $SEM_{\text{opposite-to-grating}} = 25.94$; $M_{\text{same-to-plaid}} = 494.94$, $SEM_{\text{same-to-plaid}} = 23.53$; and $M_{\text{same-to-grating}} = 479.55$, $SEM_{\text{same-to-grating}} = 24.36$) in comparison to control condition ($M_{\text{control}} = 545.45$, $SEM_{\text{control}} = 16.86$), where all F statistics were $F(1, 9) = 18.907$, $p = 0.002$, $\eta_p^2 = 0.678$; $F(1, 9) = 9.488$, $p = 0.013$, $\eta_p^2 = 0.513$; $F(1, 9) = 7.121$, $p = 0.026$, $\eta_p^2 = 0.442$; and $F(1, 9) = 9.785$, $p = 0.012$, $\eta_p^2 = 0.521$, respectively (Figure 6A).

If the compression effects were regulated by a higher level extrastriatal cortical motion area, then one might have expected these effects to be particularly significant in conditions, where the drifting trajectory of the standard is vertical with respect to that of the global motion of the adaptor (i.e., up or down), a prediction not satisfied by our aforementioned results. Our results in Experiment 1, together with Experiment 2, indicate that the behavioral duration compression effect is not selective for the *same* or the *opposite* directions of the

adaptor with respect to that of the standard using both paradigms with RDKs and the plaids.

Experiment 2B: Prior control for perceived speeds in gratings and plaids

In a similar procedure as in Experiment 1B but this time using a plaid adaptor and the grating tests (Figure 4), the perceived speed of the standard was identified individually for each condition to be then used in the main duration experiment (Experiment 2A) to match the perceived speed of the two test stimuli.

Stimuli and procedure

In this speed-judgment task, the speed of the standard grating was fixed at $2.5^\circ/\text{s}$, but the speed of the comparison was varied from trial to trial to take one of the seven levels of speeds defined on an equally distributed logarithmic scale, from $1.25^\circ/\text{s}$ to $5^\circ/\text{s}$. All stimuli, including the adaptor and the tests, lasted for 600 ms on the screen. For the follow-up speed experiment, the same speed task was modified to correspond the changed speeds of standard and test stimulus.

Results

Similar to Experiment 1B, the perceived speed was identified for each condition and participant separately in a procedure shown in Figure 4. Manipulating the relative direction of the standard with respect to that of the adaptor as was done in Experiment 2A, participants made speed judgments (rather than duration judgments) in Experiment 2B. Following the analyses, main effect was found to be significant, $F(4, 76) = 15.880$, $p < 0.001$, $\eta_p^2 = 0.455$. Planned contrasts also revealed that in each adaptor condition (i.e., $M_{\text{opposite-to-plaid}} = 2.28$, $SEM_{\text{opposite-to-plaid}} = 0.05$; $M_{\text{opposite-to-grating}} = 2.36$, $SEM_{\text{opposite-to-grating}} = 0.06$; $M_{\text{same-to-plaid}} = 2.23$, $SEM_{\text{same-to-plaid}} = 0.05$; and $M_{\text{same-to-grating}} = 2.34$, $SEM_{\text{same-to-grating}} = 0.05$) the speed was underestimated, in comparison to nonadaptor condition ($M_{\text{control}} = 2.46$, $SEM_{\text{control}} = 0.03$). The statistical results for contrasts were $F(1, 19) = 36.598$, $p < 0.001$, $\eta_p^2 = 0.658$; $F(1, 19) = 6.429$, $p = 0.020$, $\eta_p^2 = 0.253$; $F(1, 19) = 37.129$, $p < 0.001$, $\eta_p^2 = 0.661$; and $F(1, 19) = 10.390$, $p = 0.004$, $\eta_p^2 = 0.354$, respectively (Figure 5B).

For the follow-up experiments, again a one-way repeated-measures ANOVA with the same five levels of main effect was conducted. Main effect was found significant, $F(4, 36) = 7.641$, $p < 0.001$, $\eta_p^2 = 0.459$. In two adaptor conditions (i.e., $M_{\text{opposite-to-plaid}} = 1.09$, $SEM_{\text{opposite-to-plaid}} = 0.07$; $M_{\text{same-to-plaid}} = 1.08$, $SEM_{\text{same-to-plaid}} = 0.07$) the speed was underestimated,

in comparison to nonadaptor condition ($M_{\text{control}} = 1.25$, $SEM_{\text{control}} = 0.07$), whereas the difference was not significant in two other conditions ($M_{\text{opposite-to-grating}} = 1.20$, $SEM_{\text{opposite-to-grating}} = 0.07$; $M_{\text{same-to-grating}} = 1.21$, $SEM_{\text{same-to-grating}} = 0.07$), as revealed after planned contrasts, $F(1, 9) = 16.198$, $p = 0.003$, $\eta_p^2 = 0.643$; $F(1, 9) = 1.005$, $p = 0.342$, $\eta_p^2 = 0.100$; $F(1, 9) = 14.963$, $p = 0.004$, $\eta_p^2 = 0.004$; and $F(1, 9) = 0.584$, $p = 0.584$, $\eta_p^2 = 0.464$, respectively (Figure 6B).

There are two important aspects of the results to be clarified: Firstly, the perceived speed difference as indexed by percentage (i.e., 10% slower in speed) does not linearly translate into the same amount of bias in perceived duration (i.e., 10% longer in duration). Previous research observing a percent shift in the perceived duration required radically different speed differences indexed by the multitudes of those percentages. Secondly, it is crucial to put the amount of physical difference on perceived speed in perspective for our paradigm: If one were to imagine the drifting gratings as spatiotemporally moving static patterns, then for example, a “significant finding” of $0.1^\circ/\text{s}$ in speed would be translated into ~ 2 pixels of total positional change within the context of its overall trajectory, given the implemented stimulus and display properties in our paradigm. In other words, the perceived speed differences seem to emerge in consequence of using drifting patterns at slow speeds with subsecond presentation times. Note that, regardless of the amount of overall perceived speed change, individual (i.e., per participant and per condition) speed corrections were applied to the main duration experiment.

Experiment 3A: Interocular adaptation effect transfer using shutter glasses

That the short-term adaptation-induced changes in perceived duration depends on the presence of global motion coherence (Experiment 1) and the relative directions of the adaptor and the test (Experiment 2) points to a high-level origin in the brain. Further support to this premise could come from an investigation of the adaptation effects within the context of interocular transfer. If the locus of the effect were some higher level motion processing areas, then it would mean that it is induced at or beyond the primary visual cortex, where the visual information received monocularly from each eye would have already been integrated. If that is the case in fact, then presenting the adaptor to one eye and displaying test stimuli to the other eye would still induce a significant temporal compression effect.

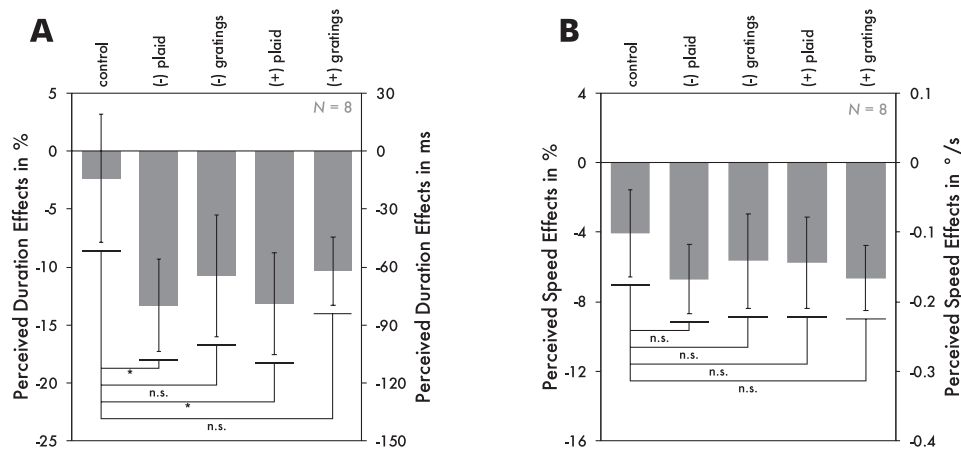


Figure 7. Results of Experiment 3A and B (i.e., interocular adaptation effect transfer using shutter glasses). The main results on the interocular transfer experiment, where the adaptor was presented monocularly to one eye and the test stimuli onto the nonadapted eye and participants were asked to judge either the duration in Experiment 3A (Figure 7A, left panel) or the speed in Experiment 3B (Figure 7B, right panel) of the two drifting grating stimuli were visualized as bar graphs. In all graphs, labels above the x-axis indicate experimental conditions using five levels of adaptor type, where labels as control, (-)plaid, (-)grating, (+)plaid, and (+)grating denote control blocks without adaptor and all four possible relative direction of standard to that of the adaptor (i.e., opposite to plaid, opposite to grating, same to plaid, and same to grating directions, respectively). Note that, the physical speed of the comparison was matched individually to the perceived speed of the standard in the duration judgment experiment. Y-axes indicate either effects of perceived duration or speed. Bar values were calculated as the difference of means between and control and testing conditions. Error bars indicate the standard error of the means (*SEMs*) of these difference scores. Whenever available, n.s. indicates a non-significant and * indicates a significant result, in this case using contrasts after a repeated-measures ANOVA. Whereas the perceived duration effects showed significant interocular transfer, the perceived speed effects were nonsignificant.

Stimuli and procedure

Stimuli and the experimental procedure were similar with minor adjustments such that here, the adaptor and the test stimuli were displayed monocularly to different eyes. Although our LED display worked at 120 Hz resulting in a refresh rate of 60 Hz per eye, it was possible to double this rate (i.e., 240 Hz) by inserting additional in-between frames, which helped reduce motion blur induced by the procedure. Stimuli were also presented at relatively lower contrasts in this experiment (i.e., 80% C_M for the standard and the comparison, 40% C_M for the adaptor) in order to avoid stimuli ghosting on the covered eye. Note that the perceived speeds of the two test stimuli were matched individually for each condition according to the values obtained in the interocular speed judgments experiments (Experiment 3B). In this experiment, we used test gratings with vertical directions (same vs. different) to those of the adaptor plaid (component vs. pattern direction).

Results

A repeated-measures ANOVA revealed that the main effect was significant, $F(4, 28) = 4.019$, $p = 0.011$, $\eta_p^2 = 0.365$, which was further broken down using simple contrasts. As seen in Figure 7A, whereas perceived durations in conditions with opposite-to-plaid ($M = 520.26$, $SEM = 23.79$) and same-to-plaid

directions ($M = 521.06$, $SEM = 26.10$) was significantly shorter than those in the control conditions ($M = 585.81$, $SEM = 33.06$, as yielded by F statistics, $F(1, 7) = 29.906$, $p = 0.001$, $\eta_p^2 = 0.810$, and $F(1, 7) = 22.918$, $p = 0.002$, $\eta_p^2 = 0.766$, perceived durations in the conditions with opposite-to-grating ($M = 535.21$, $SEM = 31.49$) and same-to-grating directions ($M = 538.08$, $SEM = 17.90$) were not different than those in the control conditions, $F(1, 7) = 3.554$, $p = 0.101$, $\eta_p^2 = 0.337$, and $F(1, 7) = 4.044$, $p = 0.084$, $\eta_p^2 = 0.366$, respectively.

These results show that adapting one eye and testing the other preserved the short-term adaptation-based duration change in either conditions for plaid directions. Although we observed that the duration compression in conditions for the same- and the opposite-to-grating directions abolished statistically, this might be due to the noise indicated by the large error bars (Figure 7A). Interocular transfer itself suggests that the neural locus of the brief adaptation effects is at a region, where the information coming from the two eyes are already integrated, i.e., post-LGN.

Experiment 3B: Prior control for perceived speeds

Similar to the previous speed control experiments, the aim was to obtain perceived speeds as indexed by

PSEs so that they could be used in the matched-speed conditions of the duration experiment 3A.

Stimuli and procedure

Analogous to the previous speed control experiments, participant made speed judgments in a 2AFC paradigm, where the adaptor was presented to one eye, and the test stimuli onto the other.

Results

A repeated-measures ANOVA revealed that mean perceived speeds did not differ significantly across five different experimental conditions, $F(4, 28) = 0.630$, $p = 0.645$, $\eta_p^2 = 0.083$. As can be seen in Figure 7B, none of the four conditions (i.e., $M_{\text{opposite-to-plaid}} = 2.33$, $SEM_{\text{opposite-to-plaid}} = 0.05$; $M_{\text{opposite-to-grating}} = 2.36$, $SEM_{\text{opposite-to-grating}} = 0.06$; $M_{\text{same-to-plaid}} = 2.36$, $SEM_{\text{same-to-plaid}} = 0.05$; and $M_{\text{same-to-grating}} = 2.33$, $SEM_{\text{same-to-grating}} = 0.05$) showed any significant difference in comparison to the no-adaptation condition (Figure 7B).

Discussion

Here, we introduced a new effect, where a brief global motion adaptation made a significant change in the perceived duration—but only a slight shift in the perceived speed—of a subsequently presented dynamic stimulus. Our results provided evidence for the followings:

- In RDKs, significant short-term motion adaptation effects on duration compression are present for adaptors with 50% global motion coherence but not for those with 0% global motion coherence, implying the involvement of higher level visual brain areas such as area MT+.
- This effect is dissociable from changes in perceived speed following adaptation, suggesting separate mechanisms for processing visual speed and duration.
- Potential changes or biases in the judgments of stimulus onset and offset cannot account for the adaptation-induced temporal effects, which indicates that the brief adaptation-induced duration compression is not due to a failure in marking the event boundaries of the test.
- Short-term adaptation-induced duration compression does not show a specific direction and 2-D versus 1-D motion selectivity: A significant change with respect to baseline values is obtained for all adaptation conditions, where the test

grating moves in a relatively vertical direction with respect to either the plaid adaptor or the adaptor plaid's component directions, which suggests that the effect is not necessarily modulated in the pattern (versus component) cells.

- Tested using shutter glasses, adaptation effect transfers interocularly across the two eyes, providing further evidence for a cortical or extracortical origin.

Internal clock models generally assume that timing is centralized, and the same neural circuitry applies to every modality and interval. The specificity of the brief motion adaptation-induced duration compression to a coherent global motion signal contradicts such a generic centralized clock (Creelman, 1962; Treisman, 1963; Treisman et al., 1990), which inherently implies a high-level cognitive mechanism. The presented effect being spatially localized to the position of the adaptor provides evidence that time and space are linked in the visual system and that there exist distributed, modality-specific (i.e., visual) timing mechanisms (for a discussion on distributed versus specialized timing theories, see Ivry & Schlerf, 2008; Ivry & Spencer, 2004). We know that all sensory processing eventually relies upon spatiotemporal patterns of neural activity. We suggest that if time is also considered a sensory attribute like color and motion, then one may find a neural circuit for the encoding of duration, which extends from the sensory surface of retina to the subcortical and cortical parts of the brain. This time pathway might also be using the same units as the motion processing system, an idea originally coined by Johnston et al. (2006). This theory is supported by the evidence that sensory areas involved in spatial vision and motion perception (i.e., MT+) are also involved in visual duration perception (Buetti, Bahrami, & Walsh, 2008; Buetti & Walsh, 2009).

Following the event time theory that links long-term temporal frequency adaptation effects to the contrast gain mechanisms in the early-level regions—such as LGN (Johnston, 2010)—one might argue that the duration compression effect induced by brief visual motion we report here might also have a similar origin. The disappearance of the effect at 0% global motion coherence, however, together with the interocular transfer suggest rather a higher level source, potentially at the area MT+. Although the loci where take place *the long-term temporal frequency adaptation* Johnston et al. (2006) have reported and *the brief motion adaptation* on perceived duration we report here seem to be different in the visual pathway, we think that the mechanisms might be common, though; namely, the temporal phase shifts in the response of neurons resulting from different temporal adaptation regimes. In a neurophysiology study, Priebe and Lisberger (2002) showed that short motion-adaptation regimes cause a shift in the phase of temporal impulse response—i.e., latency of

response—of MT+ cells, a higher level contrast gain effect to which our empirical data indicating coherent motion selectivity here (Experiment 1A and C) may be linked. This theoretical frame is also compatible with the *event time theory*, where long-term adaptation-dependent changes in the amplitude of the transient cells are linked to the changes in the subjective temporal frequency, whereas compression of the temporal impulse function is linked to the apparent duration compression (Johnston et al., 2006). Supportingly, our results demonstrate that the effects of short-term motion adaptation on perceived duration and speed are dissociable, as the changes in perceived speed following the adaptation are not significant (Experiment 1B) as opposed to those in perceived duration (Experiment 1A). Although the perceived speed bias was found to be significant in Experiment 2B, notice that all duration effects we report here were conducted following an individual and condition-based speed matching between the two test stimuli, so the effects of changes in perceived speed after adaptation were all controlled in the duration judgment tasks.

The pattern cells in area MT+ are known to be sensitive to the true direction of complex patterns at the global motion processing level, whereas component cells process the signal coming from the 1-D components of a moving pattern (see Wang & Movshon, 2016). The results of our Experiments 2A and C have shown that brief plaid adaptors induce significant duration changes on gratings moving either in the same or opposite direction of motion with respect to the combined direction of the pattern, or the individual directions of component gratings of the plaid in blocked trials. These results demonstrate that brief-adaptation-induced duration changes are not direction selective (Figures 5A and 6A). In Priebe and Lisberger's (2002) neurophysiology study, however, the changes in the *latency* of the neurons were only found to be for the adaptors moving in the *opposite* direction relative to that of the test; thus, the direction selectivity effect being non-existing in our behavioral data makes it difficult to establish a direct link between the two. There seems to be different contrast-gain mechanisms at each hierarchical level of the motion processing pathway playing part in interval timing, however (i.e., early-level contrast gain being also present in MT+ cells; Kohn & Movshon, 2003); thus how these may interact to yield our current behavioral results might not be as straightforward and require further modeling in the future.

In a long-term adaptation paradigm with an initial adaptation of 30- and 5-s top-ups, Curran and Benton (2011) showed a direction-selective adaptation-induced duration compression. In this study, they demonstrated that the subjective duration of test stimulus gets reduced only when a slow array of dots moved in the

same direction as the adaptor. They also used plaid adaptors to provide evidence that this effect is direction-selective for the pattern, rather than the component motions, indicating an extrastriatal involvement. Although, at first sight, the results of this study might seem to be controversial to our findings, as we have not obtained a strong evidence for direction selectivity, neurophysiology studies have shown that prolonged and short-term adaptation, used in Curran and Benton's and our studies, respectively, have dissociable influence on the contrast gain response characteristics of the MT+ cells (Kohn & Movshon, 2003; Priebe & Lisberger, 2002). Thus, we think that these two effects might take source from different mechanisms of contrast gain. Yet they, together, provide evidence for high-level visual mechanisms of event timing.

Recent evidence in the literature showed that long-term adaptation-induced duration compression is selective for only translational motion and that complex motion trajectories, such as radial or circular motion, have a negligible effect on perceived duration (Fornaciai, Arrighi, & Burr, 2016). On the basis of their results, the authors concluded that adaptation-induced duration compression is necessarily specific to unidirectional adaptation and that any multidirectional adaptation has no influence on perceived duration. Our current results here, however, suggest that this is not necessarily the case, and that significant duration effects could still be observed using complex texture adaptors with multidirections (i.e., plaids) if suitable adaptation regimes are applied (i.e., with slower speeds and brief adaptation periods). We argue that this discrepancy across long- and short-term adaptation effects might suggest that manipulations known to change the shape of temporal impulse response at different stages in the motion processing pathway are specific to different stimulus parameters and that they may result in differential effects on perceived duration.

There is a controversy in the literature with regard to both the frame of reference and the interocular transfer for the long-term adaptation-induced duration compression. Whereas Bruno et al. (2010) found the adaptation effects to be purely retinotopic and non-transferrable from one eye into the other using various paradigms (i.e., pursuit and saccadic), Burr et al. (2007) provided evidence for both spatiotopy and interocular transfer, implying a rather higher level cortical origin. This controversy was recently addressed by Latimer and Curran (2016) using plaid adaptors rather than drifting gratings as had been used by previous studies. Their results showed evidence for both retinotopic and spatiotopic adaptation. Thus, Latimer and Curran (2016) argued that one needs to use a suitable stimulus set in order to reveal spatiotopic effects. This argument is in line with our conclusion that stimulus parameters

are important in revealing duration effects taking place at different levels of visual hierarchy. In fact, here, using a very brief adaptation regime in a complex motion setup, we also provided evidence for an interocular transfer.

In a timing model suggested by Buonomano, Karmarkar, Merzenich, and their colleagues (Buonomano & Karmarkar, 2002; Buonomano & Merzenich, 1995; Karmarkar & Buonomano, 2007; Mauk & Buonomano, 2004), neural circuits are inherently capable of temporal processing by means of their time-dependent neuronal properties. In this model, time is encoded in the population activity of neurons that might be facilitated/depressed by a physiological learning process, which in turn changes the responses to following pulses. Here, the presented adaptation effects on subjective time, however, are selective for global motion signal rather than duration per se, a feature hard to accommodate within a population clock framework. Our results, revealing compression in subjective duration following a rather brief adaptation cannot find an explanation by alternative *duration-channel* accounts either (e.g., Heron et al., 2012), which would predict an expansion rather than a reduction following an adaptation to a relatively short interval within the context of a population coding model composed of a series of broadband duration channels.

As for spatial priming by the adaptor, one might argue that the temporal effects we report here could be accounted by attention drawn to the location of the standard stimulus following adaptation. Attention, however, is known to dilate, rather than compress subjective duration (Tse et al., 2004). Moreover, the precisions as indexed by the width of psychometric functions did not show a significantly different trend across conditions, which eliminates the possibility that the source of the reported duration compression effect is attentional.

Onset and offset transients might be used as cues to interval timing, which would imply an indirect process, where the estimates would be based on tagged intervals for which the neural system remains active (Johnston & Nishida, 2001). Here, we introduced temporal jitter at the onset and offset of our random dot stimuli in Experiment 1 in order to prevent our participants' use of abrupt transients as cues. In a separate control, in Experiment 1D, we have also investigated individual points of subjective simultaneity, where—in separate blocks—participants judged the temporal order of the onset and the offset of the standard test to an audio tone. The results of this experiment demonstrated that the changes in perceived duration of the standard following adaptation cannot be explained by changes in latency at onset relative to offset, thus, discarding the explanations within the context of a failure in marking the event boundaries of the test.

All in all, we demonstrate evidence for sensory mechanisms mediating duration effects in higher level motion areas. We also show that the effects of adaptation on perceived duration are dissociable from those on perceived speed such that (a) the average of perceived speeds following adaptation does not show a significant difference across different coherence conditions, as opposed to the trend observed in subjective duration effects, and more importantly, (b) the duration compression effect survives even after the speeds of the test stimuli are matched using individual corrections per condition. Unlike the traditional approach to time perception—the underlying mechanisms of which are supposed to be in the brain and mostly isolated from the sensory encoding strategies—following the seminal Johnston et al. study (2006), together with our aforementioned early work (Ayhan et al., 2009, 2011; Bruno et al., 2010) and our current results, we suggest that there might be a sensory time pathway for processing brief time intervals in the visual system, starting from the early-level regions towards the higher level areas in the visual cortex, the latter of which is supported by our current findings. This is a novel approach that is gaining increasing evidence in the field.

Keywords: time perception, motion perception, adaptation, motion pathway

Acknowledgments

We provide our special thanks to Alan Johnston for reading and providing comments on an earlier version of this manuscript as part of the first author's thesis defense. We also provide our thanks to Dilce Tanriverdi for helping us with the part of data collection. Our research is funded by Bogazici University Scientific Research Projects, Project No: 9248.

Commercial relationships: none.

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Supplementary material

Supplementary Movie S1. Random Dot Kinematogram (RDK) Paradigm, where participants are asked to judge the duration of the two RDK stimuli following a brief adaptation phase within a 2AFC design. Here, the adaptor dot array has a motion coherence of 0%

Supplementary Movie S2. Random Dot Kinematogram (RDK) Paradigm, where participants are asked to judge the duration of the two RDK stimuli following a brief adaptation phase within a 2AFC design. Here, the adaptor dot array has a motion coherence of 50%

Supplementary Movie S3. Plaids and Gratings Paradigm, where participants are asked to judge the duration of two drifting grating stimuli following a brief adaptation to a plaid stimulus within a 2AFC design. Here the drift direction of the standard grating is opposite to that of one of the plaid adaptor's component directions

Supplementary Movie S4. Plaids and Gratings Paradigm, where participants are asked to judge the duration of two drifting grating stimuli following a brief adaptation to a plaid stimulus within a 2AFC design. Here the drift direction of the standard grating is opposite to that of the plaid adaptor