Changes in apparent duration follow shifts in perceptual timing

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It is well established that the apparent duration of moving visual objects is greater at higher as compared to slower speeds. Here we report the effects of acceleration and deceleration on the perceived duration of a drifting grating with average speed kept constant (10°/s). For acceleration, increasing the speed range progressively reduced perceived duration. The magnitude of apparent duration compression was determined by speed rather than temporal frequency and was proportional to speed range (independent of standard duration) rather than acceleration. The perceived duration reduction was also proportional to the standard length. The effects of increases and decreases in speed were highly asymmetric. Reducing speed through the interval induced a moderate increase in perceived duration. These results could not be explained by changes in apparent onset or offset or differences in perceived average speed between intervals containing increasing speed and intervals containing decreasing speed. Paradoxically, for intervals combining increasing speed and decreasing speed, compression only occurred when increasing speed occurred in the second half of the interval. We show that this pattern of results in the duration domain was concomitant with changes in the reported direction of apparent motion of Gaussian blobs, embedded in intervals of increasing or decreasing speed, that could be predicted from adaptive changes in the temporal impulse response function. We detected similar changes after flicker adaptation, suggesting that the two effects might be linked through changes in the temporal tuning of visual filters.

Introduction

Our judgment of the duration of a subsecond interval can be biased by either generic, supramodal factors or modality- and stimulus-specific factors. Some studies have shown that manipulating attention (Cicchini & Morrone, 2009; Tse, Intriligator, Rivest, & Cavanagh, 2004) or stimulus novelty (Matthews, 2011b; Pariyadath & Eagleman, 2007, 2008) can alter the apparent duration of an interval containing a visual stimulus. These factors can be considered generic and cognitive in nature, and their influence on our perception of subsecond duration might be ascribed to the effect of supramodal mechanisms like, for instance, those that link duration processing to arousal (Droit-Volet & Wearden, 2002) or coding efficiency (Eagleman & Pariyadath, 2009).

However, in the visual domain we can find several examples of changes in perceived duration caused by modality-specific manipulations. High-temporal-frequency adaptation to motion or flicker (Ayhan, Bruno, Nishida, & Johnston, 2009, 2011; Bruno, Ayhan, & Johnston, 2010; Burr, Tozzi, & Morrone, 2007; Johnston, Arnold, & Nishida, 2006; Johnston et al., 2008), fast contrast adaptation (Bruno & Johnston, 2010), and dark adaptation (Bruno et al., 2011) have all been shown to affect duration judgments for subsequently displayed stimuli. A generic, cognitive approach cannot readily accommodate these results, as they are often spatially localized. An alternative model, which assumes that visual duration processes share the

Citation: Bruno, A., Ayhan, I., & Johnston, A. (2015). Changes in apparent duration follow shifts in perceptual timing. *Journal of Vision, 15*(6):2, 1–18, http://www.journalofvision.org/content/15/6/2, doi:10.1167/15.6.2.

doi: 10.1167/15.6.2 Received October 20, 2014; published May 1, 2015 ISSN 1534-7362

same early mechanisms used for visual motion and temporal change processing, has been proposed (Johnston, 2010, 2014). This model attempts to link the aforementioned changes in apparent duration after adaptation to concurrent changes in the temporal impulse response of early visual neurons.

The perceived duration of an interval has been shown to depend, to some extent, on its content. The relationship between apparent duration and stimulus speed (or temporal frequency) has been the preferred route to study the effect of content on time perception. Dynamic stimuli are perceived to last longer than stationary stimuli (J. F. Brown, 1931; S. W. Brown, 1995) and higher speeds (Kaneko & Murakami, 2009) or higher temporal frequencies (Kanai, Paffen, Hogendoorn, & Verstraten, 2006) induce duration overestimation relative to lower change rates. Traditionally, this dependency of perceived duration on stimulus speed (or temporal frequency) has been ascribed to the effect of a change-sensitive mechanism (Block & Reed, 1978; Fraisse, 1963; Poynter, 1989): The higher the number of temporal changes detected within a given interval, the longer the duration is perceived to be. Faster stimuli contain more changes, and therefore the duration of the intervals that contain them is overestimated relative to that of intervals containing slower or stationary stimuli.

In this study, we measured perceived duration for intervals that contain stimuli with increasing or decreasing speed across the interval, but with the same average speed (and therefore containing the same number of temporal changes). Previous work has shown that acceleration can induce perceived duration compression. Matthews (2011a) addressed the effect of speed changes on the apparent duration of visual stimuli using various shapes that rotated around their center or translated across the screen. For translation, when subjects categorized duration, apparent duration compression was found to be greater for accelerating than decelerating patterns, with both compressed relative to constant-speed patterns. There was no difference for acceleration and deceleration for reproduction. Binetti, Lecce, and Doricchi (2012) investigated how rate changes can affect the perceived duration of flickering and drifting patterns. They analyzed duration estimates for Gabor patterns whose grating carriers could be accelerating, decelerating, or drifting at constant speed in different sessions. They showed that acceleration induced a strong apparent duration compression (between ~20% and ~40%, according to different stimulus manipulations), whereas deceleration caused only a slight apparent dilation. Using similar stimuli, Sasaki, Yamamoto, and Miura (2013) also found that the apparent duration of an interval containing acceleration was compressed relative to that of an interval containing deceleration. No change in apparent average speed was observed between the two conditions.

Here we extend the investigation of speed change on duration perception to a wider range of stimulus conditions. We found that, when we systematically increased the speed of the embedded stimulus, the duration of the interval was underestimated, whereas decreasing speed caused only a mild apparent duration dilation. The effect was substantial (up to ~30% reduction) but limited to duration perception, as no difference emerged for either duration discrimination, perceived onset/offset, or perceived average speed. We also show that these perceived duration changes are accompanied by the advent of apparent motion between simultaneously presented Gaussian blobs that were transiently superimposed on the increasing- or decreasing-speed stimuli. Similar apparent motion effects were observed after flicker adaptation, a manipulation that has previously been shown to induce apparent duration compression (Johnston et al., 2006).

These results suggest a link between adaptation-induced and content-dependent distortions of apparent duration. Changes in the temporal tuning of early visual neurons, revealed by changes in the temporal impulse response measured psychophysically, might be the common mechanism underlying these phenomena.

General methods

Observers

Five observers (AB, IA, and three naïve observers) participated in the perceived-duration (Experiment 1) and perceived-onset/offset (Experiment 2) experiments. Five observers (AB, AJ, and three naïve observers) participated in the experiments on perceived average speed (Experiment 3), perceived duration with matched average speed (Experiment 4), perceived duration with half increasing, half decreasing speed (Experiment 5), and perceived duration with different combinations of temporal and spatial frequencies (Experiment 6). Ten observers (AB, AJ, and eight naïve observers) participated in the apparent-motion experiment (Experiment 7). We chose to include a larger number of observers in this experiment because we noted that the size of the effect was small in pilot experiments. Finally, five observers (AB, IA, and three naïve observers) participated in the adaptation experiment (Experiment 8).

Apparatus

Stimuli were displayed, in a darkened room, on a gamma-corrected 19-in. Sony Trinitron Multiscan

500PS monitor with a refresh rate of 100 Hz. The stimuli were generated in MATLAB using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997) and viewed from a distance of 57 cm.

Stimuli

In Experiments 1–6, the visual stimuli we used were luminance-modulated sinusoidal gratings (spatial frequency: 1 c/°, diameter: 5°, distance from center of screen: 5°, 80% Michelson contrast). All stimulus waveforms were amplitude modulated by a temporal Gaussian envelope ($\sigma =$ standard duration/6) to avoid sudden signal onset or offset effects. In Experiment 7, we used the same luminance-modulated sinusoidal gratings, except the Michelson contrast was lower (50%) and luminance-modulated Gaussian blobs ($\sigma = 0.83°$ of visual angle, 80% Michelson contrast in the center of the patch) were superimposed on the gratings. The same Gaussian blobs were also used in Experiment 8.

Experiment 1: Effect of speed changes on perceived duration

Two intervals, identical in terms of duration, do not appear to have the same extent in time if the rates of change of the embedded stimuli are different. Higher speed (Kaneko & Murakami, 2009) and higher temporal frequency (Kanai et al., 2006) both lead to duration overestimation. However, a change model (Block & Reed, 1978; Fraisse, 1963; Poynter, 1989) would predict no difference in apparent duration between two intervals containing the same number of temporal changes (i.e., same number of cycles in a drifting sinusoidal grating). We showed in a previous study (Bruno et al., 2012) that the apparent duration of intervals containing an equal amount of static and moving stimuli did not correspond to the average of their components, a finding that is inconsistent with the change model. Here, we measured the influence of speed changes on the ability to correctly estimate the duration of a subsecond interval. In particular, we measured the perceived duration of an interval containing either increasing or decreasing speed (same average speed, 10°/s, therefore the same number of temporal changes) relative to an interval containing constant speed (10°/s, Figure 1A).

Methods

Participants were asked to fixate the center of the screen while the two tests were displayed sequentially on either side of fixation, separated by a 500-ms blank interval. We randomized the presentation order and side on a trial-by-trial basis. The standard had fixed duration across trials (300, 600, or 900 ms in different sessions), whereas we varied the comparison duration in seven steps (between 0.33 × standard duration and 1.67 × standard duration) in order to generate a psychometric function (fitted with a cumulative Gaussian function; each function was based on at least 140 trials, depending on subject availability—i.e., 20 repetitions per data point). The comparison drifted at 10°/s in all conditions. In each experimental session, we interleaved trials where the speed of the standard linearly increased from Speed 1 (which could be 0°/s, 2°/s, 4°/s, 6°/s, 8°/s, or 10°/s in different sessions) to Speed 2 (which was 20°/s, 18°/s, 16°/s, 14°/s, 12°/s, or 10°/s, respectively) with trials where it decreased linearly from Speed 2 to Speed 1 across the interval. The average speed was 10°/s for all the Speed 1–Speed 2 pairs. At the end of each trial, subjects had to indicate which test stimulus appeared to last longer by a key press. The point of subjective equality of the resulting psychometric function provided a measure of perceived duration. The discrimination threshold was defined as the width of the underlying Gaussian error distribution σ (corresponding to the difference between the 50% and 84% points on the psychometric function).

Results

Figure 2A shows apparent duration expressed as percentage differences relative to the standard durations (300, 600, or 900 ms) for the two speed conditions (increasing and decreasing) and for the six different speed ranges (see Figure 1B). Figure 2B plots the duration discrimination thresholds expressed as a percentage of the standard duration for the same conditions as in Figure 2A. Apparent duration compression was found for the increasing-speed condition (maximum ~30%), whereas a very mild apparent expansion (maximum ~10%) was observed for the decreasing-speed condition (general-linear-model repeated-measures ANOVA): main effect of speed condition, $F(1, 4) = 11.389$, $p < 0.05$. Statistical analyses did not reveal any significant effect for duration discrimination. The size of the perceived duration change differed with speed range: main effect, $F(5, 20) = 21.581$, $p < 0.001$. The effect of speed range depended on speed condition, as revealed by a significant interaction between the two factors, $F(5, 20) = 12.602$, $p < 0.001$. We conducted a trend analysis to investigate the nature of this dependency. We found a significant linear trend for speed range, $F(1, 4) = 34.623$, $p < 0.005$, and also for the interaction between speed range and speed condition, $F(1, 4) = 29.596$, $p < 0.01$. When we then analyzed the increasing- and decreasing-

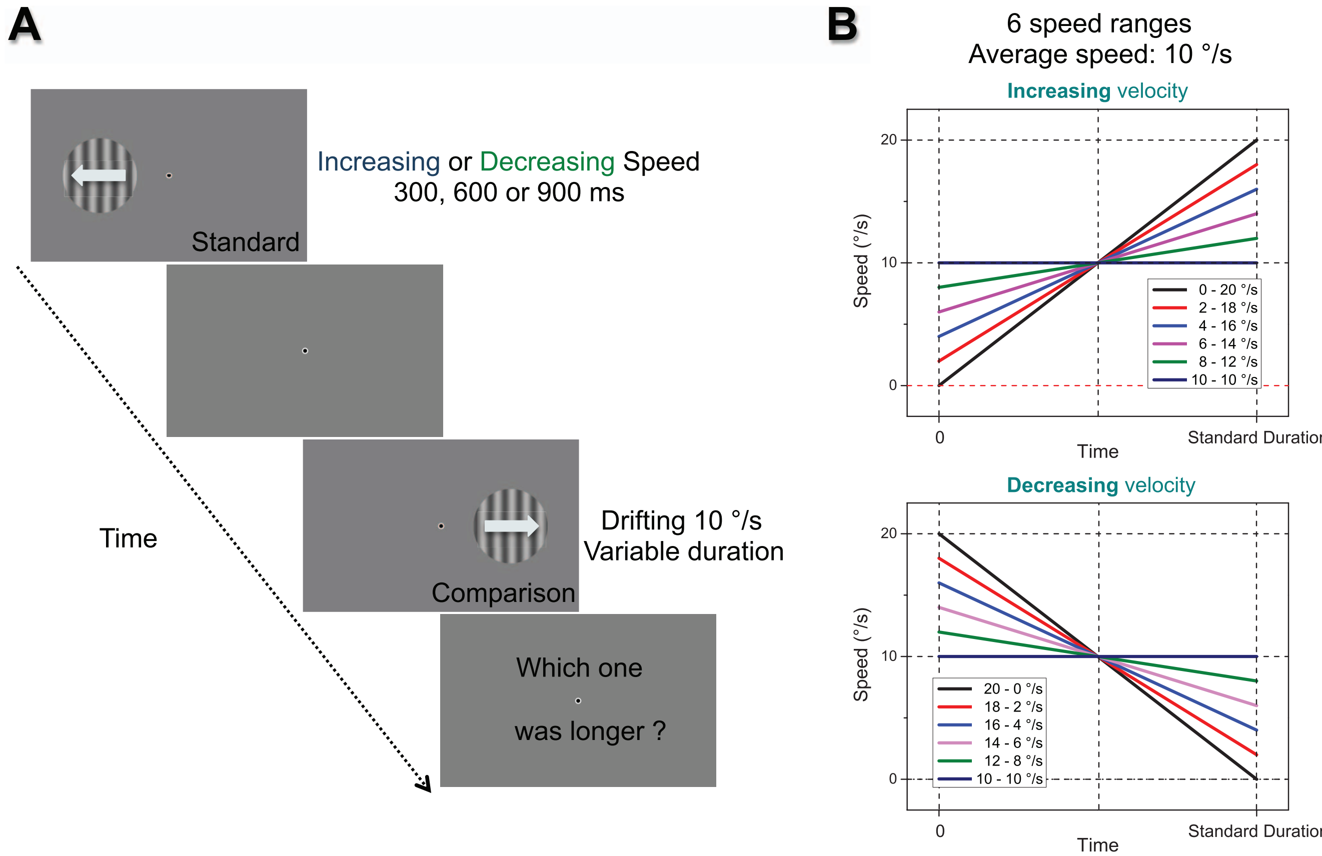

Figure 1. Schematic representations of the stimuli and the task. (A) Participants fixated the middle of the screen while two intervals (the standard, with fixed duration, and the comparison, with variable duration across trials) were sequentially displayed on either side of the fixation spot. We interleaved trials where the standard contained a drifting sinusoidal grating that linearly increased its speed across the interval with trials where the standard contained the same type of stimulus but decreasing its speed within the same range. The comparison always drifted at a constant speed that corresponded to the average speed of the standard (10°/s). (B) In different sessions, the standard interval could contain a stimulus that increased or decreased its speed following one of six possible combinations of initial and final speed (i.e., six speed ranges). The absolute values of the ranges for increasing and decreasing speed were the same; we simply swapped the initial and final speeds. For each speed range, speed increased (or decreased) linearly from the onset of the interval to its offset, and the average speed was always the same, 10°/s. The 10°/s–10°/s range corresponded to a constant 10°/s drifting speed across the interval.

speed data separately, in order to disentangle their contributions to the observed trend, we found a significant linear trend for speed range only in the increasing-speed data, $F(1, 4) = 133.781$, $p < 0.0001$, for which compression increased with speed range, whereas for decreasing speed there was no dependency on speed range.

The observed pattern was consistent across the three standard durations, as revealed by a nonsignificant main effect of the standard duration, $F(2, 8) = 0.159$, $p = 0.856$, and by nonsignificant interactions between the standard duration and both speed range, $F(10, 40) = 1.449$, $p = 0.195$, and speed condition, $F(2, 8) = 1.91$, $p = 0.21$. This observation suggests that the speed range, which did not change across standard durations, could be more important than acceleration or deceleration, which changes with the interval duration since the initial and final speed are kept constant. To illustrate this, we replotted the same perceived-duration results from Figure 1B as a function of acceleration (Figure 3A) and deceleration (Figure 3B), defined as the ratio between the speed range and the standard duration. Apparent duration compression was more pronounced for higher acceleration values, whereas the opposite pattern is observable for deceleration, with the peak apparent expansion occurring for low deceleration values. More importantly, one can see that there are multiple data points with the same acceleration value which do not have the same apparent duration change (for instance, the second lowest value for 300 ms has the same acceleration value as both the third lowest for 600 ms and the fourth lowest for 900 ms, but this condition clearly has a much lower perceived duration change associated with it). In Figure 3C and D, the same data presented in Figure 2A for different standard durations are plotted on the same graph for increasing

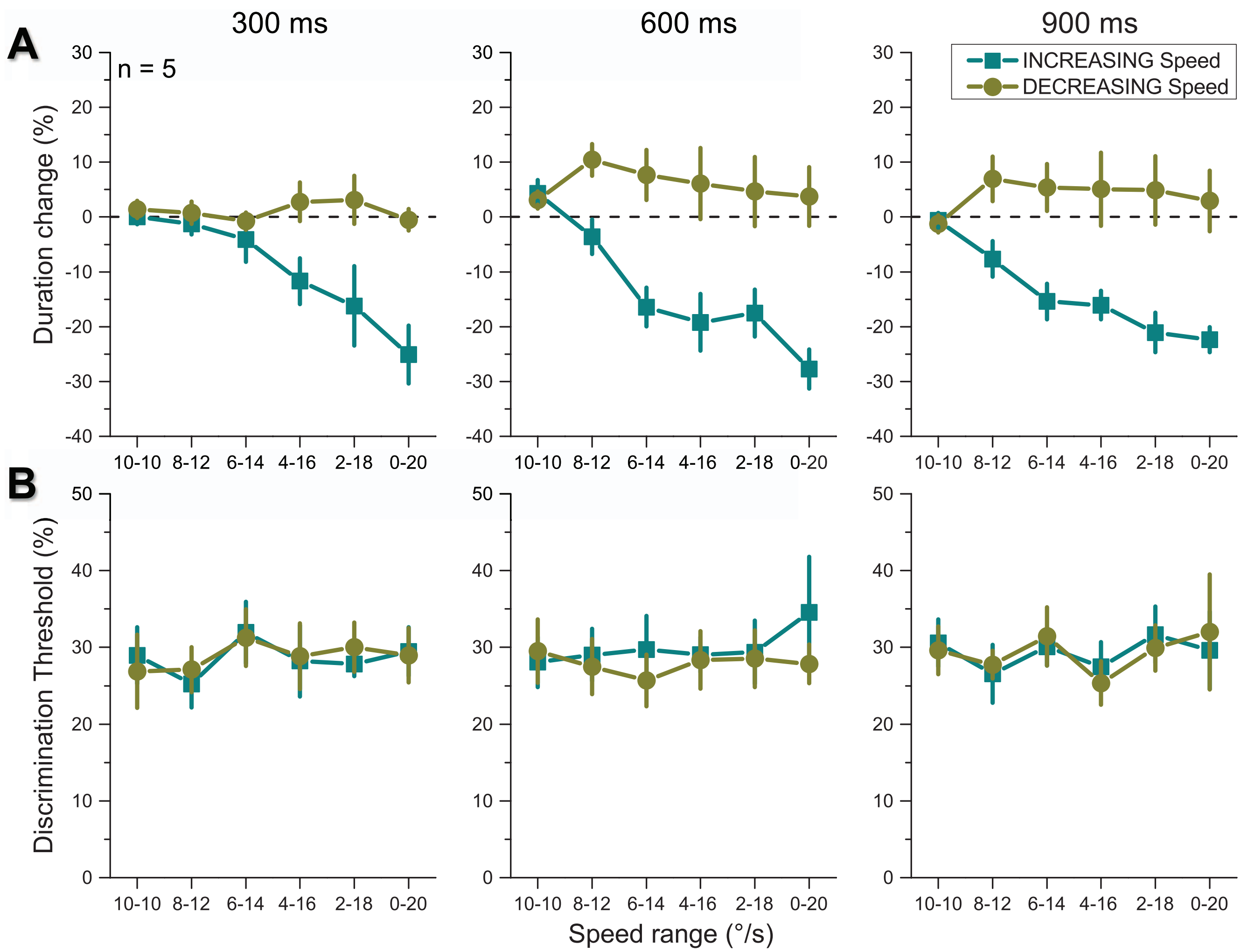

Figure 2. Effect of speed changes on apparent duration and discrimination thresholds. (A) Mean apparent duration change (calculated as the percentage change in perceived duration, as indicated by the point of subjective equality, relative to the actual interval duration) across five subjects for three standard durations (different panels) and two stimulus configurations (increasing speed: dark cyan squares; decreasing speed: dark yellow circles) plotted as a function of speed range. Note that, in order not to clutter the graph text, we only report the initial and final speeds of the increasing-speed conditions. For the decreasing-speed conditions, the two values were simply swapped. (See text for further details.) Dashed lines represent no change relative to the actual standard durations. Error bars indicate ±1 standard error of the mean. (B) Average discrimination thresholds (defined as the difference between the 50% and 84% points on the psychometric function, expressed as percentage of the standard duration) for the same participants and conditions as in (A). Note: Here and in subsequent figures, *duration* refers to apparent duration. Error bars indicate ±1 standard error of the mean.

and decreasing speed, respectively. The degree of overlap for the increasing-speed condition is clearly higher than in Figure 3A, whereas there is no obvious difference for the decreasing-speed condition. Figure 3C also shows that, for increasing speed, the linear correlation between the apparent duration change and the difference between initial and final speed (the error on the y-axis was taken into account when the fit was calculated) was highly significant for all the standard durations (all $ps < 0.005$). More specifically, the amount of perceived duration compression progressively increased with the difference between initial and final speed (all Pearson's $Rs < -0.94$). In comparison, none of the correlations were significant for decreasing speed, indicating that no particular linear trend emerged there.

Experiment 2: Changes in perceived stimulus onset/offset cannot account for the apparent duration effect

One might argue that the asymmetric effect of increasing versus decreasing speed on perceived duration is due to differences in latencies at onset relative to

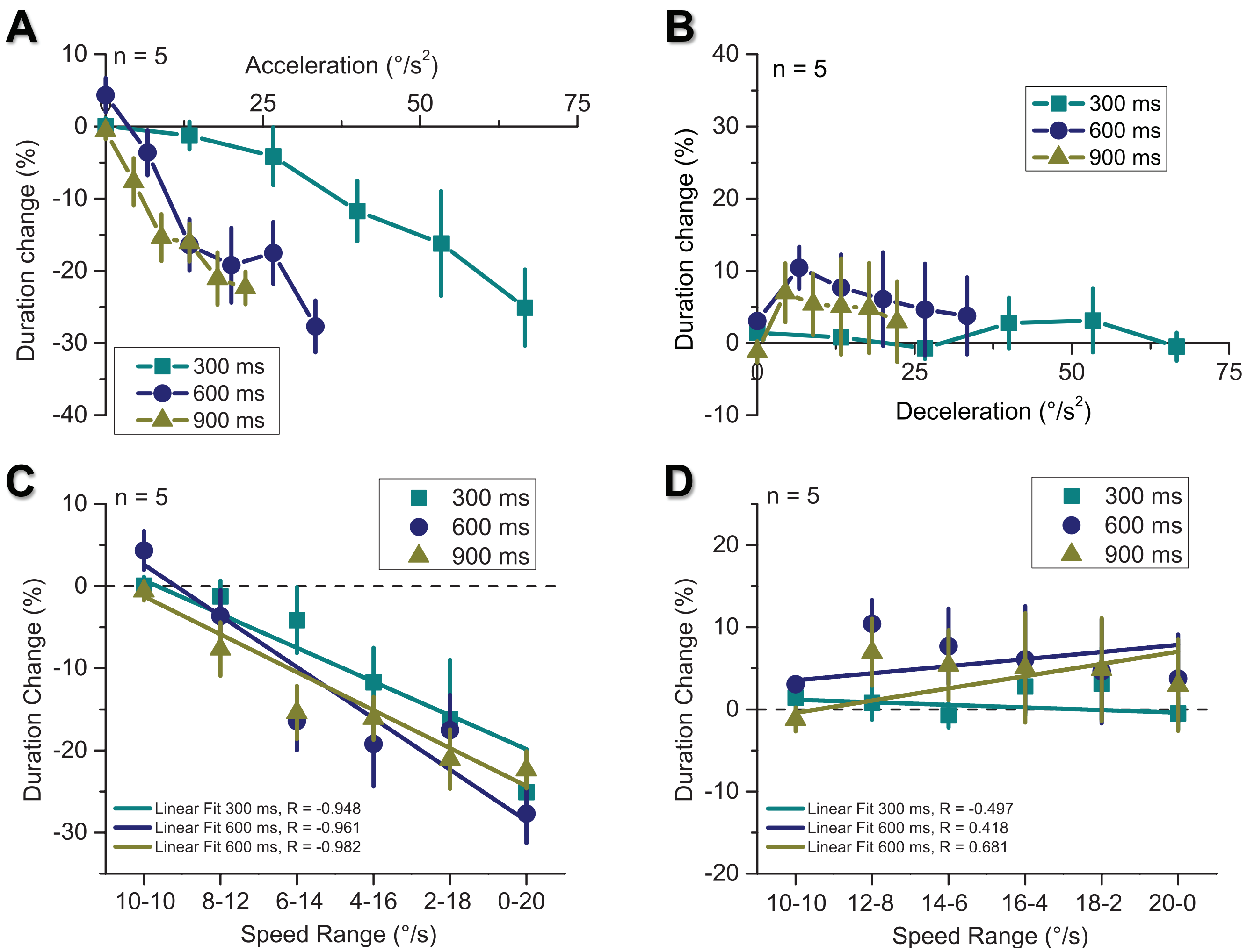

Figure 3. Comparison between the effect of acceleration/deceleration and that of speed range on apparent duration. (A) The same results reported in Figure 2A for the increasing-speed conditions were recalculated here as a function of acceleration (speed range/standard duration), rather than speed range, for three standard durations. The color and symbol coding is the same as in Figure 2A. Error bars indicate ±1 standard error of the mean. (B) The decreasing-speed results plotted in Figure 2A are reported here as a function of deceleration. Error bars indicate ±1 standard error of the mean. (C) For each standard duration separately, we calculated and plotted here the linear fits for the same results reported in Figure 2A for the increasing-speed conditions. Pearson's *R*s are reported at the bottom of the graph. The dashed line represents no change relative to the actual standard durations. Error bars indicate ±1 standard error of the mean. (D) The same as in (C), but for the decreasing-speed conditions.

offset. In fact, for each speed range, in the two main conditions (increasing and decreasing speed), initial and final speeds are reversed, and we know that stimulus visibility also depends on speed. Even though all the test stimuli were contained within a Gaussian temporal envelope to avoid sudden perceptual effects at onset or offset, we wanted to make sure that the perceived start and end points of our intervals were not a key contributor to the perceived duration effects. Our observers were thus required to perform a cross-modal temporal-order task, in which they compared the onset or the offset of a visual stimulus of the same type as those used previously with the onset of a brief auditory stimulus while we varied their relative timing (Figure 4A).

Methods

The visual stimuli were identical to those used in the Experiment 1. The auditory stimulus was a 30-ms 3-kHz tone generated by a TDT Basic Psychoacoustic Workstation (Tucker-Davis Technologies, Alachua, FL) and delivered binaurally by Sennheiser HD 265 linear headphones at 80 dB. On a trial-by-trial basis, we varied the time at which the tone was presented from 200 ms before to 200 ms after the onset or the offset (in different sessions) of a single visual stimulus. Subjects

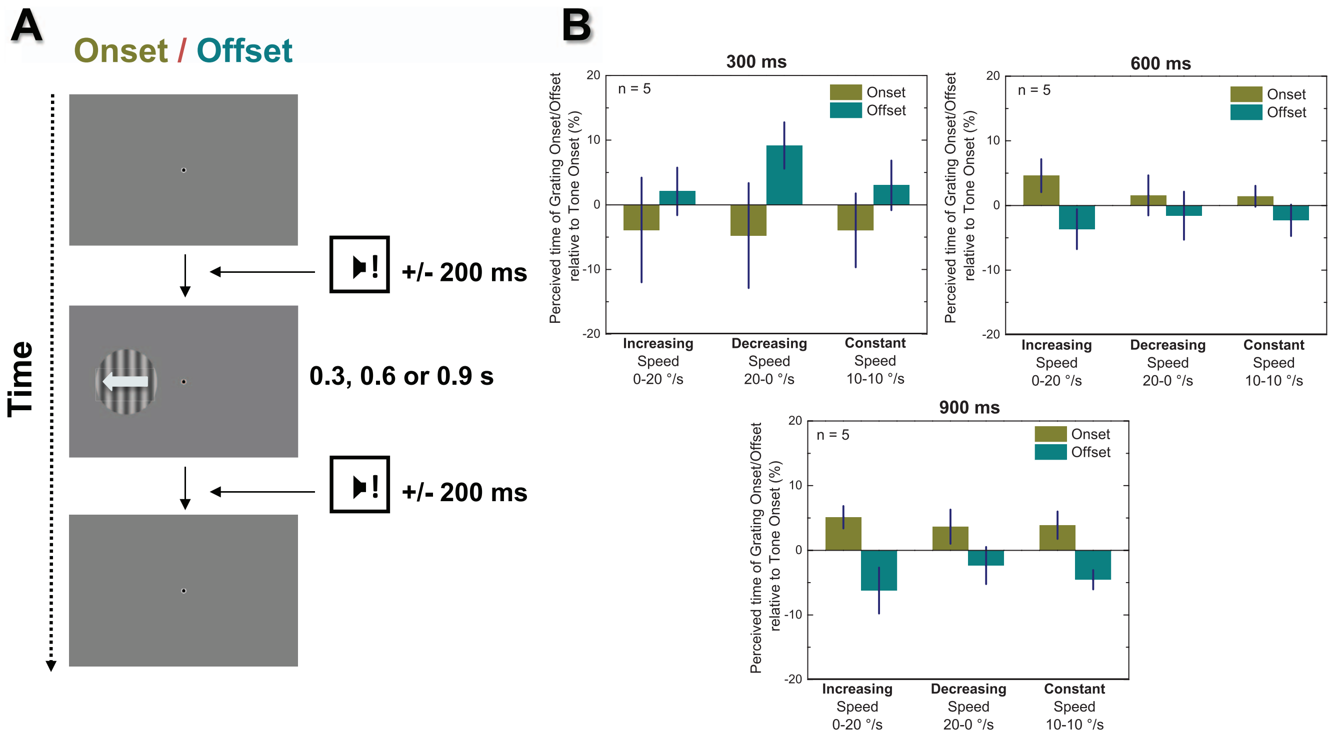

Figure 4. Effect of speed changes on perceived onset and offset. (A) Participants had to fixate the center of the screen while a visual stimulus (the same as those used in the perceived-duration experiment) was displayed to the left of the fixation spot. In different sessions, a brief tone was generated at different latencies close in time to either the onset or the offset of the visual stimulus. Participants had to decide whether the tone onset occurred before or after the stimulus onset (or offset). (B) We plotted here the mean points of subjective simultaneity, expressed as a percentage of the standard duration for the two main conditions (onset and offset), for three standard durations and three speed conditions (increasing, decreasing, and constant speed). Positive values indicate that the onset (or the offset) of the visual stimulus was perceived to occur earlier than the tone onset, whereas negative values indicate that it was perceived later. For this experiment, only two speed ranges were used, one for the constant-speed condition (10°/s–10°/s) and the other for increasing (0°/s–20°/s) and decreasing (20°/s–0°/s) speed. Error bars indicate ±1 standard error of the mean.

had to report which occurred first. We blocked the three different durations of the visual stimulus (300, 600, and 900 ms), whereas we interleaved trials where the visual interval contained increasing speed (initial speed: 0°/s, final speed: 20°/s) with trials with intervals containing decreasing (initial speed: 20°/s, final speed: 0°/s) or constant speed (10°/s). The point of subjective simultaneity (PSS) provided a measure of perceived temporal simultaneity.

Results

The results are presented in Figure 4B. For all three speed conditions tested (from this experiment on, we only used the most extreme speed ranges: increasing speed, speed range 0°/s–20°/s; decreasing speed, speed range 20°/s–0°/s; constant speed, 10°/s), the changes in perceived onset or offset were minimal. More specifically, for each standard duration, the pattern of results did not differ across speed conditions (no statistically significant main effects or interactions).

Experiment 3: Speed changes have a negligible effect on perceived average speed

Stimuli with the same duration but with different speeds or temporal frequencies appear to have different durations (Kanai et al., 2006; Kaneko & Murakami, 2009). Sasaki et al. (2013) found no difference in perceived speed between an accelerating and a decelerating Gabor stimulus when compared to a stimulus drifting at a constant speed. In our stimuli, the average speed was the same (10°/s) across speed conditions, but the perceived average speed may be affected by acceleration or deceleration. If, for instance, our observers had perceived the average speed in the increasing-speed condition to be lower than that in the decreasing-speed condition, then this biased perception could have influenced the duration judgment and could potentially have explained the pattern of results observed here. In order to investigate this issue, we measured apparent average speed for the different speed conditions using the paradigm described in Figure 1A.

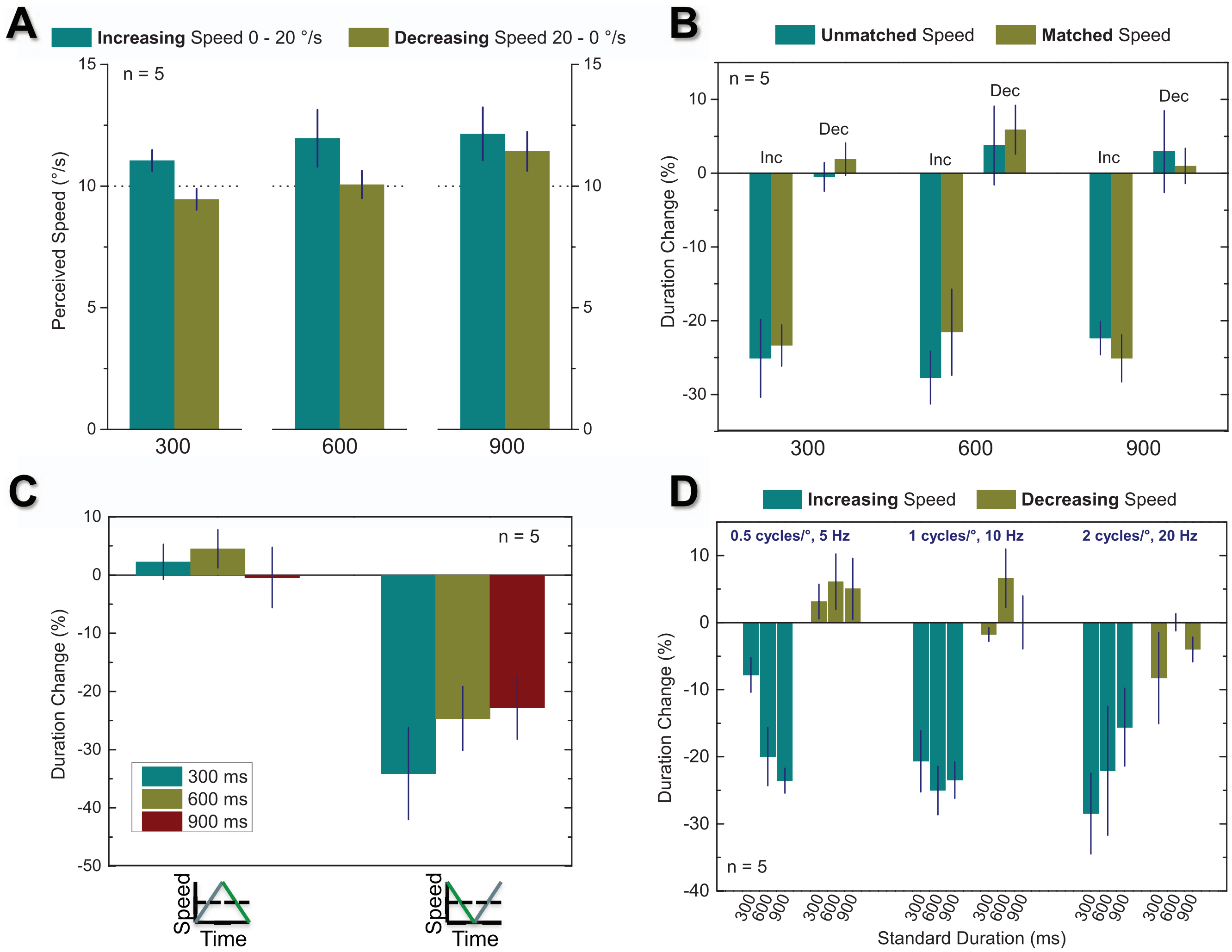

Figure 5. Effects of perceived average speed, speed profile, and temporal frequency on apparent duration. (A) Mean perceived average speeds are plotted for two speed conditions. Dashed lines indicate the actual average speed. Error bars indicate ±1 standard error of the mean. (B) Mean perceived duration change obtained when the perceived average speed of the two tests was not matched and when it was matched. (C) Mean perceived duration change for two different speed profiles: On the left side of the graph, the speed of the stimulus increased between 0°/s and 20°/s until half interval and then decreased back to 0°/s; on the right side, the increasing-speed half followed the decreasing-speed half. (D) Average perceived duration change for three combinations of spatial and temporal frequency that were chosen to keep the average speed constant (10°/s).

Methods

The stimuli and procedure were the same as in the perceived-duration experiment, with the following exceptions: Both test intervals had the same duration (300, 600, or 900 ms in different sessions), while we varied the speed of the comparison stimulus (no speed changes across the interval) in seven steps (between 2°/s and 18°/s) across trials in order to generate a psychometric function. The standard interval could contain either increasing (initial speed: 0°/s, final speed: 20°/s) or decreasing speed (initial speed: 20°/s, final speed: 0°/s). In both cases, the average speed was 10°/s. Subjects had to report the stimulus with the higher average speed. The point of subjective equality provided a measure of perceived speed.

Results

The apparent average speed for decreasing speed was generally lower than for increasing speed (Figure 5A), but the effect did not reach statistical significance: main effect of speed condition, $F(1, 4) = 1.113$, $p = 0.351$. In general, the perceived average speed increased with standard duration: main effect of standard duration, $F(2, 8) = 17.769$, $p < 0.005$. However, the difference in apparent speed between standard durations did not depend on the speed condition, as revealed by a statistically nonsignificant interaction between the two factors, $F(2, 8) = 0.669$, $p = 0.539$.

Experiment 4: Matching for perceived average speed does not cancel the apparent duration effect

We used the speed estimates obtained individually in Experiment 3 to match the apparent average speed of the two tests (one with constant speed, the other with increasing or decreasing speed) in a perceived-duration task.

Methods

The stimuli and procedure were the same as in the Experiment 1, with the exception that the speed of the comparison stimulus (which drifted at a constant rate) was adjusted individually (and separately for the increasing- and decreasing-speed conditions) in order to match that of the standard stimulus. Once again, we interleaved two conditions—increasing (initial speed: 0°/s, final speed: 20°/s) and decreasing speed (initial speed: 20°/s, final speed: 0°/s)—and we used three standard durations (300, 600, and 900 ms).

Results

As in Experiment 1, a strong apparent duration compression of around 25% was observed for the increasing-speed condition (Figure 5B), whereas an expansion of less than 5% on average was found for the decreasing-speed condition: main effect of speed condition, $F(1, 4) = 34.689$, $p < 0.005$. Furthermore, the pattern is statistically indistinguishable across standard durations—there is no significant main effect of standard duration, $F(2, 8) = 2.6$, $p = 0.135$, and no significant interaction between standard duration and speed condition, $F(2, 8) = 0.61$, $p = 0.942$. The difference between matched and unmatched estimates is negligible—main effect of matched versus unmatched, $F(1, 8) = 0.231$, $p = 0.643$—indicating that changes in apparent average speed are unlikely to be the key factor in the apparent duration effect.

Experiment 5: Apparent duration compression occurs only when increasing speed is contained in the second half of a visual interval

Experiment 4 showed that the perceived-duration effect observed in Experiment 1 was dissociable from changes in apparent average speed. However, observers might have weighed the first half of an interval more than the second half when they judged its duration. This could explain apparent duration compression for the increasing-speed condition, as we know that stimuli moving slowly are perceived to last for less time than faster-moving stimuli (Kanai et al., 2006; Kaneko & Murakami, 2009). To address this issue, we designed two new test stimuli, which both contained the same amount of increasing and decreasing speed (same average speed); the only difference was the order in which they were presented.

Methods

We used two different standard stimuli in different sessions. For one of them, the speed increased linearly from 0°/s at the beginning of the interval to 20°/s at half interval and then decreased back to 0°/s by the end. For the other, the opposite happened. In both cases, the average speed in the two halves was the same (10°/s). The procedure was identical to that used in the Experiment 1. We interleaved these two standards and asked our participants to judge their duration against a comparison interval containing constant speed (10°/s).

Results

Figure 5C shows the results for this experiment. Perhaps surprisingly, a strong apparent duration compression was observed when increasing speed followed decreasing speed, but not when it preceded it—main effect of speed condition, $F(1, 4) = 22.01$, $p < 0.01$—as if our participants ignored the first half of the interval and based their duration judgment entirely on the second half. However, this strategy cannot explain the apparent duration effect observed in Experiment 1, because in the second half of the stimulus with speed increasing along the entire interval, the average speed was actually higher (15°/s) than in the first half (5°/s). This should have led to perceived duration dilation rather than the compression we observed. Once again, the effect was similar across standard durations, with no significant main effect, $F(2, 8) = 1.62$, $p = 0.257$, or interaction, $F(2, 8) = 1.916$, $p = 0.209$, between the two factors.

Experiment 6: Changes in speed rather than temporal frequency cause the perceived duration effect

In all the experiments described thus far, we cannot tell whether the observed effect on perceived duration was determined by changes in stimulus speed or by changes in temporal frequency. In fact, since we used a constant spatial frequency of 1 c/°, the nominal value of speed and temporal frequency for our stimuli were the same. Therefore, in Experiment 6 we manipulated the spatial and temporal frequency of our stimuli (while maintaining the same average speed), and then we measured apparent duration again.

Methods

We designed three different comparison stimuli with the same average speed (10°/s) but different combinations of spatial frequency (0.5, 1, or 2 c/°) and temporal frequency (5, 10, or 20 Hz, respectively), which were interleaved to measure perceived duration. The speed range (0°/s–20°/s for the increasing-speed condition, 20°/s–0°/s for the decreasing-speed condition) was kept constant. We varied the temporal frequency of the stimuli to obtain the changes in speed across the test intervals. Otherwise, the procedure was identical to that used in Experiment 1.

Results

Figure 5D shows that the difference between increasing and decreasing speed remained clear across all the combinations of spatial and temporal frequency: main effect of speed condition, $F(1, 4) = 23.053$, $p < 0.01$. We observed no difference between the three combinations of spatial and temporal frequency that we used in terms of perceived duration—main effect of combinations of spatial and temporal frequency, $F(2, 8) = 1.556$, $p = 0.269$—suggesting that changes in speed might be more crucial than changes in temporal frequency to explain the apparent duration effect we found here. However, we should note that the magnitude of the perceived duration change for different combinations of spatial and temporal frequency varied slightly across standard durations, as revealed by a significant interaction between the two factors, $F(4, 16) = 7.374$, $p < 0.005$, and that this difference also depended on the speed condition, as revealed by a significant three-way interaction, $F(4, 16) = 3.12$, $p = 0.045$.

Experiment 7: Increasing stimulus speed affects perceived simultaneity in an apparent-motion task

In the final two experiments, we investigated the connection between changes in apparent duration in the subsecond range and changes in the temporal tuning of neurons in the early stages of the visual system, as suggested by previous adaptation studies (Ayhan et al., 2009; Bruno et al., 2010, 2011; Bruno & Johnston, 2010; Burr et al., 2007; Johnston et al., 2006). Specifically, we investigated whether the same changes in speed that, as we showed here, cause biases in duration perception are related to changes in temporal tuning that are associated with changes in the temporal impulse response function. Contrast-gain changes sharpen and advance the temporal impulse response measured physiologically (Shapley & Victor, 1978). The effect of this is to temporally advance the physiological signal. We reasoned that this advance could potentially induce apparent motion in a pair of simultaneously presented targets. In order to estimate changes in the temporal impulse response, in Experiment 7 we superimposed two sequentially displayed Gaussian blobs on two adjacent stimuli, one of which drifted at a constant speed and the other of which increased or decreased in speed (Figure 6A). The physical distance between the stimuli and the relative timing of the presentation of the Gaussians were chosen to induce a clear sensation of a single Gaussian blob moving from one location to another for the longest interstimulus interval. Changes in the shape of the impulse response should be revealed through changes in the PSS, the point at which observers did not perceive a clear impression of apparent motion.

Methods

The drifting stimuli were identical to those used previously, except for the lower Michelson contrast (50%) so as not to interfere with the visibility of the flashes, which were luminance-modulated Gaussian blobs ($\sigma = 0.83°$ of visual angle, 80% Michelson contrast in the center of the patch). While fixating the center of the screen, participants were presented with two adjacent and simultaneous stimuli for 900 ms, one of them always containing drifting motion at a constant speed (10°/s) whereas the other contained increasing speed (0°/s–20°/s) in half of the trials and decreasing speed (20°/s–0°/s) in the other half. The stimuli were displayed in one of four possible positions (top, bottom, left, and right) within a notional annulus centered on the fixation spot, to reduce local long-term temporal-frequency adaptation (distance from the center: 5°, distance between the centers of the two gratings: 5°). Participants were aware of where the stimuli would be displayed in the next trial. The Gaussian blobs were centered on each of the two gratings and were displayed sequentially for 50 ms each in order to induce a sensation of apparent motion. Participants had to report the direction of apparent motion. On a trial-by-trial basis, we varied the interstimulus interval between 0 and 80 ms (presentation order was randomized, i.e., either Gaussian blob could be presented before the other in each given trial) in order to generate a psychometric function. In different sessions, we also changed the time at which the Gaussians were flashed relative to the onset of the grating stimuli (corresponding to one third, one half, or

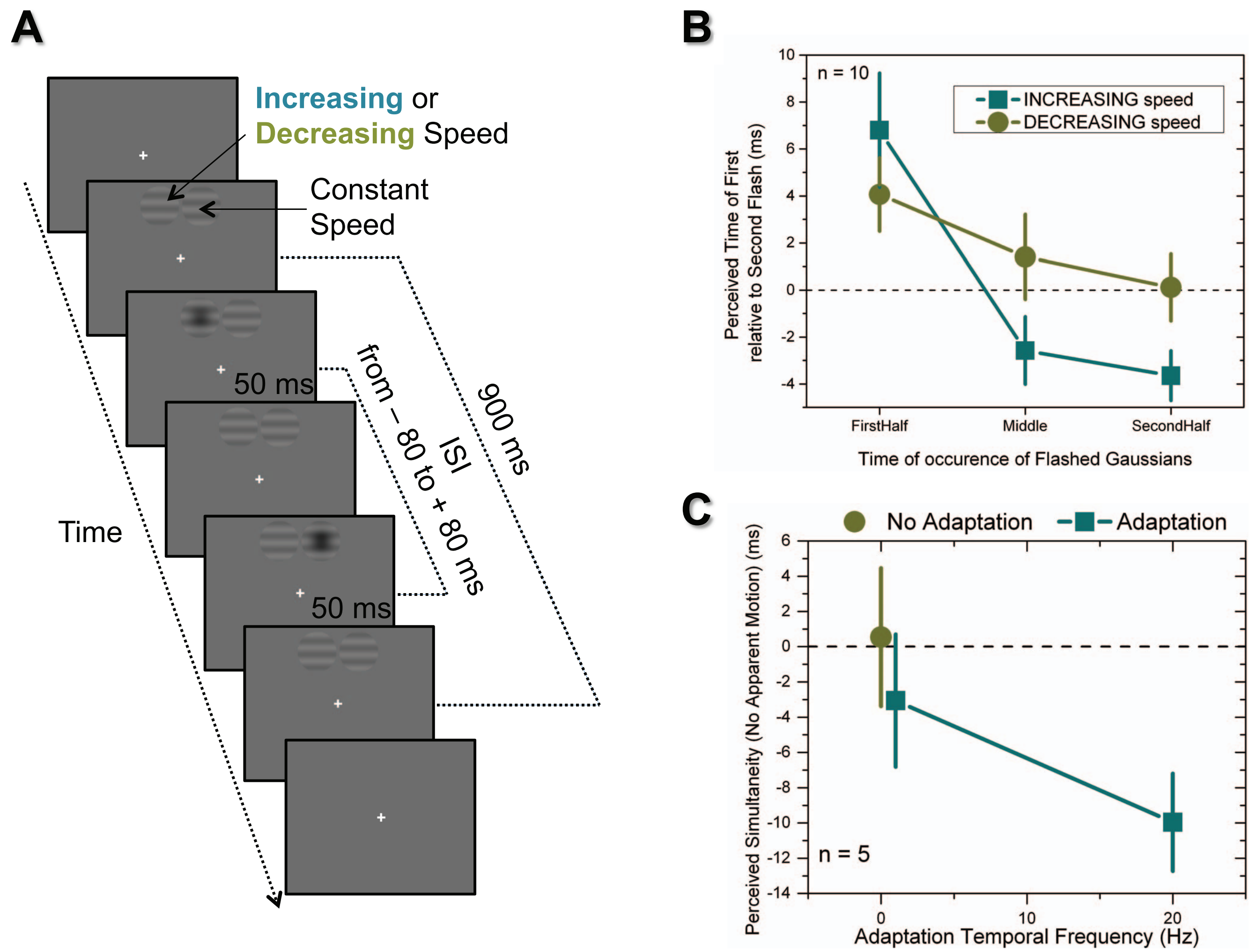

Figure 6. Effect of speed changes and flicker adaptation on the perceived direction of apparent motion. (A) Schematic representation of the apparent-motion experiment. Participants had to keep fixation on the center of the screen, while two adjacent drifting gratings were simultaneously displayed in one of four possible locations around the fixation cross (only the top location is shown here). One of them drifted at a constant speed, whereas the other increased (or decreased) its speed across the interval. Two Gaussian blobs were briefly flashed on top of each grating sequentially, separated by an interstimulus interval of variable duration. Participants had to indicate the direction of apparent motion. (B) Average point of subjective simultaneity for the two Gaussian blobs as a function of their time of occurrence (in "FirstHalf" they were displayed at one third of the interval, in "Middle" in the center, and in "SecondHalf" at two thirds of the sequence duration). Negative values indicate that the blob superimposed on the grating with increasing or decreasing speed was perceived to occur earlier than the other blob; positive values indicate that it was perceived to occur later. Error bars indicate ±1 standard error of the mean. (C) Mean point of subjective simultaneity for the two Gaussian blobs after flicker adaptation as a function of the adapting frequency. Negative values indicate that the adapted blob was perceived to occur earlier than the unadapted one; positive values indicate that it was perceived to occur later.

two thirds of the sequence duration). Subjects had to indicate the direction of apparent motion. The PSS was our measure of apparent simultaneity.

Results

Figure 6B shows that the point in time at which the Gaussian blobs were displayed in the interval had an influence on the PSS: main effect of time of occurrence, $F(2, 18) = 31.004$, $p < 0.001$. When presented in the middle or second half of the interval, the Gaussian was seen to appear earlier when superimposed on the speed-change stimulus than when superimposed on the constant-speed stimulus, as compared to when it was presented in the first half of the interval. Importantly, this effect depended on the speed condition: interaction of speed condition × time of occurrence, $F(2, 18) = 5.399$, $p < 0.05$. To test the significance of simple main effects, we conducted two one-way repeated-measures ANOVAs for increasing and decreasing speed separately. The main effects of time of occurrence were found to be significant in both cases—increasing speed:

$F(2, 18) = 17.162$, $p < 0.001$; decreasing speed: $F(2, 18) = 10.521$, $p < 0.005$. However, since (as previously reported) the interaction between speed condition and time of occurrence was also significant, this implies that the magnitude of the effect was greater for increasing speed. This was also confirmed by the observation that only when the Gaussian blob was presented in the second half of the interval containing increasing speed was the PSS significantly below zero: one-sample t test against 0, $t(9) = -3.345$, $p < 0.01$.

Experiment 8: Flicker adaptation also causes a shift in apparent simultaneity

We considered that the perceptual shift in the temporal order of the two stimuli due to increasing speed that we showed in Experiment 7 could be related to the phase advance in the impulse response that has also been proposed to be a causal factor (Johnston, 2010, 2014) in adaptation-based apparent duration compression (Johnston et al., 2006). In Experiment 8, in order to obtain psychophysical evidence for adaptation-based impulse response sharpening, we measured the PSS for two Gaussians after adaptation to flicker using the apparent-motion technique.

Methods

The stimuli we used were Gaussian blobs, identical to those in Experiment 7. An adaptation phase preceded a test phase. In the adaptation phase, participants fixated the center of the screen while they adapted to a flickering Gaussian patch (the Michelson contrast of which varied according to a sinusoidal function with a modulation depth of 0.8) located 5° right of the vertical midline and centered 2.5° above the horizontal midline, which stayed on initially for 30 s (8-s top-ups). In the test phase, after a 500-ms blank mean-luminance interval, two stationary Gaussian blobs were briefly (50 ms) and sequentially displayed (separated by an interstimulus interval within the range 0–80 ms), one in the same spatial position as the adaptor and the other in the opposite position (unadapted) relative to the horizontal midline. Participants were required to report the direction of apparent motion. The flicker frequency of the Gaussian adaptor could be either 1 or 20 Hz, in different sessions. A control condition without adaptation was also run. The PSS was our measure of apparent motion.

Results

When no adaptation preceded the test phase, the PSS corresponded to the physical simultaneity of the two Gaussians (Figure 6C): one-sample t test against 0, $t(4) = 0.139$, $p = 0.896$. When the adapting frequency was low (1 Hz), subjects' performance did not differ from that obtained without adaptation: paired-samples t test, $t(4) = 1.231$, $p = 0.286$. However, when we increased the adapting frequency to 20 Hz, the PSS was substantially shifted relative to the baseline (no-adaptation) condition: paired-samples t test, $t(4) = 3.147$, $p < 0.05$. More specifically, the direction of the shift suggests that the Gaussian in the adapted region was perceived to occur earlier than that presented in the unadapted location.

Discussion

We investigated the effect of speed change on the perceived duration of a subsecond interval. We found the following:

- The apparent duration of a stimulus that linearly increased its speed across an interval appeared substantially compressed (maximum compression: ~30% of standard duration) relative to a stimulus that drifted at a constant rate (10°/s), with the effect size increasing with speed range.
- When the speed of the embedded interval decreased linearly, only a mild perceived duration expansion (maximum dilation: ~10% of standard duration) was observed, and it affected all the tested speed ranges equally.
- No substantial differences in duration discrimination emerged between the increasing- and decreasing-speed conditions.
- The amount of apparent duration compression observed in the increasing-speed condition increased linearly with speed range (rather than acceleration) and was proportional to standard stimulus duration, whereas no specific relationships were detected for decreasing speed.
- The differences in perceived onset and offset (measured against an auditory stimulus) between increasing-, decreasing-, and constant-speed conditions were negligible and could not explain the observed pattern of results for perceived duration.
- The perceived average speed of a stimulus with increasing speed was marginally higher than that of a stimulus with decreasing speed.
- When the perceived average speeds of the two test stimuli (one drifting with increasing or decreasing speed, the other drifting at constant speed) were matched, the difference in apparent duration between the conditions remained.
- When we compared the relative duration of a stimulus moving at constant speed with that of a stimulus that contained the same amount of increasing and decreasing speed, we observed significant apparent

duration compression only when the increasing-speed half followed the decreasing-speed half.

- The qualitative differences in apparent duration between increasing and decreasing speed remained when we manipulated the spatial and temporal frequency of the test stimuli (keeping the average speed the same). However, the magnitude of the difference depended on the spatiotemporal content.
- Increasing the stimulus speed generated a change in the perceived simultaneity of superimposed Gaussian blobs. In the later part of the interval, a blob flashed on a stimulus with increasing speed appeared to occur earlier than one flashed on a stimulus with constant speed. For the decreasing-speed condition, this trend did not reach significance.
- Flicker adaptation induced a similar change in perceived simultaneity: At 20 Hz, a Gaussian blob that was subsequently flashed in an adapted location appeared to occur earlier than in an unadapted location, whereas at 1 Hz no such effect was observed.

The pattern of results described here presents a level of complexity that cannot be explained by a simple change model (Fraisse, 1963; Poynter, 1989). The change model postulates that, when our brain has to estimate the duration of an interval containing a sensory stimulus, it adopts the strategy of detecting and counting the number of temporal changes that occur within that interval. According to this view, intervals that have the same actual duration might be perceived to have a different extension in time if they contain a different number of temporal subunits. The observations that moving stimuli appear to last longer than stationary stimuli and that slower stimuli are perceived to be more short-lived than faster stimuli (S. W. Brown, 1995; Kanai et al., 2006; Kaneko & Murakami, 2009) seem to support a change-based coding of time perception. In the present study, all the stimuli we used had the same average speed (10°/s), and therefore the number of changes (defined here as the number of cycles occurring per time unit) within each given interval did not differ. However, we showed here that decreasing stimulus speed induced small apparent duration dilation regardless of the speed range (not necessarily contradicting the predictions of the change model), whereas increasing stimulus speed caused a perceived duration compression that increased as we widened the speed range (see Figure 1B). This latter finding is at odds with the predictions of the change model.

In previous studies of the effect of speed change on apparent duration, there are other results that seem to be problematic for a change-based explanation. Our group recently compared duration estimates for static, drifting, and mixed stimuli composed of a balanced alternation of static and drifting subintervals (Bruno et al., 2012). The number of temporal changes contained in the mixed stimulus was intermediate between the numbers of those contained in the static and drifting stimuli, and therefore, according to the change model, its perceived duration should have roughly corresponded to an average of the duration estimates obtained for the other two stimuli. What we actually observed was that the mixed stimulus appeared significantly more compressed than the mean of the static and drifting estimates. For durations that approximated those used in this study (588–1647 ms), Matthews (2011a, experiment 3a) reported that both accelerating and decelerating patterns were perceived to be compressed relative to a pattern translating at constant speed when a categorical judgment was required, whereas he observed a smaller reduction for deceleration for duration reproduction.

The discrepancy between Matthews's and the present results might be ascribed to the many methodological differences between the two studies. First, he used simple geometrical shapes, whereas we used sinusoidal gratings. Second, the type of motion was also different: object translation in his study, a windowed drifting pattern in ours. Third, he used only one speed range per speed condition (average speed: 6.6°/s for rotational motion), whereas we used six (average speed: 10°/s). Finally, the most important difference relates to the chosen method of measuring apparent duration. In all the experiments reported in the present study, participants were asked to compare the relative duration of two test stimuli, and we always used the method of constant stimuli to determine a complete psychometric function (the 50% point represented our measure of perceived duration). In different sessions and conditions, Matthews's participants were required to estimate duration by rating it on a scale ranging from "very short" to "very long" or reproducing it holding down a mouse button. Matthews explained the main finding of his study (i.e., constant speed longer than deceleration, deceleration longer than acceleration) by referring to a modified version of the classic pacemaker model (Creelman, 1962; Treisman, 1963; Treisman, Faulkner, Naish, & Brogan, 1990) with the additional proposals that the relationship between speed and accumulation rate should be logarithmic rather than linear and that the pulses accumulated in the initial and final parts of the stimulus should be weighted differently (Matthews, 2013). In fact, our participants seemed to base their duration judgement almost entirely on the second half of the stimulus, virtually ignoring the first half (Figure 5C).

In their experimental condition that was most similar to the main task of the present study, Binetti et al. (2012) reported judgments for accelerating and decelerating Gabor patterns. They used only one speed range and a slower average speed (1.23°/s) than the present study, but they also found a strong compression for acceleration and a mild dilation for deceleration. Sasaki et al. (2013), using the same average speed as in the present study (10°/s), also replicated these findings. These studies, and our own, are at odds with the predictions of the change model, but we are left with the need for a satisfactory alternative theoretical frame of reference to explain first how and why speed influences duration perception, and second what this relationship tells us about how visual time is encoded in our brain.

We have previously highlighted a potential link between perceived duration distortions and changes in the shape of the temporal impulse response function of magnocellular visual neurons (Johnston, 2010, 2014). The temporal impulse response function of a cell describes how the cell responds (i.e., number of spikes per second) to brief pulses of contrast. More specifically, it is a transform to the time domain of the temporal-frequency responsivity of a cell, and therefore it provides a representation of the temporal tuning of that particular neuron. The temporal impulse response to luminance-modulated stimuli sharpens during a saccadic eye movement (Burr & Morrone, 1996), which is associated with apparent duration compression (Morrone, Ross, & Burr, 2005) and magnocellular pathway suppression (Burr, Morrone, & Ross, 1994; Ross, Morrone, Goldberg, & Burr, 2001). There is also some evidence that the impulse response sharpens after high-temporal-frequency adaptation in the wallaby (Clifford, Ibbotson, & Langley, 1997; Ibbotson, 2005; Ibbotson, Clifford, & Mark, 1998). Our group has reported that adaptation to high- but not low-temporal-frequency motion (20 vs. 5 Hz) or flicker induced duration underestimation for a 10-Hz stimulus displayed in the same location as the adaptor for luminance-modulated (Johnston et al., 2006) but not for isoluminant chromaticity-modulated stimuli that are more likely to selectively activate P-cells (Ayhan et al., 2011). The temporal impulse response has also been shown to sharpen at high contrast (Stromeyer & Martini, 2003) and, in primates, as a consequence of contrast gain control in M-cells (Benardete & Kaplan, 1999; Kaplan & Benardete, 2001). Bruno and Johnston (2010) have reported perceived duration compression after fast luminance but not chromatic contrast adaptation. Finally, the temporal impulse response lengthens at low luminance (Kelly, 1961; Peterson, Ohzawa, & Freeman, 2001; Takeuchi & De Valois, 1997, 2009) and, as a consequence, also induces apparent duration dilation (Bruno et al., 2011).

To summarize, changes in perceived duration seem to be linked to changes in the shape of the temporal impulse response in the following way: Experimental conditions that induce a shortening of the temporal impulse response also cause an underestimation of perceived duration, whereas a lengthening coincides with perceived duration expansion. To explain the relationship between shortening/lengthening of the impulse response and apparent duration compression/expansion, and to accommodate the very different temporal scales of the two effects, Johnston (2010, 2014) developed a "predict and compare" model (Figure 7A). Once our visual system individuates the visual interval to estimate, it predicts what the embedded object will look like after a given time and then continuously compares this prediction with the stimulus appearance represented in the sensory input. This comparison process continues until the stimulus appearance matches the prediction; then a tick is generated and stored in an accumulator, and the prediction reset. At the end of the interval, the number of ticks in the accumulator (each of them corresponding to the same subinterval duration) represents the duration of the chosen interval. Thus the large temporal compression can be explained as an accumulation of many small errors. The model assumes that the forward prediction signal is carried by band-pass filters, like those of magnocellular neurons (the parvocellular cells act as temporally low-pass filters), which, being temporally differentiating filters, can be used to project visual representations forward in time (Figure 7B through D). All the experimental manipulations we report in this article seem to be magno-specific. Therefore, we can assume that a phase advance (due to the impulse response shortening) in the magnocellular signal will shift the prediction forward in time relative to the current input carried by the parvocellular signal, which is relatively unaffected by high-temporal-frequency adaptation, contrast adaptation, or saccades. This shift will cause the match between the two signals to be reached later than under normal conditions; therefore, at the end of the interval, there will be fewer ticks in the accumulator, resulting in duration underestimation. The same logic predicts apparent temporal expansion after the lengthening of the temporal impulse response.

In order to determine whether the predict-and-compare model might also explain the apparent duration distortions we found here, we investigated whether changes in perceived duration covary with changes in the temporal impulse response measured psychophysically in the same stimulus conditions. Under conditions of increasing speed, where we observed a substantial apparent duration compression (see Figure 2A), there was also a concurrent shortening of the impulse response. This correspondence extended to the dependency on the position of stimuli within the test temporal interval. Apparent duration compression required a speed increase in the second

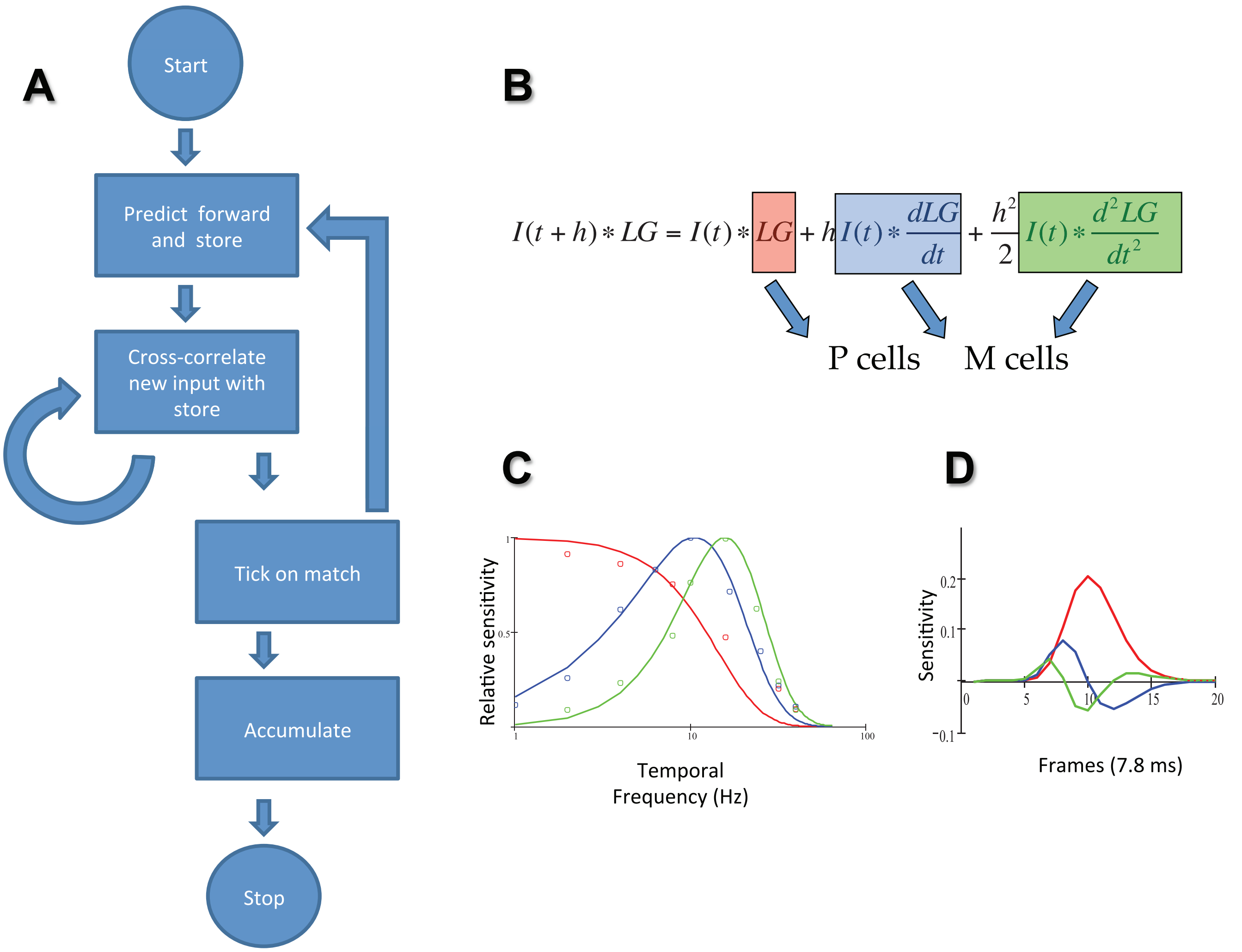

Figure 7. "Predict and compare" model of vision-based mechanisms of time perception (reproduced with permission from Johnston, 2014). (A) Schematic representation of a content-dependent clock model. An interval duration is estimated by comparing (cross-correlation) a forward prediction of the stimulus's appearance at the end of the interval with a constantly updated sensory input. When the prediction matches the current image, a tick is sent to the accumulator and the prediction is reset. (B) A Taylor series is used to predict the image brightness $I(t)$ forward in time. (C) The temporal tuning functions of P-cells, which carry the new input signal in (A), have a low-pass profile (red curve), whereas those of M-cells (which carry the prediction signal) have a band-pass profile (green and blue curves). (D) An inverse Fourier transform of the tuning curves in (C) generates the corresponding temporal impulse responses for magnocellular and parvocellular filters.

half of the interval (Figure 5C). In the increasing-speed condition (Figure 6B), the direction of apparent motion followed a forward shift and compression of the temporal impulse response for the second half of the interval but not for the first half. For the decreasing-speed condition, there was a small apparent temporal dilation, a less pronounced change in the temporal impulse response as measured by the apparent motion paradigm, and notably no significant difference from simultaneity in the second half of the interval. To establish if a change in temporal impulse can be measured psychophysically in the previously described adaptation-based apparent duration compression paradigm (Johnston et al., 2006), we also measured the PSS after flicker adaptation. Duration underestimation was found only after high-temporal-frequency adaptation. Adaptation to 20-Hz drift gratings induced a negative PSS shift, reflecting a forward shift in time of the perceived occurrence of the Gaussian blob displayed in the adapted position corresponding to a shortening of the impulse response.

The predict-and-compare model assumes that the early components of the mechanism that determines the duration of visual intervals are the same as those used to process visual motion and temporal change. The same strategy may be used in other modalities so long as there is a continuous time-varying signal that would support a forward prediction. For example, adaptation-based apparent duration compression has also been found in the tactile domain (Watanabe, Amemiya, Nishida, & Johnston, 2010). As in the visual system, sustained and transient channels (which are not called parvocellular and magnocellular) operate in the tactile system, but with different activation parameters. In fact, the perceived duration compression was observed only at a higher frequency (35 Hz) than for vision. It is possible to conclude that, as in the visual domain, time-perception mechanisms in the tactile domain have a sensory component, which is also subject to adaptation. In the auditory domain, Matthews (2013) has reported apparent duration compression that was larger for acceleration than for deceleration using sequences of consecutive tones of increasing pitch. This may point to another commonality in time-processing strategies across modalities.

In conclusion, we show here that a linear increase in stimulus speed has a specific effect on apparent duration that is dissociable from concurrent changes in perceived speed or onset/offset. More importantly, we provide evidence, for the first time, that local adaptation to motion or flicker and the visual content of an interval affect perceived duration through the same mechanism, namely changes in the temporal tuning of visual filters.

Keywords: time perception, perceived duration, speed changes, temporal tuning

Acknowledgments

We would like to acknowledge the support of the Wellcome Trust and the Leverhulme Trust.

Commercial relationships: none.
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References

Ayhan, I., Bruno, A., Nishida, S., & Johnston, A. (2011). Effect of the luminance signal on adaptation-based time compression. *Journal of Vision, 11*(7):22, 1–17, http://www.journalofvision.org/content/11/7/22, doi:10.1167/11.7.22. [PubMed] [Article]

Ayhan, I., Bruno, A., Nishida, S., & Johnston, A. (2009). The spatial tuning of adaptation-based time compression. *Journal of Vision, 9*(11):2, 1–12, http://www.journalofvision.org/content/9/11/2, doi:10.1167/9.11.2. [PubMed] [Article]

Benardete, E. A., & Kaplan, E. (1999). The dynamics of primate M retinal ganglion cells. *Visual Neuroscience, 16*(2), 355–368.

Binetti, N., Lecce, F., & Doricchi, F. (2012). Time-dilation and time-contraction in an anisochronous and anisometric visual scenery. *Journal of Vision, 12*(7):8, 1–19, http://www.journalofvision.org/content/12/7/8, doi:10.1167/12.7.8. [PubMed] [Article]

Block, R. A., & Reed, M. A. (1978). Remembered duration: Evidence for a contextual-change hypothesis. *Journal of Experimental Psychology: Human Learning and Memory, 4*(6), 656–665.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*(4), 433–436.

Brown, J. F. (1931). On time perception in visual movement fields. *Psychological Research, 14*(1), 233–248.

Brown, S. W. (1995). Time, change, and motion: The effects of stimulus movement on temporal perception. *Perception & Psychophysics, 57*(1), 105–116.

Bruno, A., Ayhan, I., & Johnston, A. (2010). Retinotopic adaptation-based visual duration compression. *Journal of Vision, 10*(10):30, 1–18, http://www.journalofvision.org/content/10/10/30, doi:10.1167/10.10.30. [PubMed] [Article]

Bruno, A., Ayhan, I., & Johnston, A. (2011). Duration expansion at low luminance levels. *Journal of Vision, 11*(14):13, 1–13, http://www.journalofvision.org/content/11/14/13, doi:10.1167/11.14.13. [PubMed] [Article]

Bruno, A., Ayhan, I., & Johnston, A. (2012). Effects of temporal features and order on the apparent duration of a visual stimulus. *Frontiers in Psychology, 3*(90), 1–7.

Bruno, A., & Johnston, A. (2010). Contrast gain shapes visual time. *Frontiers in Psychology, 1*(170), 1–8.

Burr, D. C., & Morrone, M. C. (1996). Temporal impulse response functions for luminance and colour during saccades. *Vision Research, 36,* 2069–2078.

Burr, D. C., Morrone, M. C., & Ross, J. (1994). Selective suppression of the magnocellular visual pathway during saccadic eye movements. *Nature, 371,* 511–513.

Burr, D., Tozzi, A., & Morrone, M. C. (2007). Neural mechanisms for timing visual events are spatially selective in real-world coordinates. *Nature Neuroscience, 10*(4), 423–425.

Cicchini, G. M., & Morrone, M. C. (2009). Shifts in spatial attention affect the perceived duration of events. *Journal of Vision, 9*(1):9, 1–13, http://www.journalofvision.org/content/9/1/9, doi:10.1167/9.1.9. [PubMed] [Article]

Clifford, C. W., Ibbotson, M. R., & Langley, K. (1997). An adaptive Reichardt detector model of motion adaptation in insects and mammals. *Visual Neuroscience, 14*(4), 741–749.

Creelman, C. D. (1962). Human discrimination of auditory duration. *The Journal of the Acoustical Society of America, 34*(5), 582–593.

Droit-Volet, S., & Wearden, J. (2002). Speeding up an internal clock in children? Effects of visual flicker on subjective duration. *Quarterly Journal of Experimental Psychology B, 55*(3), 193–211.

Eagleman, D. M., & Pariyadath, V. (2009). Is subjective duration a signature of coding efficiency? *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 364*(1525), 1841–1851.

Fraisse, P. (1963). *The psychology of time*. New York: Harper and Row.

Ibbotson, M. R. (2005). Contrast and temporal frequency-related adaptation in the pretectal nucleus of the optic tract. *Journal of Neurophysiology, 94*(1), 136–146.

Ibbotson, M. R., Clifford, C. W., & Mark, R. F. (1998). Adaptation to visual motion in directional neurons of the nucleus of the optic tract. *Journal of Neurophysiology, 79*(3), 1481–1493.

Johnston, A. (2010). Modulation of time perception by visual adaptation. In A. C. Nobre & J. T. Coull (Eds.), *Attention and time* (pp. 187–200). Oxford, UK: Oxford University Press.

Johnston, A. (2014). Visual time perception. In J. S. Werner & L. M. Chalupa (Eds.), *The new visual neurosciences* (pp. 749–762). Cambridge, MA: MIT Press.

Johnston, A., Arnold, D. H., & Nishida, S. (2006). Spatially localized distortions of event time. *Current Biology, 16*(5), 472–479.

Johnston, A., Bruno, A., Watanabe, J., Quansah, B., Patel, N., Dakin, S., … Nishida, S. (2008). Visually-based temporal distortion in dyslexia. *Vision Research, 48*(17), 1852–1858.

Kanai, R., Paffen, C. L., Hogendoorn, H., & Verstraten, F. A. (2006). Time dilation in dynamic visual display. *Journal of Vision, 6*(12):8, 1421–1430, http://www.journalofvision.org/content/6/12/8, doi:10.1167/6.12.8. [PubMed] [Article]

Kaneko, S., & Murakami, I. (2009). Perceived duration of visual motion increases with speed. *Journal of Vision, 9*(7):14, 1–12, http://www.journalofvision.org/content/9/7/14, doi:10.1167/9.7.14. [PubMed] [Article]

Kaplan, E., & Benardete, E. (2001). The dynamics of primate retinal ganglion cells. *Progress in Brain Research, 134,* 17–34.

Kelly, D. H. (1961). Visual response to time dependent stimuli. I. Amplitude sensitivity measurements. *Journal of the Optical Society of America, 51,* 422–429.

Matthews, W. J. (2011a). How do changes in speed affect the perception of duration? *Journal of Experimental Psychology: Human Perception and Performance, 37*(5), 1617–1627.

Matthews, W. J. (2011b). Stimulus repetition and the perception of time: The effects of prior exposure on temporal discrimination, judgment, and production. *PLoS One, 6*(5), e19815.

Matthews, W. J. (2013). How does sequence structure affect the judgment of time? Exploring a weighted sum of segments model. *Cognitive Psychology, 66*(3), 259–282.

Morrone, M. C., Ross, J., & Burr, D. (2005). Saccadic eye movements cause compression of time as well as space. *Nature Neuroscience, 8*(7), 950–954.

Pariyadath, V., & Eagleman, D. (2007). The effect of predictability on subjective duration. *PLoS One, 2*(11), e1264.

Pariyadath, V., & Eagleman, D. M. (2008). Brief subjective durations contract with repetition. *Journal of Vision, 8*(16):11, 1–16, http://www.journalofvision.org/content/8/16/11, doi:10.1167/8.16.11. [PubMed] [Article]

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10*(4), 437–442.

Peterson, M., Ohzawa, I., & Freeman, R. (2001). Neural and perceptual adjustments to dim light. *Visual Neuroscience, 18*(2), 203–208.

Poynter, W. D. (1989). Judging the duration of time intervals: A process of remembering segments of experience. In L. Iris & Z. Dan (Eds.), *Advances in psychology: Vol. 59* (pp. 305–331). Oxford, UK: North-Holland.

Ross, J., Morrone, M. C., Goldberg, M. E., & Burr, D. C. (2001). Changes in visual perception at the time of saccades. *Trends in Neuroscience, 24,* 131–121.

Sasaki, K., Yamamoto, K., & Miura, K. (2013). The difference in speed sequence influences perceived duration. *Perception, 42*(2), 198–207.

Shapley, R. M., & Victor, J. D. (1978). The effect of contrast on the transfer properties of cat retinal ganglion cells. *The Journal of Physiology, 285,* 275–298.

Stromeyer, C. F., 3rd, & Martini, P. (2003). Human temporal impulse response speeds up with increased stimulus contrast. *Vision Research, 43*(3), 285–298.

Takeuchi, T., & De Valois, K. K. (1997). Motion-reversal reveals two motion mechanisms functioning in scotopic vision. *Vision Research, 37*(6), 745–755.

Takeuchi, T., & De Valois, K. K. (2009). Visual motion mechanisms under low retinal illuminance revealed by motion reversal. *Vision Research, 49*(8), 801–809.

Treisman, M. (1963). Temporal discrimination and the indifference interval: Implications for a model of the "internal clock." *Psychological Monographs, 77*(13), 1–31.

Treisman, M., Faulkner, A., Naish, P. L., & Brogan, D. (1990). The internal clock: Evidence for a temporal oscillator underlying time perception with some estimates of its characteristic frequency. *Perception, 19*(6), 705–743.

Tse, P. U., Intriligator, J., Rivest, J., & Cavanagh, P. (2004). Attention and the subjective expansion of time. *Perception & Psychophysics, 66*(7), 1171–1189.

Watanabe, J., Amemiya, T., Nishida, S., & Johnston, A. (2010). Tactile duration compression by vibrotactile adaptation. *NeuroReport, 21*(13), 856–860.