

Retinotopic adaptation-based visual duration compression

Aurelio Bruno

Cognitive, Perceptual and Brain Sciences,
Division of Psychology and Language Sciences,
University College London, London, UK



Inci Ayhan

Cognitive, Perceptual and Brain Sciences,
Division of Psychology and Language Sciences,
University College London, London, UK



Alan Johnston

Cognitive, Perceptual and Brain Sciences,
Division of Psychology and Language Sciences,
University College London, London, UK, &
CoMPLEX, University College London, London, UK



Eye movements present the visual system with the challenge of providing the experience of a stable world. This appears to require the location of objects to be mapped from retinal to head and body referenced coordinates. Following D. Burr, A. Tozzi, and M. C. Morrone (2007), here we address the issue of whether adaptation-based duration compression (A. Johnston, D. H. Arnold, & S. Nishida, 2006) takes place in a retinocentric or head-centric frame of reference. Duration compression may be associated with shifts in apparent temporal frequency. However, using an adaptation schedule that minimizes any effect of adaptation on apparent temporal frequency, we still find substantial apparent duration compression. Duration compression remains when the adaptor continuously translates in head-centered coordinates but is fixed on the retina, isolating retinal adaptation. Apparent duration was also measured after a change in gaze direction—a strategy which allows eye-centered and head-centered components of adaptation-induced duration compression to be distinguished. In two different paradigms, we found significant compression was elicited by retinotopic adaptation, with no significant change in apparent duration following spatiotopic adaptation. We also observed no interocular transfer of adaptation. These findings point to an early locus for the adaptation-based duration compression effect.

Keywords: temporal vision, magnocellular/parvocellular, eye movements

Citation: 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.

Introduction

The duration of events lasting hours or days is most likely encoded in a different way from events in the millisecond range (Buonomano & Karmarkar, 2002; Mauk & Buonomano, 2004). Here we focus on the millisecond range within which duration can be considered a perceptual property of an event. The most well-established view of how we judge duration is embodied in the centralized supramodal clock model (Creelman, 1962; Treisman, 1963; Treisman, Faulkner, Naish, & Brogan, 1990). A pacemaker generates ticks at a set rate, which are stored in an accumulator. At the end of the interval the gate to the accumulator is shut, and interval duration is indicated by the number of ticks. In this model, distortions in apparent duration can be explained either by a speeding or slowing of the clock rate or by an incorrect start or end point to the interval. Typically, changes in

duration are explained in terms of changes in arousal or attention. This view has been recently challenged by the finding that a spatially specific adaptation to 20 Hz oscillating motion (or flicker) induces a reduction in the perceived duration of a 10 Hz drifting (or flickering) visual stimulus displayed in the same position as the adaptor (Johnston, Arnold, & Nishida, 2006). There was also a small apparent compression of the duration of the 10-Hz stimulus after adaptation to 5 Hz oscillating motion or flicker. This finding points to the existence of domain-specific components within mechanisms for the encoding of duration.

Adaptation-induced time compression is not diminished when the orientation of the adaptor and test differ by 90° (Johnston et al., 2006) and is present for adaptors that exceed the critical flicker fusion threshold (Johnston et al., 2008). Moreover, it has been recently shown that this compression effect is abolished for test locations just 1 degree of visual angle from the adaptor location (Ayhan, Bruno, Nishida, & Johnston, 2009). Taken together, these

results point to an early site for the adaptation. However, this interpretation has been challenged by Burr, Tozzi, and Morrone (2007). They extended the Johnston et al. (2006) paradigm to investigate whether adaptation occurs within a retinotopic or spatiotopic frame of reference. Fixation was shifted between the adaptation and test phases of the duration compression experiment, allowing the independent measurement of retinotopic (same retinal position after the gaze shift) and spatiotopic (same position relative to the head after the gaze shift) components of adaptation as well as combined spatial and retinotopic adaptation (static head and eye). They report time compression in both head-centric and retinocentric coordinates but also that the retinotopic effect was eliminated when they matched the perceived speed of the two tests. They also showed interocular transfer for full and spatiotopic, but not for retinotopic adaptation. They interpreted these results as implying a cortical location for the adaptation effect.

The Johnston et al. (2006) study did not distinguish between retinotopic and spatiotopic adaptation. In their study, and in the Burr et al. (2007) study, there was clear apparent duration compression for test patterns matched in perceived temporal frequency after adaptation, when the test was in the same retinal and spatial location as the adaptor. The purely retinotopic effect in the Burr et al. study was attributed to perceived speed differences since it disappeared when test patterns were matched in perceived speed. Apparent duration has been shown to change as a function of speed (Brown, 1995; Kaneko & Murakami, 2009) or temporal frequency (Johnston et al., 2006; Kanai, Paffen, Hogendoorn, & Verstraten, 2006). Adaptation to high or low temporal frequency can also shift the apparent temporal frequency of a test pattern. Thus, changes in perceived duration may be mediated by changes in perceived temporal frequency or speed. To investigate whether one can find purely retinotopic adaptation without changes in perceived speed at test, we adopted the paradigm used by Ayhan et al. (2009) in which 5 and 20 Hz adaptors are interleaved, with the relative durations of each frequency chosen to null any change in perceived temporal frequency. This procedure minimizes the effect of adaptation on perceived speed (or temporal frequency) (Experiment 1). We then measured duration compression for an adaptor that was yoked to a pursuit target adapting a single retinal location continuously but many head-referenced directions only briefly (Experiments 2 and 3). We found clear adaptation-based duration compression.

We also measured apparent duration after full, retinotopic and spatiotopic adaptation in two slightly modified versions (Experiments 4 and 5) of the Burr et al. (2007) paradigm. In both cases, we found very a strong retinotopic effect but no clear evidence of spatiotopic adaptation. Finally, using an identical procedure to that used by Burr et al., we measured apparent duration after binocular adaptation (Experiment 6) and after switching between the adapted and unadapted eye in a dichoptic presentation (Experiment 7). In the Burr et al. paradigm,

the standard stimulus (presented in the adapted position) was always presented before the comparison stimulus (displayed in the unadapted position). We, in addition, compared trials in which the standard was presented first and second. A nonsignificant trend in the direction of a spatiotopic adaptation effect was only seen in standard first conditions. There was no suggestion of spatiotopic adaptation effects or interocular transfer for the standard second conditions, whereas the full and retinotopic adaptation effect remained strong.

General methods

Observers

Twelve observers participated in the study. Two authors (AB and IA) participated in all the experiments. In addition, one further observer (naïve to the aim of the experiment) participated in Experiments 1–4, two naïves participated in Experiment 5, another author (AJ) and eight naïves participated in Experiment 6, and three naïves participated in Experiment 7. All participants had normal or corrected-to-normal visual acuity.

Apparatus

Observers sat in a darkened room in front of a 19-inch Sony Trinitron Multiscan 500PS monitor, with a refresh rate of 100 Hz, driven by a VSG 2/5 visual stimulus generator (Cambridge Research Systems). The resolution of the monitor was 800×600 pixels. The monitor subtended 40×30 degrees of visual angle at a viewing distance of 57 cm.

Procedure

All the experiments were composed of an adaptation phase followed by a test phase. In the adaptation phase, subjects were required to maintain fixation, while a luminance modulated sinusoidal grating reversed direction every 250 ms (Experiments 1–4) or every 2 s (Experiments 5–7) to avoid inducing a directional motion after-effect. The spatial frequency was always 1 cycle/degree; thus, the numerical values of speed and temporal frequency are the same. The Michelson contrast of the adaptor was 50% in Experiments 1–5 and 90% in Experiments 5–7. The oscillating adaptor was presented for an initial period (20 seconds for Experiments 1–4 and 45 seconds for Experiments 5–7) with top-ups between trials (10 seconds in Experiments 1–4 and 8 seconds in Experiments 5–7). In the test phase, subjects were asked to judge the relative speed (Experiment 1) or the relative duration (Experiments 2–7) of two sequentially displayed

drifting sinusoidal gratings modulated in luminance (spatial frequency: 1 cycle/degree, Michelson contrast = 100% in Experiments 1–4, 90% in Experiments 5–7). One grating, the standard stimulus, with either a fixed speed or a fixed duration across trials, was displayed in the same position as the adaptor, while the other, the comparison stimulus, varied in speed or duration across trials in order to generate a psychometric function. Observers had to report which test stimulus drifted faster (Experiment 1) or stayed on for longer (Experiments 2–7). The 50% point on the derived psychometric functions provided an estimate of apparent speed or duration of the standard, depending upon task. A more detailed description of the stimuli in each experiment can be found in the methods of the relevant section.

Retinotopic effects in the absence of temporal frequency shifts

Increasing the speed of motion or temporal frequency of a stimulus can produce an expansion of its perceived duration (Brown, 1995; Kanai et al., 2006; Kaneko & Murakami, 2009). The apparent temporal frequency of a 10-Hz stimulus is reduced to around 7 Hz after adapting to 20 Hz; therefore, it is possible that the duration compression effect described by Johnston et al. (2006) may have been mediated by the change in apparent temporal frequency. Burr et al. (2007) and Johnston et al. reported that full adaptation-induced duration compression remained when the temporal frequency of the test stimuli were matched. However, Burr et al. also reported that purely retinotopic apparent duration compression disappeared when the two tests had the same perceived speed. Note that the function relating perceived duration to temporal frequency saturates at around 4–8 Hz or 8 deg/sec (Johnston et al., 2006; Kanai et al., 2006; Kaneko & Murakami, 2009), and therefore changes in apparent temporal frequency in the range tested should have little effect on perceived duration (Johnston et al., 2006). Nevertheless, a more effective means of distinguishing the effect of motion or flicker adaptation on perceived duration from its effect on apparent temporal frequency would be to construct an adaptor that had little or no effect on apparent temporal frequency. Fortunately, both 20 and 5 Hz adaptors reduce the apparent duration of a subsequently displayed interval containing a 10-Hz drifting grating, whereas 20 Hz reduces and 5 Hz increases its apparent temporal frequency (Johnston et al., 2006).

In order to obtain retinotopic adaptation without distortions of perceived test temporal frequency, we first measured perceived temporal frequency after adaptation to oscillating motion (Experiment 1). The temporal frequency of the adaptor was alternated between 5 and 20 Hz over time (different 5/20 Hz duty cycles were tested

in different sessions). For each subject, in different sessions, we determined the duty cycle that had no effect on perceived temporal frequency. We then used this stimulus to measure apparent duration in a pursuit task, in which the position of the adaptor changed continuously relative to the head but remained constant relative to the eye (Experiment 2). In order to ensure that the two test positions differed only in the amount of retinotopic adaptation, we included an experiment with two adaptors (one for each test location) translating in opposite directions so that only one of them maintained the same position relative to the retina (Experiment 3).

Methods

In Experiment 1, observers had to fixate the center of the monitor and were required to judge the relative temporal frequency or speed of two sequentially displayed drifting gratings sinusoidally modulated in luminance after adapting to an oscillating drifting sinusoidal grating (which was located 5° right to the center of the screen within a 5° diameter circular patch). Each subject was tested in different sessions with five different proportions of 5/20 Hz adaptation (0% 5 Hz–100% 20 Hz; 25% 5 Hz–75% 20 Hz; 50% 5 Hz–50% 20 Hz; 75% 5 Hz–25% 20 Hz; and 100% 5 Hz–0% 20 Hz) in order to determine the duty cycle that had no effect on the perceived temporal frequency of the tests. Each cycle lasted 4 s during the initial adaptation (which lasted 20 s) and 2 s during the top-ups (which lasted 10 s). Once the adaptor had disappeared, there was a blank interval lasting 500 ms, followed by two test gratings that were displayed sequentially (separated by a 500-ms interval). The standard stimulus was displayed in the same spatial position as the adaptor and drifted at a fixed rate (10 Hz) across trials. The comparison stimulus drifted at a variable rate (range 2–18 Hz) from trial to trial in order to generate a psychometric function. The durations of both tests were fixed (600 ms). They drifted in opposite directions and the presentation order was randomized across trials. They were both presented in a Gaussian temporal window (amplitude 1.0; Standard: $SD = 100$ ms; Comparison: $SD = \text{comparison duration}/6$). Observers had to report which of the tests drifted at the lower rate. The 50% point on the psychometric function (point of subjective equality, PSE) provided a measure of the perceived temporal frequency of the comparison required to match the frequency of the standard.

In Experiment 2 (Figure 1A), the adaptor (an oscillating sinusoidal grating within a 5° circular window, Michelson contrast = 50%) was located 5° below the fixation spot. Both the fixation spot and the adaptor oscillated slowly ($\sim 6^\circ/\text{s}$) across the screen for 20 s (with 10 s top-ups between trials). Subjects were required to track the fixation spot. The adaptor was oriented horizontally and drifted in a direction orthogonal to the eye movement at 5

or 20 Hz in separate sessions or with the two frequencies interleaved according to the duty cycle that was individually determined in Experiment 1 to minimize the effect of adaptation on perceived temporal frequency. The horizontal starting point of the fixation spot was randomly selected at the beginning of each trial in a range of 20° (from 10° left to 10° right to the center of the screen), while its vertical position was randomly chosen on a trial-by-trial basis between the center of the screen and 6° below or above it. Thus, any head-referenced direction was typically stimulated around 4 times for 1 s in the first adaptation stage and at most twice for 1 s at the top-up stage. Note on two out of three trials that the head-referenced track would be different from in the initial adaptation period; therefore, there was no sustained consistent adaptation at any particular head-referenced location in the pursuit adaptation task. At the end of the adaptation phase, the fixation spot stopped, and 500 ms after the adaptor had disappeared, two test stimuli (Michelson contrast = 100%), separated by a 500-ms interval, were displayed sequentially. The standard stimulus had a fixed duration across trials (600 ms) and was located in the last spatial position occupied by the adaptor. The comparison stimulus (variable duration, range 300–1200 ms) was displayed in the opposite position relative to the fixation spot. The tests drifted in opposite direction at the same rate (10 Hz). Subjects reported which test appeared to stay on for a longer duration, and the PSE of the derived psychometric function provided an estimate of the perceived duration of the standard stimulus.

Experiment 3 differed from Experiment 2 only in the adaptation phase. A second adaptor, identical to that presented in Experiment 2, was simultaneously displayed in the opposite position relative to the fixation spot (5° above it). The two adaptors translated across the screen at the same velocity, but in opposite directions (randomized across trials). As in Experiment 2, subjects were instructed to track the fixation spot that oscillated together with the adaptor displayed 5° below it, and the vertical displacement of the stimuli was randomly varied on a trial-by-trial basis. The horizontal starting point of the fixation spot was randomly selected in a narrow range of positions around the center of the screen to further minimize the retinotopic contribution to the adaptation of the region covered by the second adaptor (i.e., where the comparison stimulus is displayed during the test phase). Both adaptors drifted at the optimal 5 to 20 Hz ratio determined in Experiment 1.

Results

For each subject, we determined the duty cycle of 5 and 20 Hz adaptation that had no effect on perceived temporal frequency. Figure 1B shows the perceived temporal frequency of the stimulus in the adapted region after different proportions of 5 and 20 Hz adaptation. A preponderance of 20 Hz adaptation (left part of the graph)

induced a reduction ($\sim 2\text{--}4$ Hz) of the perceived temporal frequency of the stimulus displayed in the adapted position, while a preponderance of 5 Hz adaptation caused a similar increase in apparent temporal frequency. The duty cycle that minimized the effect on apparent temporal frequency (in the figure, the intersection between the linear fit to the data points and the dashed line that represents the frequency of the standard stimulus) was around 0.25 for two subjects and around 0.66 for the third subject. We then used this stimulus to measure apparent duration in the pursuit task (Figure 1A). Observers were also exposed to continuous 5 and 20 Hz adaptation in different sessions. As reported previously (Johnston et al., 2006), 20 Hz adaptation induced a strong compression of perceived duration (~ 200 ms, mean bottom = 414.9 ms; mean center = 424.2 ms; mean top = 411.3 ms; one-sample t tests revealed a significant difference from 600 for all position conditions, $p < 0.05$), but there was considerably less duration compression (~ 50 ms, mean bottom = 565.8 ms; mean center = 546.6 ms; mean top = 537.9 ms; only the center condition was significantly different from 600, $p = 0.01$) after 5 Hz adaptation (Figure 1C, left panel). More importantly, an adaptor composed of the combination of 5 and 20 Hz that elicited no change in apparent temporal frequency induced a significant reduction of perceived duration (~ 120 ms, mean bottom = 484.8 ms; mean center = 481.2 ms; mean top = 475.3 ms; all the position conditions were significantly different from 600, $p < 0.05$), demonstrating the existence of a retinotopic component of adaptation induced time effects that is independent of changes in apparent temporal frequency. In addition, this effect (and that for continuous 5 and 20 Hz adaptation) is independent of the vertical position on the screen of the stimuli (reported on the abscissa), showing that there is no modulating effect of gaze angle on the magnitude of the duration compression. Finally, when we used two adaptors, one for each test region, simultaneously translating in opposite directions in order to completely match the amount of spatiotopic adaptation for the two areas, the observed reduction in apparent duration remained substantial (Figure 1C, right panel, Mean 2 adaptors = 494.1, one-sample t test revealed a significant difference from 600, $p < 0.01$) and did not significantly differ from that observed when only one adaptor was presented (paired sample t test, $p = 0.22$).

Retinotopic and spatiotopic components of duration compression

From Experiments 2 and 3, it is clear that retinotopic adaptation produces an effect on apparent duration with-

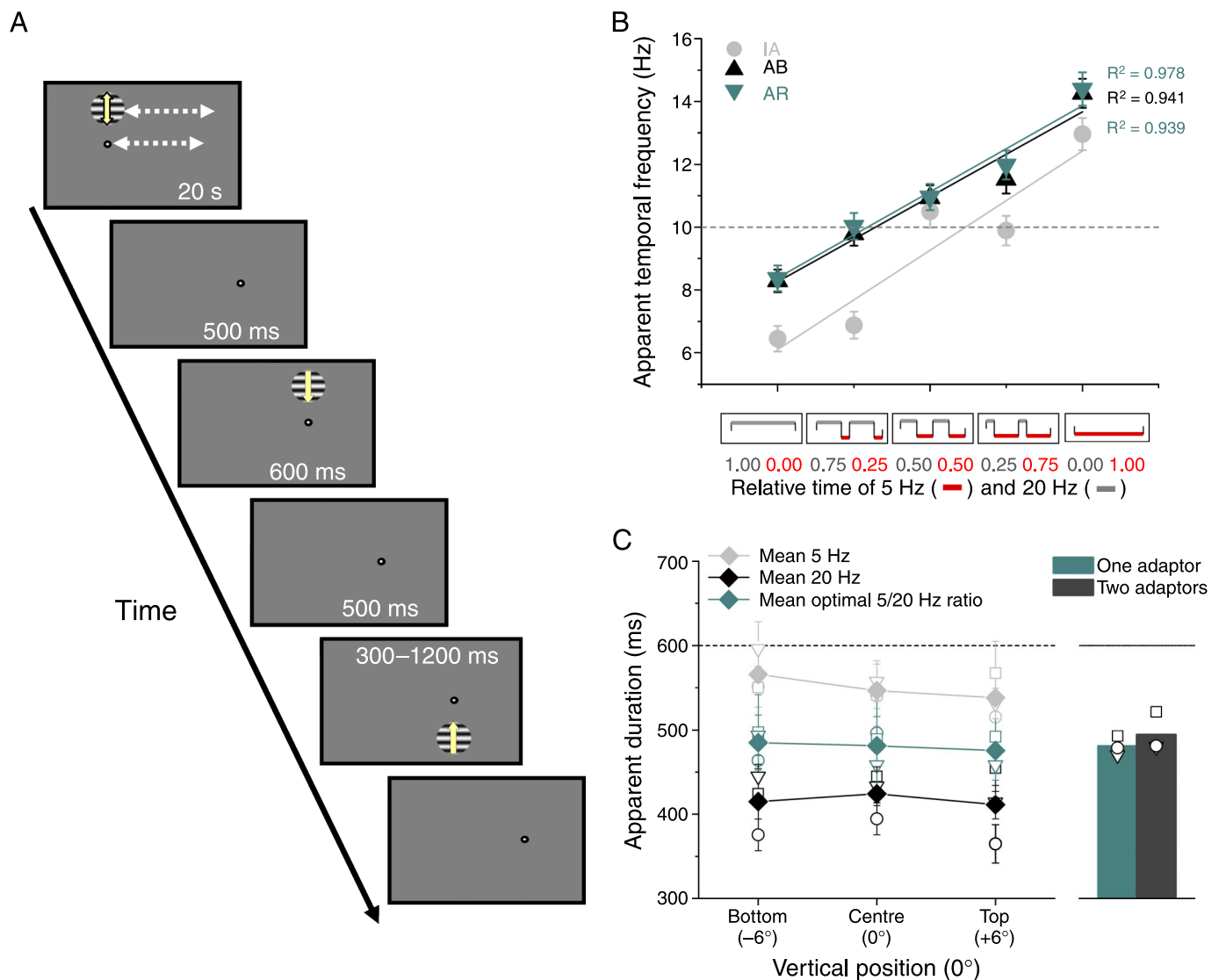


Figure 1. Effects of retinotopic adaptation on duration judgments in the absence of temporal frequency distortions. (A) Schematic illustration of the time course of the pursuit experiment, in which subjects had to judge the relative duration of two sequentially displayed drifting gratings after an adaptation to a vertically oriented drifting grating (which changed direction every second) which was yoked to a fixation spot that slowly oscillated horizontally across the screen. (B) Results of Experiment 1 (temporal frequency experiment, schematic illustration not shown) for three different subjects (two authors and a naïve). The PSEs (chosen as an estimate of apparent temporal frequency) are plotted as a function of the relative time of 5 and 20 Hz adaptation that were used in different sessions. Straight lines describe the linear fits of the data for each subject. The dashed line indicates the temporal frequency of the standard stimulus. The correlation coefficient R^2 is also reported in the legend for each subject separately. Error bars show ± 1 SEM. (C) Results of the pursuit experiments (Experiments 2 and 3) for the same subjects displayed in Figure 1B. (Left panel) The duration judgments are plotted as a function of three fixation tracks. Empty symbols describe individual data, while filled symbols indicate average data. Results obtained after adaptation to 5 Hz (light gray symbols), 20 Hz (black symbols), and to the combination of 5 and 20 Hz (dark cyan symbols) that elicited no change in temporal frequency in the first experiment (Figure 1B) are shown. The dashed line indicates the duration of the standard stimulus. Error bars show ± 1 SEM. (Right panel) Mean results (averaged across three subjects and three fixation tracks) for the condition in which two adaptors, drifting at the optimal ratio of 5 to 20 Hz and translating in opposite directions, were displayed (one for each test region) are reported (dark gray column), alongside mean results for the condition with one adaptor (already displayed in the left panel, dark cyan column). Empty symbols indicate individual results for the same conditions (triangles, subject AB; circles, subject IA; squares, subject AR).

out any change in perceived temporal frequency. We have previously shown that, during fixation, duration compression is similar whether changes in apparent temporal frequency are compensated for or not (Johnston et al., 2006), and there is little change in perceived duration as a function of physical temporal frequency over the range of likely changes (10–7 Hz) in perceived temporal frequency (Johnston et al., 2006; Kanai et al., 2006); therefore, in the subsequent experiments, we used our simpler standard paradigm, testing the effects of 20 Hz adaptation on 10 Hz drifting test gratings. This should provide stronger adaptation than the mixed adaptor paradigm, and in this case comparisons are made in relation to the durations of physically identical stimuli. Note that Burr et al. (2007) reported little or no change in apparent temporal frequency in purely spatiotopic conditions. In Experiment 4, we used a gaze shift paradigm to gauge the strength of spatiotopic adaptation. This paradigm differed from the one used by Burr et al. in some respects. Our stimuli were smaller and the oscillation rate was higher in keeping with the Johnston et al. (2006) study, and the relative position of the two tests was always the same in our paradigm (above and below the horizontal midline of the monitor, Figure 2A), whereas in their study the comparison in the spatiotopic and control conditions was across hemifield whereas the retinotopic condition was within hemifield. At least one study has reported that the durations of stimuli in the right hemifield appear expanded (Vicario et al., 2008), and it is possible that the allocation of attentional resources to locations might be more variable when observers must compare the relative duration of stimuli displayed in unpredictable positions. Later in Experiment 5 (Figure 3A) we adopted the same spatial configuration as used by Burr et al.

Methods

In the adaptation phase of Experiment 4 (Figure 2A), subjects fixated a circular spot that was located 5° left to the center of the monitor, while a luminance modulated sinusoidal grating (located 5° above the center of the screen within a 5° diameter patch) that oscillated at 20 Hz (reversing direction every 250 ms, spatial frequency = 1 cycle/degree, Michelson contrast = 50%) was presented for 20 s with 10 s top-ups between trials. After the disappearance of the adaptor, the fixation spot could randomly either jump 5° rightward (retinotopic and spatiotopic adaptation) or stay in the same position (full adaptation). In the retinotopic and spatiotopic cases, but not in the full adaptation case, subjects were required to saccade to the new target position. At the beginning of each trial, an acoustic signal informed them which condition (full, retinotopic, or spatiotopic) was about to be displayed. In the full and retinotopic adaptation conditions, the test stimuli (1 cycle/degree vertical gratings,

Michelson contrast = 100%, drifting at 10 Hz in opposite directions, displayed sequentially 800 ms after the adaptor had disappeared) were displayed 5° right of the fixation spot, while in the spatiotopic condition they were displayed 5° left of the fixation spot. The standard (600 ms) and the comparison (range 300–1200 ms) stimuli were displayed in opposite positions relative to the horizontal midline. At the end of each trial, observers reported which test seemed to have the longer duration. Control conditions, in which observers viewed a gray field during the adaptation period in order to keep timing constant, were also run in separate sessions. The PSE provided an estimate of the perceived duration of the standard stimulus.

In Experiment 5 (Figure 3A), subjects had to fixate a black spot that was located 15° left of the center of the screen, while a 1 cycle/degree horizontal grating (the adaptor, Michelson contrast = 50%) drifting at 20 Hz was displayed for 44 s (with 8 s top-ups between trials). The adaptor reversed direction every 2 s, and it was displayed within a 12° diameter patch centered 8° left of the center of the screen. At the end of the adaptation phase, the fixation spot jumped 15° rightward and subjects had to saccade to it. Some 800 ms after the fixation spot had changed position, a standard stimulus (600 ms) was randomly displayed in one out of three possible positions. In the retinotopic trials, it was displayed to the right of the fixation spot and above the horizontal midline. In the spatiotopic trials, it was presented to the left of the fixation spot and above the midline. In the control trials, it was displayed left of the fixation spot and below the midline. Some 500 ms later, a comparison stimulus (300–1200 ms) was displayed to the right of the fixation spot and below the midline. Michelson contrast of both tests was 100%. A full adaptation condition (where no saccade was required and the adaptor and the standard were in the same physical position) was also run in a separate session. The two tests drifted at 10 Hz in opposite direction. Subjects reported which test was perceived to be longer in duration. A psychometric function was fitted to the resulting data and the PSE provided an estimate of the perceived duration of the standard stimulus.

Results

In Experiment 4 (Figure 2B), a significant reduction of perceived duration was observed both for the full (mean FULL baseline = 636.3 ± 17.93 ; mean FULL adaptation = 398.4 ± 9.43 ; paired t test: $t(2) = 14.15$, $p = 0.005$) and the retinotopic (mean RETINO baseline = 606.3 ± 12.75 ; mean RETINO adaptation = 429.9 ± 21.91 ; paired t test: $t(2) = 11.65$, $p = 0.007$) adaptation conditions, while the spatiotopic adaptation results did not differ from the baseline (mean SPATIO baseline = 631.5 ± 18.62 ; mean SPATIO adaptation = 630.6 ± 12.08 ; paired t test: $t(2) = 0.042$, $p = 0.97$, not significant). The pattern was the same

for all three subjects we tested (individual data compared using bootstrap statistics from the fits of the psychometric functions). If we plot the size of the duration reduction (determined as the difference between adaptation and baseline PSEs) obtained in the retinotopic or spatiotopic adaptation condition as a function of the reduction observed in the full adaptation condition (Figure 2C), we can see that the magnitude of the time compression observed in the retinotopic condition was similar to that obtained in the

full condition. The data points are close to the diagonal dashed equality line. However, there was no such relationship with the spatiotopic condition. In this case, the data points are close to the horizontal dashed line, which represents an absence of correlation between the two conditions.

In Experiment 5, (Figure 3), which was more similar in format to the Burr et al. (2007) study, we found a significant reduction in perceived duration (CONTROL

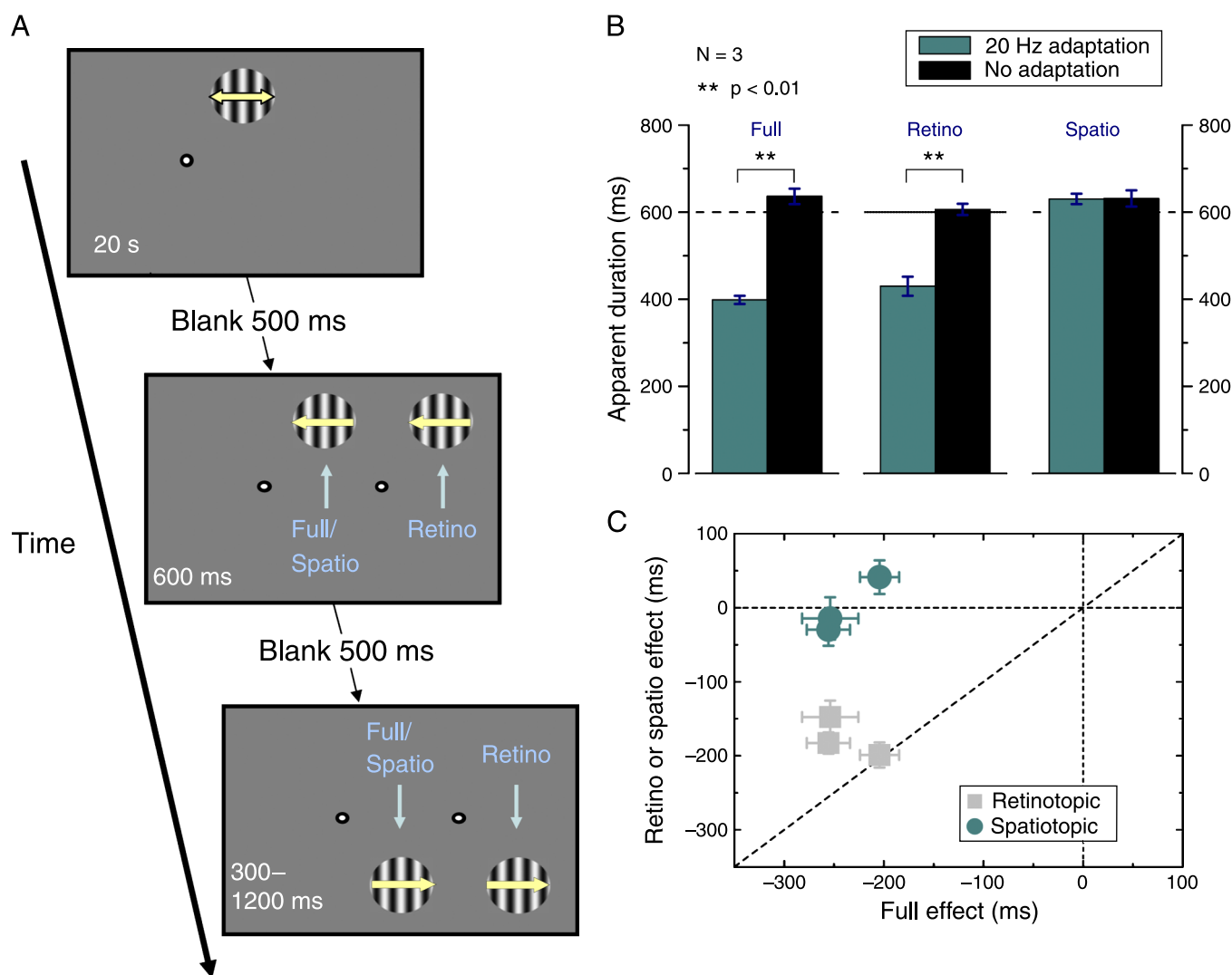


Figure 2. Effects of retinotopic and spatiotopic adaptation on perceived duration. (A) Schematic illustration of the time course of Experiment 4 (duration), in which the standard stimulus was randomly presented in one of three possible spatial positions: same physical position of the adaptor (FULL), same position of the adaptor in retinocentric (RETINO) or head-centric (SPATIO) coordinates. The comparison stimulus was displayed in the opposite position relative to the horizontal midline and the subjects were asked to report which of the tests seemed to last longer. (B) Average results for three subjects (two authors and a naïve). Duration judgments (PSEs) are plotted for 20 Hz adaptation (dark cyan columns) and for a condition in which no adaptation was presented (black columns). The dashed line indicates the duration of the standard stimulus. Error bars show ± 1 SEM. (C) Duration change in the adaptation conditions relative to the control conditions (no adaptation). Duration change after retinotopic (light gray symbols) and spatiotopic (dark cyan symbols) adaptation are plotted as a function of the change in the full adaptation condition. The horizontal dashed line indicated no effect on duration in the retinotopic or spatiotopic condition, the vertical dashed line indicated no effect in the full condition. The diagonal is the equality line. Error bars show ± 1 SEM.

mean = 670.57 ± 29.34) following both the full (FULL mean = 475.81 ± 50.71 ms; paired t test: $t(3) = 4.42$, $p = 0.022$) and the retinotopic (RETINO mean = 450.6 ± 56.24 ms; paired t test: $t(3) = 3.97$, $p = 0.029$) but not the spatiotopic adaptation (631.2 ± 24.14 ; paired t test: $t(3) = 2.89$, $p = 0.063$, not significant). The amount of reduction in apparent duration obtained when the standard was in the same physical position of the adaptor was comparable in magnitude to the compression observed when standard and comparison were in the same position relative to the

eye but not to the head (Figure 3C). No substantive relationship between full and spatiotopic reduction was observed.

Order effect

Unlike the Burr et al. (2007) study, we find that adaptation-based duration compression is robustly retino-

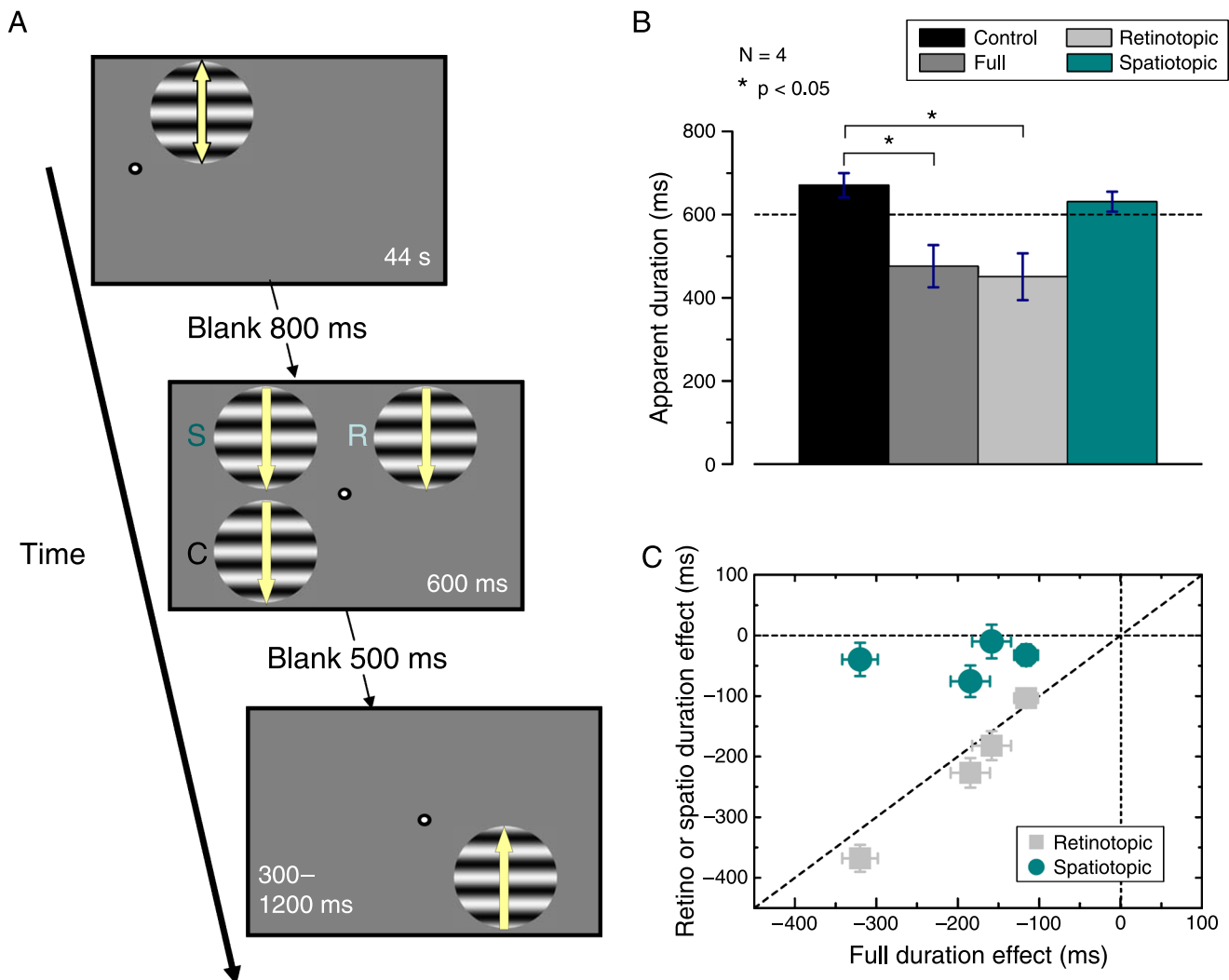


Figure 3. Effects of adaptation on perceived duration in the paradigm following Burr et al. (2007). (A) Schematic illustration of Experiment 5 (saccadic task). After a saccadic eye movement, the standard stimulus randomly appeared in the same retinotopic or spatiotopic position of the adaptor or in a control position. The comparison stimulus was subsequently displayed on the bottom-right. A condition in which no saccade was required and the standard was in the same physical position of the adaptor (full adaptation, not shown in the illustration) was also run. (B) Duration judgments averaged over four subjects (two authors and two naives) are plotted for four different conditions: control (black column), full (dark gray column). Retinotopic (light gray column) and spatiotopic (dark cyan column). The dashed line indicates the standard stimulus duration. Error bars show ± 1 SEM. (C) Apparent duration change in the adaptation conditions relative to the control condition (unadapted location) (from Figure 2B). Apparent duration change after retinotopic (light gray symbols) and spatiotopic (dark cyan symbols) adaptation are plotted as a function of the apparent duration change in the full adaptation condition. The horizontal dashed line indicated no effect on duration in the retinotopic or spatiotopic condition; the vertical dashed line indicated no effect in the full condition. The diagonal is the equality line. Error bars show ± 1 SEM.

topic. The second of a pair of intervals is generally perceived as having a greater magnitude than the first one (Jamieson & Petrusic, 1975; Nachmias, 2006) and for 2IFC designs the discrimination threshold is lower when the standard comes before the comparison (Lapid, Ulrich, & Rammsayer, 2008; Nachmias, 2006). One methodological difference that may contribute to the different outcomes of the two studies is the method in which order effects are controlled. In the Burr et al. paradigm, the standard stimulus (presented in the adapted position) was always presented before the comparison stimulus (displayed in the unadapted position), while in Experiments 2–5 and in our previous reports (Ayhan et al., 2009; Johnston et al., 2006, 2008), the stimulus order was randomized on a trial-by-trial basis. Although in the Burr et al. adaptation conditions the order effect is potentially confounded with any adaptation effect, Burr et al. reported differences between adaptation and control conditions, which should be affected similarly by the presence of an order effect in any subject's data. Nevertheless, there may be an interaction between the order effect and the adaptation conditions reflecting a greater order effect after a period of adaptation. To assess any dependence of a spatiotopic effect or interocular transfer on classical presentation order effects (Fechner, 1860; Woodrow, 1951; Woodworth & Schlosberg, 1954), we measured perceived duration after full, retinotopic, and spatiotopic adaptation for trials for which the stimulus in the adapted region was presented first or second in separate sessions (Experiment 6). The same procedure was used to study the interocular transfer effect, in which we adapted one eye and tested the other eye (Experiment 7). Both these experiments were run using the same MATLAB script generated by Burr et al. for their experiment, adapted to control order of presentation. Adopting the procedure of Burr et al. means that rather than being drawn from a predetermined set of intervals, the level of the comparison stimuli is now controlled by an adaptive staircase. This, of itself, is not expected to have any effect on duration discrimination (Lapid et al., 2008).

Methods

In Experiment 6, subjects adapted to a luminance modulated sinusoidal grating (which was located 7.5° above the center of the screen within a 12° diameter patch) that oscillated at 20 Hz (inverting direction every 2 s, spatial frequency = 1 cycle/degree, Michelson contrast = 90%) while fixating a circular spot that was located 6.5° left of the center of the monitor. The adaptor was presented for 45 s with 8 s top-ups between trials. Immediately after the disappearance of the adaptor, the circular spot jumped 13° to the right and subjects were instructed to execute a saccade to the new position. Some 800 ms later, the two tests (11° diameter, 10 Hz, 1 cycle/degree, Michelson contrast = 90%) were displayed sequentially (separated by

500 ms blank gray interval), one (standard stimulus, fixed duration across trials, 600 ms) in either the same spatiotopic or retinotopic position as the adaptor (in separate sessions), the other (comparison stimulus, variable duration across trials) in the opposite position relative to the monitor horizontal midline. Note that the location of the comparison for this version of the Burr et al. (2007) paradigm differs from that reported by Burr et al. and in our Experiment 4. In the full adaptation condition, the fixation spot remained in place at the end of the adaptation phase, and the standard stimulus was displayed in the same physical position as the adaptor. For each adaptation condition (full, retinotopic, and spatiotopic), three stimulus orders were used in different sessions: the standard was the first test to be displayed in all trials (standard first) or was always displayed second (standard second) or its position in the test sequence was randomized (standard random). Baseline conditions, in which no adaptation was presented, were also run in separate sessions. The duration of the comparison stimulus was determined on a trial-by-trial basis using the adaptive QUEST procedure (Watson & Pelli, 1983).

The stimuli, conditions, and procedure employed in Experiment 7 were the same as in Experiment 6 with the only difference that observers were required to wear a pair of ferroelectric liquid crystal shutter goggles (Cambridge Research Systems FE-1 Goggles) for the whole duration of the experiment. During the adaptation phase, the left lens of the goggles was shut so that observers could see the monitor (and the adaptor displayed on it) monocularly through the right eye. At the end of the adaptation phase, the left lens switched to the open state and the right one was shut, allowing subjects to see the tests monocularly with the left eye.

Results

Experiment 6 followed the methods used by Burr et al. (2007) except, to simplify the procedure, we used our standard paradigm rather than matching the perceived temporal frequencies of the test pattern or eliminating any changes in perceived temporal frequency, since we have shown changes in apparent duration can be dissociated from changes in apparent temporal frequency. Data for the full, retinotopic and spatiotopic manipulations are plotted against separate control conditions in Figure 4. We first compared the mean apparent durations against the standard duration (600 ms) using one-sample *t* tests. The average perceived duration in all adaptation conditions (FULL, RETINO, and SPATIO) and for all the stimulus orders (standard first, standard second, and standard random) is less than 600 ms, apart from in the standard second spatiotopic condition ($p = 0.568$, *ns*). However, the data may also contain a general tendency for the standard to appear compressed relative to the comparison and an order effect, in that the first interval may appear com-

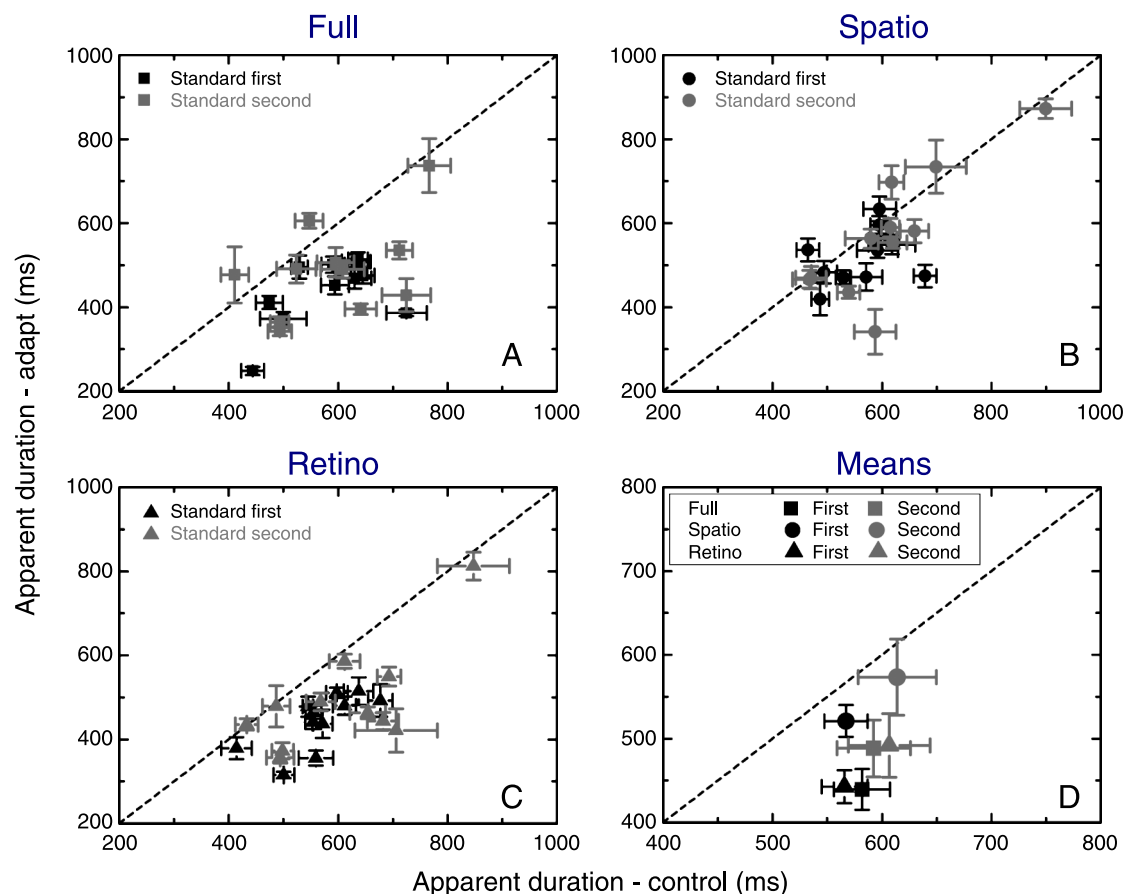


Figure 4. Effect of adaptation and presentation order on apparent duration (Experiment 6). (A) Duration estimates after adaptation in the full condition are plotted as a function of the estimates obtained in the control (no adaptation) condition for two stimulus orders: standard stimulus (600 ms) constantly displayed before (standard first, black) or after (standard second, dark gray) the comparison stimulus. Error bars show ± 1 SEM. (B and C) Same as in Figure 4A for spatiotopic and retinotopic adaptation, respectively. (D) Means for full, spatiotopic, and retinotopic adaptation conditions.

pressed relative to the second interval, or an order contingency, in that there may be apparent compression or expansion contingent on whether the standard was presented first or second. To explore these alternatives, standard first and standard second conditions are plotted separately (Figure 4). In these graphs, a line passing through the origin and the point (600, 600) indicates zero adaptation. Data points falling on this line indicate subjects for whom the perceived duration of the standard in the adaptation condition is equal to the perceived duration of the standard in the control condition. Points falling below this line indicate compression in the adaptation conditions relative to controls. Contours parallel to the opposite diagonal through the point (600, 600) indicate an equal average tendency for the standard to appear expanded or contracted relative to the comparison, with increasing distance from the origin indicating expansion. First, we observed a significant difference between the means of the adaptation conditions (including the standard random condition) when compared using ANOVA (main effect adaptation: $p < 0.005$). Planned comparisons show both the full and retinotopic conditions

show significantly greater compression than the spatiotopic condition ($p < 0.05$ and $p < 0.05$, respectively). To test for a compression effect, that is whether the mean of the data points is below the line, we compared the difference between adaptation conditions and control conditions for each of the three adaptation conditions (full, retinotopic, and spatiotopic) and each of the stimulus orders (standard first, standard second, and standard random) separately against zero using one-sample t tests (Figure 6A). We found that perceived duration was significantly compressed after adaptation only in the full and retinotopic conditions. The adaptation effect in the spatiotopic condition for standard first trials approached significance ($p = 0.06$) but there was no observable effect in the case of standard second or standard random conditions. All full and retinotopic conditions apart from the full standard second condition survived Bonferroni correction (0.05/number of comparisons; number of comparisons = 9; Bonferroni corrected criterion = 0.0056).

We also plot the perceived duration for conditions in which the standard came second relative to when the

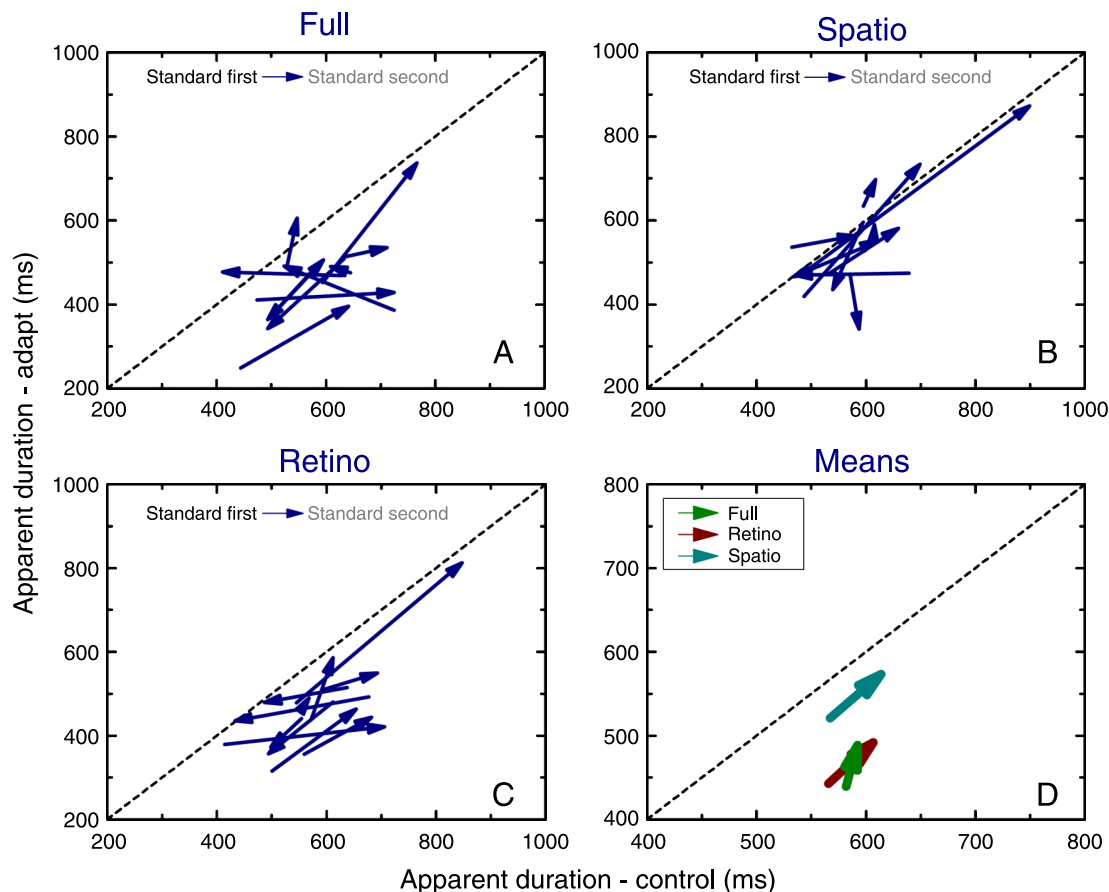


Figure 5. Direction of the presentation order effect on apparent duration (Experiment 6). (A) Blue arrows connect standard first to standard second judgments as presented in Figure 4A for each subject separately. (B and C) Same as in Figure 5A for spatiotopic and retinotopic adaptation, respectively. (D) Mean arrows for full, spatiotopic, and retinotopic adaptation connect [mean standard first for control, mean standard first after adaptation] with [mean standard second for control, mean standard second after adaptation].

standard came first as a vector along with vectors relating the means of these conditions (arrows in Figure 5). We can see that, for all three adaptation and control conditions, the standard in the first interval appears compressed relative to when it is in the second interval however the difference does not reach significance. Thus, in these data there is no overall order effect, presumably reflecting considerable intersubject variability. Also the mean trend vector relating the second interval to the first interval is parallel in the retinotopic and spatiotopic conditions to the main diagonal indicating the trend toward the second interval appearing shorter does not interact with the adaptation effect. However, it is clear from the scatter plot in each condition that there is some tendency for the degree of compression in the adaptation condition to be related to the perceived duration of the standard in the control condition, which may reflect individual differences in an order bias in both control and adaptation conditions.

Although the mean apparent duration of the standard is significantly less than 600 ms in the spatiotopic condition, this apparent spatiotopic compression disappears when compared against controls, suggesting that there is some

other influence unrelated to adaptation which tends to make the standard appear compressed, particularly when it is presented first, though we should point out none of the means of the control conditions are significantly different from 600 ms. One possibility is that when the standard appears first in blocked trials, it can be ignored and the observers can relate the variable comparison to an internal standard. This strategy has recently been shown to lead to better discrimination thresholds and therefore adoption of this strategy by the subject would make a difficult task easier (Lapid et al., 2008; Nachmias, 2006). In our results (data not shown), an analysis of variance revealed a significant main effect for the standard stimulus order ($p = 0.011$). In particular, the discrimination threshold was lower when the standard was displayed first relative to when it was displayed second (test of within-subjects contrast, $p = 0.013$) or when it was randomized ($p = 0.035$). However, if this strategy is adopted, without feedback the mean internal standard is essentially free-floating. The general expectation is that subjects use the mean of the stimulus set as an internal criterion. Because of the well known Weber Law for duration perception, it makes sense to use logarithmic or quasi-logarithmic

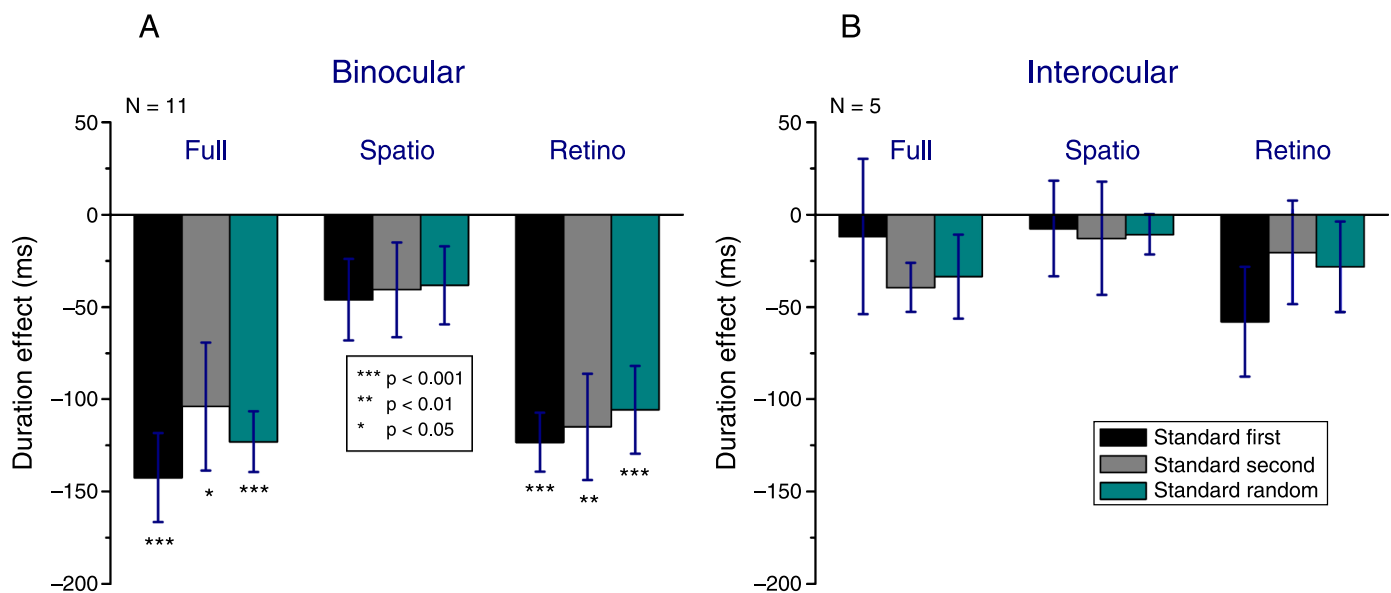


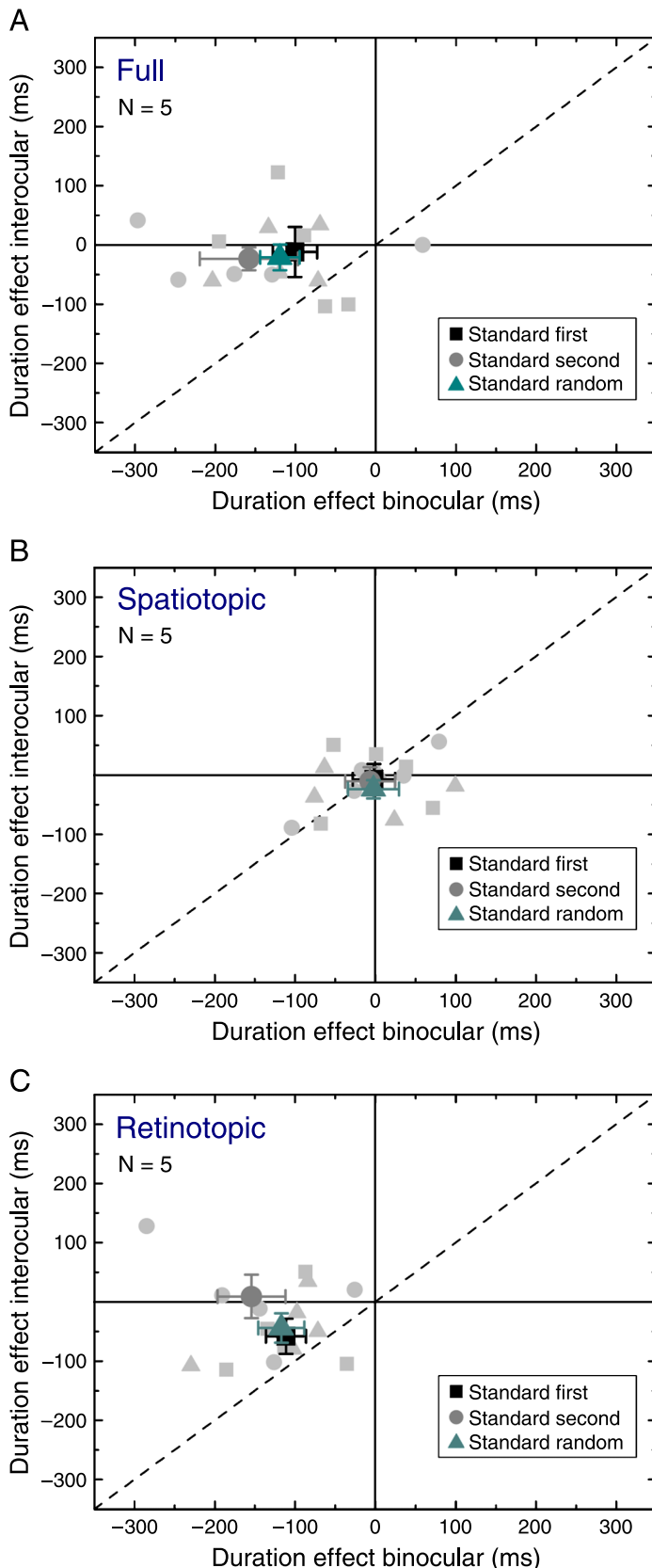
Figure 6. Effect of binocular and monocular adaptation on duration judgments for three presentation orders. (A) Apparent duration effect (relative to no adaptation condition) after binocular adaptation (Experiment 6, both eyes were adapted and tested) averaged across eleven subjects (three authors, eight naives) for standard first (black columns), standard second (dark gray columns) and standard random (dark cyan columns) conditions, and for three adaptation paradigms (full, spatiotopic, retinotopic). Error bars show ± 1 SEM. (B) Same as Figure 6A for dichoptical presentation (Experiment 7): subjects (two authors, three naives) monocularly adapted the right eye and tested the left eye.

intervals in both QUEST staircase and method of constants techniques, as was done by both Burr et al. (2007) and Johnston et al. (2006). However, in this case an internal criterion based on the mean of the set will be biased toward long intervals generating a tendency for the measured PSE to be longer (expansion) than the standard. In our replication of Burr et al. the range of the QUEST staircase was set between -0.6 and $+0.3$ logarithmic units (with 0 logarithmic units corresponding to the standard duration, 600 ms). Thus, the mean of the set of the presented comparison durations is somewhat biased toward values lower than 600 ms, which would generate a tendency for the PSE to be shorter (compression) than the standard duration. To explain the spatiotopic adaptation found by Burr et al. on this observer strategy, one would have to assume, in addition, a greater tendency for subjects to ignore the standard interval and generate an internal standard in the adaptation conditions in comparison to control conditions. However, adaptation experiments combined with QUEST or methods of constants procedures are more grueling for subjects than control conditions and therefore the potential for subjects to rely on an internal standard may be greater, particularly in the case of standard first trials. The best defense against this would be to randomize standard first and standard second trials on a trial by trial basis as we did in Experiments 2–5, where the trend is in the control and spatiotopic conditions for the standard to appear slightly longer than 600 ms. In these experiments, the intervals for the levels of the comparison

were quasi logarithmic but centered on the duration of the standard (600 ms). One should note that, even when the position of the standard is randomized, discrimination threshold is expected to be reduced in the standard first case (Nachmias, 2006).

In Experiment 7, we measured the amount of interocular transfer from the adapted eye to the test eye, first, by comparing the average apparent durations after adaptation against the actual duration (600 ms) with one-sample t tests. All the standard first and standard random conditions are significantly different from 600 ($p < 0.05$) for the three types of adaptation, while none of the standard second conditions are statistically significant. However, when we subtract the control data from the adaptation data and, then, we compare this difference against 600 with one-sample t tests, none of the conditions reach statistical significance (lowest $p = 0.12$ for retinotopic, standard first). This, again, suggests a trend for the standard to appear compressed even in control conditions. Since all the five subjects that participated in the interocular transfer experiment had also taken part to Experiment 6, we can compare their performances in the two paradigms and estimate the amount of transfer for each adaptation condition. To do so, we plotted the difference between adaptation and control data in the interocular transfer experiment as a function of the same difference in the binocular experiment (Experiment 6) for full, spatiotopic, and retinotopic adaptation separately (Figure 7). The amount of adaptation induced effect on

duration in the binocular and interocular conditions is indicated by the distance from the vertical and horizontal solid lines, respectively; the more distant the points, the bigger the difference between adaptation and control.



Moreover, if the data points fall on the diagonal dashed line (equality line), it means that the effect produced by adaptation in the interocular condition is identical to that produced in the binocular condition. It is clear that for full and retinotopic adaptation, the means for the binocular condition are substantially lower than zero. One-sample t tests against zero reveal that all the full and retinotopic means apart from the full standard second ($p = 0.061$) are significantly different from zero ($p < 0.05$). However, as shown in Figure 6B, no significant adaptation effect is observable for full and retinotopic adaptation in the interocular condition. For the spatiotopic adaptation, none of the three standard conditions (first, second, random) are significantly different from either of the two zero lines (highest $p = 0.85$ for standard second) (Figure 7).

Discussion

The idea that the apparent duration of a visual stimulus can be influenced by spatially specific visual adaptation (Ayhan et al., 2009; Burr et al., 2007; Johnston et al., 2006, 2008) implies the existence of spatially localized components within a pathway for visual duration perception. In this study, we aimed to investigate where, in the visual system, adaptation might influence time perception. We observed robust time compression following a purely retinotopic adaptation, in which the adaptor had always the same position relative to the eye, but not to the head, after we minimized changes of apparent temporal frequency by optimally alternating 5 and 20 Hz adaptation. We also found a strong reduction in apparent duration for a stimulus that was displayed in the same position of the adaptor in retinocentric coordinates in two different paradigms in which a change in the direction of gaze occurred between the adaptation and the test phase. No significant effect was observed after spatiotopic adaptation in either case. The size, spatial configuration of the stimuli and psychophysical techniques (which were different in

Figure 7. Differential effect of binocular and monocular adaptation on apparent duration (Experiment 7). (A) Differences between apparent duration after full adaptation and in the control (no adaptation) conditions in the interocular (adapt right eye, test left eye) experiment are plotted as a function of the same differences in the binocular (adapt and test both eyes) experiment. Mean (standard first, black squares; standard second, dark gray circles; standard random, dark cyan triangles) and individual (light gray symbols) results are plotted for three different stimulus orders. The diagonal is the equality line; the vertical dashed line indicates zero adaptation effect in the binocular paradigm. The horizontal dashed line indicates zero effect in the interocular paradigm. Error bars show ± 1 SEM. (B and C) Same as in Figure 7A for spatiotopic and retinotopic adaptation, respectively.

the two paradigms involving a shift in eye gaze) did not seem to make a substantial difference to the pattern of results. Moreover, we observed robust retinotopic, but no spatiotopic effect in a paradigm in which we separated out the two possible temporal orders in which the test stimuli can be presented. The relative position of the standard and the comparison stimuli in the test sequence seems to produce a small effect on apparent duration, which, at least in some cases, can be dissociated from the effect of adaptation. Finally, we showed almost no interocular transfer in a paradigm in which the right eye was adapted and the left eye was tested.

The robustness of the results we observed in all our experiments after adaptation in retinal coordinates suggest the existence of a significant retinotopic component for duration encoding. This supports the idea that the neural substrates of the spatially specific mechanisms responsible for the time compression effects reside at an early stage in the visual system. This is consistent with a number of recent results. In the first paper demonstrating an influence of adaptation to flicker or oscillating motion on apparent duration, Johnston et al. (2006) observed that duration compression was similar when the orientation of the adaptor was orthogonal to the orientation of the tests, suggesting the neural substrate of the effect was prior to the orientation tuned channels of primary visual cortex. Moreover, adapting to a invisible flicker (adaptation frequency above the flicker fusion threshold, ~50–60 Hz) thought to stimulate the magnocellular layers of the lateral geniculate nucleus (LGN), but not cortical cells, has been shown to produce a significant reduction of perceived duration (Johnston et al., 2008). Ayhan et al. (2009) investigated the spatial specificity of the adaptation induced duration compression by measuring perceived duration in locations nearby the adapted region. They found that the effect is highly specific to the adapted region (compression was abolished for test locations just 1 degree of visual angle from the adaptor location), implying that this kind of adaptation takes place in an early locus in the time pathway, where the receptive fields are relatively small (Dow, Snyder, Vautin, & Bauer, 1981; Johnston, 1989). The involvement of the magnocellular layers of the LGN is consistent with the finding that dyslexics, for whom a magnocellular-related impairment has been suggested (Stein & Walsh, 1997), do not show a reduction in apparent duration for invisible flicker adaptation (Johnston et al., 2008). There is also evidence of magnocellular suppression around the time of a saccade. Saccadic eye movements have been shown to distort time as well as space (Burr, Morrone, & Ross, 1994). The apparent duration of an interval defined by switching between two bars, one above and one below the saccade path, is compressed immediately before the execution of a saccade (Morrone, Ross, & Burr, 2005). Terao, Watanabe, Yagi, and Nishida (2008) describe a similar effect in which the interval was defined by two bars presented within a sequence of high-frequency random dynamic

luminance flicker. The high-frequency flicker was considered to suppress magnocellular pathway activity.

Burr et al. (2007) reported significant spatiotopic adaptation. Spatiotopic adaptation has been taken as evidence of feature remapping across saccades (Melcher, 2005). Melcher (2005) reported that the tilt aftereffect, a form aftereffect and the face aftereffect, but not contrast adaptation, survived a change in gaze when the test and adaptor overlapped in head-centered coordinates. The claim that spatiotopic adaptation is particularly strong for high level visual processing has been challenged by Afraz and Cavanagh (2009) who did not find spatiotopic adaptation for gender-specific face adaptation. In a different but related paradigm, Nishida, Motoyoshi, Andersen, and Shimojo (2003) reported that the motion aftereffect, tilt aftereffect, and size aftereffect show a modest enhancement if the test stimulus remains in the same position relative to the head as the adaptor, over just being on the same location on the retina, providing psychophysical evidence of eye gaze modulation of retinal adaptation. Nishida et al. also looked for a tilt aftereffect for the same head-referenced visual direction after a change in gaze but failed to find evidence for spatiotopic adaptation. In more recent subsequent studies, the claims for spatiotopic adaptation have not held up well. Knapen, Rolfs, Wexler, and Cavanagh (2010) failed to find a spatiotopic tilt aftereffect. The same group (Knapen, Rolfs, & Cavanagh, 2009) failed to find a spatiotopic motion aftereffect and Wenderoth and Wiese (2008) reported the motion direction aftereffect to be predominately retinotopic. Also, Morris et al. (2010) showed that transsaccadic motion integration reflects probability summation and integration can be minimized by reducing stimulus onset uncertainty.

There is a crucial difference between these feature-based adaptation effects and the duration aftereffect, which would make spatiotopic adaptation in the duration aftereffect more difficult to explain. The motion aftereffect, tilt, and direction aftereffects and form aftereffect are thought to arise from adaptation bias in feature gain within a population of feature coded cells. The spatiotopic effect is thought to reflect the remapping of these feature gains into a new location, which will contain the stimulus after a saccade, in order to facilitate subsequent processing. Putting aside the complexity of this, in duration-based time compression, the observers are not adapted to a change in duration, they are adapted to a change in temporal frequency. In addition, Burr et al. (2007) report that little change was required to match the speed (temporal frequency) in the spatiotopic conditions in six out of eight subjects. Since there is no substantial change in perceived temporal frequency and no opportunity for an adaptation induced bias in a population of duration channels, there is no obvious candidate feature to be remapped. Burr et al. suggest that high temporal frequency adaptation slows down processing in a network of cells such that a network pattern indicative of a particular duration arises late. The difficulty for this proposal, as with the proposal that

temporal frequency alters the time course of the neural representation of the stimulus, is that there is no change in the apparent time of onset or offset of the test intervals after adaptation (Johnston et al., 2006). In addition, if changes in perceived duration reflected temporal frequency induced changes in processing speed then perceived duration should be expected to increase after adaptation to 5 Hz drift or flicker; however, this was not found to be the case in Experiment 2 where a retinotopic adaptation to 5 Hz produced a duration reduction trend (Figure 1C).

There are some methodological differences between our experiments and Burr et al. (2007). In Experiment 4, the size of our stimuli was roughly half of those used by Burr et al. (5° vs. 12° diameter). According to some recent reports, relative size can affect time judgments (Ono & Kawahara, 2007; Xuan, Zhang, He, & Chen, 2007) but in our studies stimuli to be compared were always the same size, so we do not think stimulus size is a critical variable. In Experiment 5, we used the same size and followed the procedure described by Burr et al. Again, we could not find any substantial compression after spatiotopic adaptation. They always presented the standard first in case adaptation strength for spatiotopic adaptation diminished quickly with time. Burr et al. matched apparent speed of the test patterns. We chose to keep the test patterns speed and temporal frequency physically identical but since in the spatiotopic adaptation trials Burr et al. reported little or no change in apparent spatial frequency this difference would not explain the lack of spatiotopic compression in our study.

We investigated potential interactions between changes in apparent duration due to adaptation and changes due to the temporal order, given that people tend to overestimate the strength of the second of a pair of stimuli (Jamieson & Petrusic, 1975; Lapid et al., 2008; Nachmias, 2006). In this experiment we also had the opportunity to use the MATLAB code generated by Burr et al. (2007). Although there was a trend in the direction of spatiotopic adaptation in the Experiment 6 when the standard was presented first, there was no indication of spatiotopic adaptation when the standard was presented second or when the presentation order was randomized. A robust spatiotopic adaptation would be expected to survive a switch in order of standard and comparison, given the average length of a trial is only 1.7 seconds, and motion adaptation can survive a gap containing a uniform interval lasting many seconds (Spigel, 1962). We found a tendency for the standard (adapted position) to appear compressed when it was displayed first in the test sequence in the case of control conditions and adaptation conditions. This order effect might account, at least in part, for the discrepancy between Burr et al.'s results and our own. We suggest that the Burr et al.'s spatiotopic result reflects the trend we see in our own data for standard first conditions. Also we suggest the lack of an effect in standard second conditions is attributable to observer strategies rather than a lack of

storage or the weakness of spatiotopic adaptation, as is the standard first result, given that there is no clear mechanism for feature remapping in our paradigm. In standard first situations, some observers ignore the standard and switch to a method of single stimuli strategy (Nachmias, 2006), comparing the comparison to a biased internal reference derived from the mean of the presented stimuli. They adopt this strategy because, perhaps paradoxically, magnitude discrimination thresholds are lower for method of single stimuli and thus the task appears easier to observers. This tendency we think is more likely with naïve observers and in the more taxing adaptation conditions. This may explain the fact that we saw a trend toward what appears to be spatiotopic adaptation in Experiment 6 but no duration compression in spatiotopic conditions in Experiments 4 and 5, where we used practiced observers, had the same time course, including adapting to a blank field as in the adaptation conditions, and randomized the order in which the standard and comparison was presented.

The specificity of the adaptation effects we have described to a retinocentric frame of reference is potentially a problem for a centralized clock model (Creelman, 1962; Treisman, 1963; Treisman et al., 1990) whose supramodal nature implies high level mechanisms. Our results rather suggest that the duration of a sensory stimulus is encoded in part by low-level sensory mechanisms that are modality specific and can be adapted. To explain how low-level adaptation can induce a change in duration perception we need to introduce the idea of a content-dependent clock (Johnston, 2010).

It has been hypothesized that temporal adaptation induced time compression might be linked to changes in the temporal impulse response functions of M cells (Johnston et al., 2006). There is some evidence that high temporal frequency adaptation shifts in the temporal frequency tuning curve of the directionally selective cells of the nucleus of the optic tract (NOT) in the wallaby rightward, increasing relative sensitivity to high temporal frequencies and sharpening the temporal impulse response (Clifford, Ibbotson, & Langley, 1997; Ibbotson, 2005; Ibbotson, Clifford, & Mark, 1998). A shortening of the temporal impulse response seems to occur during saccades (Burr & Morrone, 1996), a situation in which time has been reported to be distorted (Morrone et al., 2005). This sharpening is also seen at high contrast (Stromeyer & Martini, 2003) and in M cells as a consequence of contrast gain control (Benardete & Kaplan, 1999; Kaplan & Benardete, 2001). We have recently shown that the apparent duration of a 50% contrast interval is reduced when it is preceded by a 90% contrast inducer only for temporal frequencies higher than 10 Hz (Bruno & Johnston, 2007, 2009) which is consistent with this.

To try to explain how changes in the temporal tuning of neurons may be related to duration distortions, we have recently proposed (Johnston, 2010) a content-dependent

clock model that determines the duration of an interval using a “predict and compare” strategy. We need to be able to predict what the visual world will look like in, for example, 100 ms. Then we can continuously compare the forward prediction to the sensory input. When the prediction matches the visual input, the system registers that 100 ms has passed, the clock ticks, and the prediction is reset. In this clock model, timing is intimately related to perceptual processing and sensory calibration. To predict forward in time, we require a temporal derivative in order to construct a Taylor series expansion of the time series of image brightness at a point. A temporal derivative operator has a biphasic impulse response, as do transient magnocellular neurones, whereas parvocellular neurones are temporally low-pass. Magnocellular neurones are more prone to adaptation than parvocellular neurones and adaptation has two effects—a reduction in sensitivity and a shift in temporal tuning which causes a phase advance in their response (Benardete & Kaplan, 1999; Kaplan & Benardete, 2001).

We showed in this study that, consistent with previous reports (Ayhan et al., 2009; Johnston et al., 2006, 2008), effects of adaptation on temporal frequency are separable from effects on duration. Temporal frequency can be encoded from the relative activity of band-pass and low-pass temporal filters (Smith & Edgar, 1994). We attribute changes in apparent temporal frequency to changes in relative sensitivity. The phase advance (after high temporal frequency adaptation) shifts the prediction forward in time. The consequence is that the match between the prediction (carried by the magnocellular system) and the current input (carried by the parvocellular systems) is delayed, the content dependent clock ticks later, and apparent duration is reduced. The comparison may not be possible until early stages of cortical processing when magnocellular and parvocellular signals combine (Sincich & Horton, 2005).

In conclusion we provide further evidence of robust retinotopic adaptation-based duration compression in situations which avoid any change in apparent temporal frequency and in two paradigms which can separate out retinotopic and spatiotopic components of adaptation. We saw no strong evidence of spatiotopic adaptation. We suggest any trend in this direction may reflect a mixture of order effects and range effects following a tendency for participants to reconfigure the two interval forced choice magnitude discrimination task to use a method of single stimuli strategy in standard first trials.

Acknowledgments

We would like to thank David Burr and Maria Concetta Morrone for discussions of these studies and the use of their software. We would also like to thank Julia Krupic

for her help in the data collection. This work was supported by The Leverhulme Trust and The Wellcome Trust.

Commercial relationships: none.

Corresponding author: Aurelio Bruno.

Email: a.bruno@ucl.ac.uk.

Address: Cognitive, Perceptual and Brain Sciences, Division of Psychology and Language Sciences, University College London, Gower Street, London WC1 6BT, UK.

References

- Afraz, A., & Cavanagh, P. (2009). The gender-specific face aftereffect is based in retinotopic not spatiotopic coordinates across several natural image transformations. *Journal of Vision*, 9(10):10, 11–17, <http://www.journalofvision.org/content/9/10/10>, doi:10.1167/9.10.10. [PubMed] [Article]
- Ayhan, I., Bruno, A., Nishida, S. y., & 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, 355–368.
- Brown, S. W. (1995). Time, change, and motion: The effects of stimulus movement on temporal perception. *Perception & Psychophysics*, 57, 105–116.
- Bruno, A., & Johnston, A. (2007). Contrast gain changes affect the perceived duration of visual stimuli [Abstract]. *Journal of Vision*, 7(9):376, 376a, <http://www.journalofvision.org/content/7/9/376>, doi:10.1167/7.9.376.
- Bruno, A., & Johnston, A. (2009). Contrast gain not contrast change induces apparent temporal compression [Abstract]. *Journal of Vision*, 9(8):1085, 1085a, <http://www.journalofvision.org/content/9/8/1085>, doi:10.1167/9.8.1085.
- Buonomano, D. V., & Karmarkar, U. R. (2002). How do we tell time? *Neuroscientist*, 8, 42–51.
- Burr, D., Tozzi, A., & Morrone, M. C. (2007). Neural mechanisms for timing visual events are spatially selective in real-world coordinates. *Nature Neuroscience*, 10, 423–425.
- 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.
- Clifford, C. W., Ibbotson, M. R., & Langley, K. (1997). An adaptive Reichardt detector model of motion adaptation in insects and mammals. *Visual Neuroscience*, 14, 741–749.
- Creelman, C. D. (1962). Human discrimination of auditory duration. *Journal of the Acoustical Society of America*, 34, 582–593.
- Dow, B. M., Snyder, R. G., Vautin, R. G., & Bauer, R. (1981). Magnification factor and receptive field size in foveal striate cortex of the monkey. *Experimental Brain Research*, 44, 213–228.
- Fechner, G. T. (1860). *Elemente der Psychophysik*. Leipzig: Breitkopf & Hartel.
- Ibbotson, M. R. (2005). Contrast and temporal frequency-related adaptation in the pretectal nucleus of the optic tract. *Journal of Neurophysiology*, 94, 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, 1481–1493.
- Jamieson, D. G., & Petrusic, W. M. (1975). Presentation order effects in duration discrimination. *Perception & Psychophysics*, 17, 197–202.
- Johnston, A. (1989). The geometry of the topographic map in striate cortex. *Vision Research*, 29, 1493–1500.
- Johnston, A. (2010). Modulation of time perception by visual adaptation. In A. C. Nobre & J. T. Coull (Eds.), *Attention and time* (chap. 14, pp. 187–200). Oxford: OUP.
- Johnston, A., Arnold, D. H., & Nishida, S. (2006). Spatially localized distortions of event time. *Current Biology*, 16, 472–479.
- Johnston, A., Bruno, A., Watanabe, J., Quansah, B., Patel, N., Dakin, S., et al. (2008). Visually-based temporal distortion in dyslexia. *Vision Research*, 48, 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 [Abstract]. *Journal of Vision*, 9(7):14, 14a, <http://www.journalofvision.org/content/9/7/14>, doi:10.1167/9.7.14.
- Kaplan, E., & Benardete, E. (2001). The dynamics of primate retinal ganglion cells. *Progress in Brain Research*, 134, 17–34.
- Knapen, T., Rolfs, M., & Cavanagh, P. (2009). The reference frame of the motion aftereffect is retinotopic. *Journal of Vision*, 9(5):16, 11–17, <http://www.journalofvision.org/content/9/5/16>, doi:10.1167/9.5.16. [PubMed] [Article]
- Knapen, T., Rolfs, M., Wexler, M., & Cavanagh, P. (2010). The reference frame of the tilt aftereffect. *Journal of Vision*, 10(1):8, 1–13, <http://www.journalofvision.org/content/10/1/8>, doi:10.1167/10.1.8. [PubMed] [Article]
- Lapid, E., Ulrich, R., & Rammsayer, T. (2008). On estimating the difference limen in duration discrimination tasks: A comparison of the 2AFC and the reminder task. *Perception & Psychophysics*, 70, 291–305.
- Mauk, M. D., & Buonomano, D. V. (2004). The neural basis of temporal processing. *Annual Review Neuroscience*, 27, 307–340.
- Melcher, D. (2005). Spatiotopic transfer of visual-form adaptation across saccadic eye movements. *Current Biology*, 15, 1745–1748.
- Morris, A. P., Liu, C. C., Cropper, S. J., Forte, J. D., Krekelberg, B., & Mattingley, J. B. (2010). Summation of visual motion across eye movements reflects a nonspatial decision mechanism. *Journal of Neuroscience*, 30, 9821–9830.
- Morrone, M. C., Ross, J., & Burr, D. (2005). Saccadic eye movements cause compression of time as well as space. *Nature Neuroscience*, 8, 950–954.
- Nachmias, J. (2006). The role of virtual standards in visual discrimination. *Vision Research*, 46, 2456–2464.
- Nishida, S., Motoyoshi, I., Andersen, R. A., & Shimojo, S. (2003). Gaze modulation of visual aftereffects. *Vision Research*, 43, 639–649.
- Ono, F., & Kawahara, J. (2007). The subjective size of visual stimuli affects the perceived duration of their presentation. *Perception & Psychophysics*, 69, 952–957.
- Sincich, L. C., & Horton, J. C. (2005). The circuitry of V1 and V2: Integration of color, form, and motion. *Annual Review of Neuroscience*, 28, 303–326.
- Smith, A. T., & Edgar, G. K. (1994). Antagonistic comparison of temporal frequency filter outputs as a basis for speed perception. *Vision Research*, 34, 253–265.
- Spigel, I. M. (1962). Contour absence as a critical factor in the inhibition of the decay of a movement aftereffect. *Journal of Psychology*, 54, 221–228.
- Stein, J., & Walsh, V. (1997). To see but not to read; the magnocellular theory of dyslexia. *Trends in Neurosciences*, 20, 147–152.
- Stromeyer, C. F., 3rd, & Martini, P. (2003). Human temporal impulse response speeds up with increased stimulus contrast. *Vision Research*, 43, 285–298.
- Terao, M., Watanabe, J., Yagi, A., & Nishida, S. (2008). Reduction of stimulus visibility compresses apparent time intervals. *Nature Neuroscience*, 11, 541–542.

- Treisman, M. (1963). Temporal discrimination and the indifference interval. Implications for a model of the “internal clock”. *Psychology Monographs*, 77, 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, 705–743.
- Vicario, C. M., Pecoraro, P., Turriziani, P., Koch, G., Caltagirone, C., & Oliveri, M. (2008). Relativistic compression and expansion of experiential time in the left and right space. *PLoS ONE*, 3, e1716.
- Watson, A. B., & Pelli, D. G. (1983). QUEST: A bayesian adaptive psychometric method. *Perception & Psychophysics*, 33, 113–120.
- Wenderoth, P., & Wiese, M. (2008). Retinotopic encoding of the direction aftereffect. *Vision Research*, 48, 1949–1954.
- Woodrow, H. (1951). Time perception. In S. S. Stevens & H. S. Langfeld (Eds.), *Handbook of experimental psychology*. New York: Wiley.
- Woodworth, R. S., & Schlosberg, H. (1954). *Experimental psychology* (rev. ed.). New York: Holt.
- Xuan, B., Zhang, D., He, S., & Chen, X. (2007). Larger stimuli are judged to last longer. *Journal of Vision*, 7(10):2, 1–5, <http://www.journalofvision.org/content/7/10/2>, doi:10.1167/7.10.2. [PubMed] [Article]