Effect of the luminance signal on adaptation-based time compression

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Traditionally, time perception has been considered the product of a central, generic, cognitive mechanism. Recent evidence, however, has shown that high temporal frequency adaptation induces local reductions in the apparent duration of brief intervals suggesting a distributive system with modality-specific sensory components. Here, we examine the effect of the luminance signal on these adaptation-based temporal distortions. Our results show that the luminance signal is crucial to generate duration compression as the effect disappears at isoluminance and that low visibility and task difficulty at isoluminance cannot explain the discrepancy. We also demonstrate that the effects of adaptation on perceived duration are dissociable from those on apparent temporal frequency. These results provide further evidence for the involvement of the magnocellular system in the neural encoding and representation of visual time.

Keywords: luminance channel, duration perception, magnocellular pathway, temporal, frequency

Introduction

Humans process temporal information over a large scale ranging from microseconds to daily circadian rhythms, perhaps reflecting multiple underlying neural mechanisms (Buonomano, 2007; Buonomano & Karmarkar, 2002; Mauk & Buonomano, 2004). Processing in the sub-second range is often referred as *perceptual timing* and is essential for a range of specialized perceptual and motor activities including sound localization, speech generation and recognition, motor coordination, and motion detection. In this range, duration, encoded explicitly, can also be considered to be part of the perceptual description of an event rather than a cognitive estimate of elapsed time. The underlying mechanisms of time perception in the sub-second range, however, remain obscure. The dominant models of event time have been devised around the idea of an internal clock (Creelman, 1962; Treisman, 1963; Treisman, Faulkner, Naish, & Brogan, 1990), which assumes a single centralized neural circuit serving all sensory modalities. Perceptual studies, however, have challenged the notion of a central clock showing that the apparent duration of a short interval depends on stimulus properties (Kanai, Paffen, Hogendoorn, & Verstraten, 2006; Kaneko & Murakami, 2009) and can be affected by adaptation to visual flicker or drifting motion (Ayhan, Bruno, Nishida, & Johnston, 2009; Burr, Tozzi, & Morrone, 2007; Johnston, Arnold, & Nishida, 2006; Johnston et al., 2008). The adaptation studies suggest that peripheral neural systems can be adapted by extended observation of particular stimulus features that play a role in the encoding of the duration of external events. Thus, in this perspective, time is treated as an attribute of a visual stimulus like any other low-level feature such as spatial frequency or contrast (Johnston et al., 2006; Johnston & Nishida, 2001).

In the original paradigm, Johnston et al. (2006) presented subjects with a 20-Hz dynamic adaptor in a limited region of visual space and then they sequentially displayed two 10-Hz tests, one in the adapted region and the other in an unadapted region. Subjects had to decide which interval was longer. They observed strong duration compression for the stimulus presented in the adapted position. They also demonstrated that the compression of the apparent duration of 10-Hz dynamic grating is specific to high temporal frequency adaptation and that the magnitude of

the effect is independent of the relative orientation of the adaptor and test, suggesting an early locus. Recently, the effect has been shown to have tight spatial tuning (Ayhan et al., 2009) and occur for purely retinotopic stimulation (Bruno, Ayhan, & Johnston, 2010), implying a site in the visual pathway where the receptive fields of the neurons remain relatively small and map the visual input in retinotopic coordinates. It is known that the apparent duration of a dynamic stimulus depends to some extent upon its temporal frequency for low to mid-temporal frequencies (Kanai et al., 2006). Using a procedure designed to eliminate the influence of temporal frequency adaptation on speed judgments, Ayhan et al. (2009) have demonstrated that adaptation-induced duration distortion cannot be attributed to changes in apparent speed, suggesting that changes in apparent duration after temporal frequency adaptation can be dissociated from changes in apparent temporal frequency. Temporal frequency shifts are bidirectional in that high temporal frequency adaptation reduces, whereas low temporal frequency adaptation increases the perceived temporal frequency of a 10-Hz test. However, for typical observers, a mid-temporal frequency (10 Hz) test always appears compressed in duration after low (5 Hz), mid- (10 Hz), and high (20 Hz) temporal frequency adaptation (Ayhan et al., 2009; Johnston et al., 2006). Thus, separate neural mechanisms are needed to explain these two effects. We suggest that temporal frequency shifts result from changes in the relative responses of the temporal channels following adaptation. For sine functions, temporal frequency can be recovered from the relative activity of band-pass and low-pass filters (Smith & Edgar, 1994). A stimulus drifting or flickering at 10 Hz stimulates both the low-pass and mid-range band-pass filter approximately equally. The shift in its apparent temporal frequency following high temporal frequency adaptation can be explained by a relative increase in the response of the low-pass channel as a result of reduction in sensitivity of the band-pass channel, the pattern representing a lower frequency than 10 Hz. The opposite shift arises after adaptation to a low (e.g., 5 Hz) frequency. This kind of change in activity among a pair or population of feature-dependent channels has been used successfully to explain other feature-based aftereffects, such as the tilt aftereffect (Colheart, 1971) and the spatial frequency aftereffect (Wilson & Humanski, 1993). In our duration adaptation paradigm, however, subjects adapt to temporal frequency rather than duration; thus, adaptation-induced duration compression cannot be simply explained by a duration channel population model. We previously linked duration compression (Ayhan et al., 2009; Johnston et al., 2006) to the changes in the temporal tuning of band-pass temporal filters following high temporal frequency adaptation (Ibbotson, Clifford, & Mark, 1998). It has been also demonstrated that the phase of signals carried by M cells are advanced through fast adaptation to high contrast (Benardete & Kaplan, 1999b). The observation that

intermediate high temporal contrast intervals are perceived as compressed following a 1.5-s dynamic high-contrast interval but not a low-contrast interval (Bruno & Johnston, 2010) provides further evidence for the link between contrast gain control in M cells and duration effects. In addition, cortically invisible flicker (~60 Hz) produces duration compression in normal subjects but not in dyslexics (Johnston et al., 2008) for whom a number of studies (for a review, see Stein, 2001) indicated impairment in the transient (magnocellular) mechanism. That the adaptation effects on temporal tuning of filters are unidirectional, i.e., high temporal frequency adaptation causes a phase advance in the signal but low temporal frequency adaptation does not lead to a phase delay, is consistent with the observation that both low and high temporal frequency adaptation induce duration compression.

Earlier studies (Ayhan et al., 2009; Burr et al., 2007; Johnston et al., 2006, 2008) all used achromatic luminance-modulated stimuli, so the effect of a mainly chromatic signal on the magnitude of the adaptation-induced duration compression remains unknown. Existing evidence suggests that chromatic and achromatic signals are carried in separate divisions from the retina to the primary visual cortex in the early stages of the visual system (Derrington, Krauskopf, & Lennie, 1984; De Valois, Abramov, & Jacobs, 1966; De Valois, Cottaris, Elfar, Mahon, & Wilson, 2000; Hubel & Wiesel, 1966). The chromatic signals are thought to be carried by two channels, which selectively signal the difference of L- and M-cone responses (red–green) and the difference between short-wave (S)-cone responses and a sum of L- and M-cone responses (blue–yellow). Though the L–M opponent channel has also been suggested to contribute to luminance detection and discrimination at high temporal frequencies (Gouras & Zrenner, 1979) and at high luminance contrasts (Benardete & Kaplan, 1999a), the achromatic signals are transmitted mainly through a luminance mechanism, which responds to a neural sum of L- and M-cone signals originating in the long-wave (L)- and middle-wave (M)-cones. The lateral geniculate body, where this anatomical and functional split clearly manifests itself, consists of six coaxially arranged layers. The cells in the dorsal, or upper, parvocellular layers receiving opponent signals from L- and M-cones (i.e., L–M) play an important role in color vision and in the perception of high spatial frequency patterns. The cells in the ventral, or bottom, magnocellular layers receiving additive signals (i.e., L + M) are clearly involved in the perception of motion (Livingstone & Hubel, 1987). There is also a third system, the koniocellular pathway, which has been proposed to mediate modulation along the S–(L + M) axis (Irvin, Casagrande, & Norton, 1993; Martin, White, Goodchild, Wilder, & Sefton, 1997). However, we will not consider this pathway further in this study.

Here, we test the magnocellular hypothesis of time compression by examining the effect of the luminance

signal on adaptation-based duration compression. As the apparent duration of a dynamic stimulus has been shown to be affected by its speed (Brown, 1995; Kaneko & Murakami, 2009) or temporal frequency (Kanai et al., 2006), we first minimized the effect of temporal frequency adaptation on apparent temporal frequency using a paradigm we have recently developed (Ayhan et al., 2009). We then measured adaptation-based temporal distortions for stimuli defined by chromatic (L–M) and luminance contrast (L + M). We found that the luminance signal is essential to duration compression. Apparent duration after adaptation was not significantly different from baseline at isoluminance. We also showed that duration compression is much stronger with luminance-modulated stimuli even after the perceptual strength (visibility) of isoluminance and luminance modulation conditions are matched, indicating that visibility cannot explain the discrepancy between the strength of duration compression in the two conditions. These results suggest that the effects of adaptation on perceived duration are mediated by a transient luminance channel.

General methods

Observers

The experiments were performed on 10 adults (5 males and 5 females), 7 of which were naïve to the purpose of the study. All subjects had normal or corrected-to-normal vision with no color vision deficit.

Apparatus

Observers were seated 57 cm from a 19-inch Sony Trinitron Multiscan 500PS monitor that was driven by a VSG 2/5 graphics board (Cambridge Research Systems) at a refresh rate of 100 Hz. At this distance, the monitor subtended 40×30 degrees. The head of the subject was fixed to prevent head movements using a chin rest.

A Gamma Scientific spectroradiometer was used to measure the spectra of the red, green, and blue phosphors at their maximum intensity. The primaries of the monitor had *x, y, Y* coordinates of 0.61, 0.34, 36.09 (red); 0.28, 0.61, 126.5 (green); and 0.15, 0.07, 20.95 (blue). The white point for space calculations was set at CIE chromaticity coordinates (0.28 and 0.31) with a luminance of 91.6 cd/m^2.

Procedure

Prior to all experiments, the point of subjective isoluminance was measured individually for each subject using a minimum motion technique with the same configuration and temporal frequency of the stimuli used in the temporal frequency and duration tasks (Cavanagh, MacLeod, & Anstis, 1987). On a gray background with mean luminance, a chromatic (magenta–cyan) sinewave grating (0.5 c/deg) was alternated with a luminance-modulated achromatic grating (0.5 c/deg) in a repetitive sequence, each stimulus displaced by one-quarter cycle from its predecessor to give the impression of apparent motion dependent on the relative luminance of magenta and cyan phases of the chromatic grating. Subjects were asked to adjust the luminance of magenta and cyan phases, respectively, in blocked trials, using a staircase procedure, until their perception of motion was replaced by flicker, which indicates the point of subjective isoluminance. The means of the two values obtained in two blocked trials were then used in the subsequent experiments as individual isoluminance settings.

In the temporal frequency and duration experiments, subjects were initially presented with a central fixation spot and an adaptor. The duration of the adaptation phase was 32 s with 8-s top-ups between trials. The adaptor grating reversed the direction of motion every 1 s to avoid the buildup of a directional motion aftereffect. After 500 ms, the adaptor disappeared from the screen, and two drifting test gratings were presented sequentially on the adapted (standard) and unadapted (comparison) sides of the fixation point. The contrast of the adaptor and tests was constant over time; thus, stimuli had an abrupt onset and offset. Whereas the duration or temporal frequency of the standard stimulus was fixed across trials, the values of the comparison stimulus varied in seven steps. Details of the stimuli in each experiment can be found in the methods of the relevant section. The order of presentation of the standard and comparison was randomized from trial to trial to control for time order effects (Jamieson & Petrusic, 1975). The adaptor location was also interleaved in blocked trials to control for spatial anisotropies in duration judgments (Vicario et al., 2008). The task of the subject was to determine which of the test stimuli drifted faster (in perceived temporal frequency experiments) or for longer (in perceived duration experiments). Responses were used to generate a psychometric function indicating the percent of trials in which the comparison was judged as faster or longer than the standard for each subject. The 50% point on the psychometric function provided an estimate of the effect of adaptation on the perceived duration of the standard.

Color space

The sinewave gratings were symmetric modulations around a central white point with CIE *xyY* coordinates (0.28, 0.31, 91.6). The isoluminant gratings were modulated around the white point between magenta (CIE *xyY*: 0.319, 0.303, 91.6) and cyan (CIE *xyY*: 0.245, 0.336, 91.6)

so as to isolate the L–M color-opponent mechanism (Derrington et al., 1984). Subjective isoluminance settings were made by combining the chromatic gratings with low-contrast background color (gray) achromatic gratings, thus introducing slight modulations of the violet–yellow opponent mechanism. The mean of the individual violet–yellow modulations, however, was only around 2% RMS cone contrast for the adaptor and 3% RMS cone contrast for the test (see Equation 7 for the definition of RMS cone contrast). For both isoluminant and luminance-modulated stimuli, L- and M-cone excitations generated by the magenta and cyan phases of the gratings were found by integrating the product of stimulus spectral output (readings taken in 1-nm intervals from 390 nm to 780 nm) with the L- and M-cone fundamentals for 2° stimuli (Stockman & Sharpe, 2000). Having found the L- and M-cone excitations, L- and M-cone contrasts on the steady gray background were calculated using the following formulas:

$$L_{CCmagenta} = (L_{CEmagenta} - L_{CEgray})/L_{CEgray}, \qquad (1)$$

$$M_{CCmagenta} = (M_{CEmagenta} - M_{CEgray})/M_{CEgray}, \qquad (2)$$

$$L_{CCcyan} = (L_{CEcyan} - L_{CEgray})/L_{CEgray}, \qquad (3)$$

$$M_{CCcyan} = (M_{CEcyan} - M_{CEgray})/M_{CEgray}, \qquad (4)$$

where $L_{CEmagenta}$, $M_{CEmagenta}$, L_{CEcyan}, and M_{CEcyan} refer to the cone excitations produced by the magenta and cyan phases of the gratings and L_{CEgray} refer to the cone excitation produced by the gray background. Each contrast component indicates the effective stimulus contrast in that particular class of cones.

To compare the effectiveness of luminance-modulated and isoluminant stimuli, we also computed the root-mean-square cone contrasts (RMS_{CC}) individually for each condition separately:

$$L_{CC} = (L_{CEcyan} - L_{CEmagenta})/(L_{CEcyan} + L_{CEmagenta}), \quad (5)$$

$$M_{CC} = (M_{CEcyan} - M_{CEmagenta})/(M_{CEcyan} + M_{CEmagenta}), \qquad (6)$$

$$RMS_{CC} = sqrt[(M_{CC}^2 + L_{CC}^2)/2]. \qquad (7)$$

For chromatic luminance-modulated stimuli, the root-mean-square contrast corresponds to the sum of the Michelson contrast [(Lum$_{max}$ − Lum$_{min\ n}$)] / [(Lum$_{max}$ + Lum$_{min}$)] and the RMS cone contrast of the chromatic component. For isoluminant stimuli, the resulting RMS cone contrast falls between L- and M-cone contrasts.

Experiment 1: Temporal frequency shift for equiluminance and luminance modulation

The apparent duration of a moving stimulus reduces with temporal frequency at low temporal frequencies (Kanai et al., 2006). We have previously shown that reductions in perceived durations following 20-Hz adaptation persist even after matching for perceived temporal frequency (Johnston et al., 2006), indicating that the effects of adaptation on temporal frequency and duration can be dissociated. More recently, we also introduced a new procedure to eliminate any possible influence of temporal frequency adaptation on speed judgments (Ayhan et al., 2009). Here, we use the same method to explore temporal frequency shifts following adaptation in isoluminant and luminance modulation conditions. We interleave 5- and 10-Hz oscillatory adaptors over time to find, for each subject, a ratio of durations of these two adaptor frequencies at which the perceived speed of a 7-Hz drifting test pattern does not change. We then use these critical ratios in our duration experiments to ensure that any aftereffect we observe cannot be attributed to changes in apparent temporal frequency or speed.

Methods

In Experiment 1, observers were presented with a central fixation spot and an adapting stimulus (which in half of the trials was located 5° above and in half of the trials 5° below the center of the screen within an 8° diameter circular patch), consisting of a drifting sinusoidal grating (0.5 c/deg) that alternated direction every 1 s. In the adaptation phase, the grating oscillated with a temporal frequency of 5 and 10 Hz interleaved using one of 3 different ratios: 0% (5 Hz)–100% (10 Hz); 50% (5 Hz)–50% (10 Hz); 100% (5 Hz)–0% (10 Hz). The duty cycle typically determined the proportion of time for which the two adapting temporal frequencies were displayed. The duration of the adaptation phase was 32 s. At the beginning of each subsequent trial, subjects were also adapted for a short period (8-s top-up), in order to maintain a high, constant level of adaptation. Each cycle typically lasted 4 s during the initial adaptation and 2 s during the top-ups, with the critical duration ratio of the two interleaved adaptor frequencies kept the same. After the adaptation phase, the test stimuli (sinusoidal grating with a spatial frequency of 0.5 c/deg drifting for 600 ms) were displayed

sequentially on the adapted and unadapted sides of the fixation point. The order of display was randomized for each trial. The temporal frequency of the standard stimulus, which was displayed in the same spatial position as the adaptor, was fixed across trials (7 Hz). The temporal frequency of the comparison stimulus, which was displayed in an unadapted spatial position (centered 5° above or below the central fixation point), was varied between 1 and 13 Hz in 7 steps. The RMS cone contrasts of the chromatic stimuli were set to 5% for the adaptor and 7% for the test in the isoluminant condition. The luminance-modulated chromatic stimuli were generated by combining physically isoluminant magenta–cyan gratings with achromatic luminance gratings modulated equally around the background color between black and white. The bright and dark phases of the achromatic luminance grating were overlapped with the cyan and magenta phases of the isoluminant grating, respectively, to yield chromatic luminance-modulated gratings with lighter cyan and darker magenta phases. The RMS cone contrasts of the chromatic component of the luminance-modulated adaptor and test stimuli were 2% and 2%, with an additional Michelson luminance contrast of 40% and 52%, respectively. The sum of chromatic and luminance contrasts yielded the values of 42% for the adaptor and 54% for the test. To minimize the effects of axial chromatic aberration, we used low spatial frequency gratings (0.5 c/deg) for which the luminance artifact has been shown to be smaller

than 0.5% contrast (Cavanagh & Anstis, 1986). Observers reported which of the tests appeared to drift faster.

Results

Figure 1A shows how the duty cycle of the two interleaved adaptors (5 and 10 Hz) affected the perceived temporal frequency of a subsequently displayed drifting stimulus for each subject. The dashed line indicates the temporal frequency of the standard grating. Data points show the 50% point on the psychometric function (point of subjective equality, PSE) plotted as a function of the proportion of the relative time of the 5- and 10-Hz adaptors. The straight lines are the linear fits to these data points for each subject. One-sample t-test showed that for the luminance modulation condition, perceived speed was reduced when the temporal frequency of the adaptor was greater than that of the test, $t(5) = -4.99$, $p < 0.01$, indicating a significant difference between the estimated temporal frequencies and the physical temporal frequency (7 Hz). Low temporal frequency adaptation, however, induced an increase in the perceived temporal frequency of test, $t(5) = 2.74$, $p = 0.041$. The pattern of these adaptation effects is consistent with our previous findings (Ayhan et al., 2009). For the isoluminance condition, similar to the luminance modulation condition, high temporal frequency adaptation induced a significant
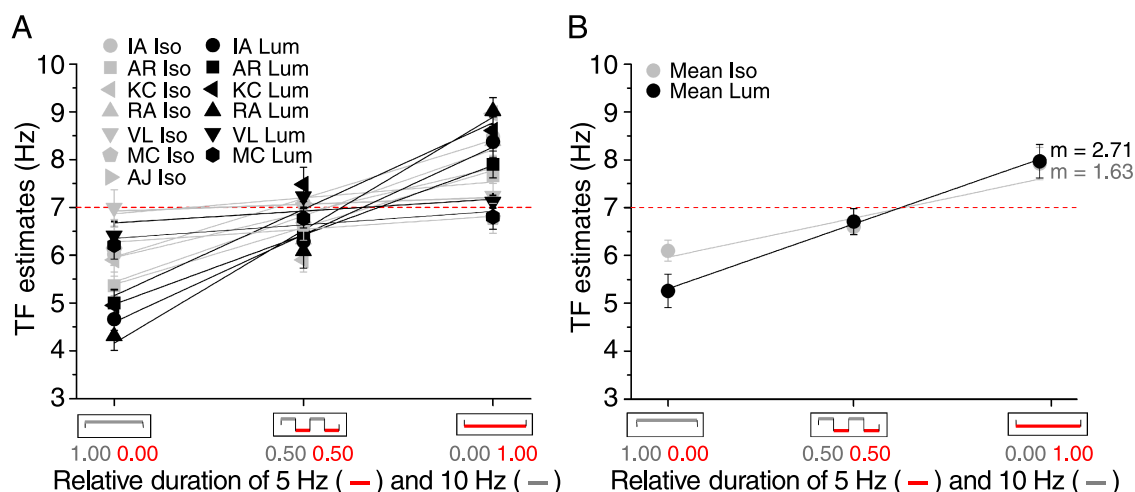

Figure 1. Eliminating the influence of temporal frequency adaptation on speed judgments for isoluminant stimuli (with 5% contrast for adaptor and 7% contrast for test) falling close to the L–M axis of the cone contrast space and for luminance-modulated stimuli (with 2% chromatic and 40% Michelson contrast for adaptor and 2% chromatic and 52% Michelson contrast for test) with 65 cd/m² (adaptor) and 85 cd/m² (test) luminance differences between the cyan and magenta phases. (A) Results of the temporal frequency experiment for 7 different subjects (three authors and four naïve subjects). The dashed line indicates the temporal frequency of the standard grating. Data points show the PSEs plotted as a function of the relative duration of the 5- and 10-Hz adaptors. The straight lines are the linear fit of these data points for each subject. Error bars show ±1 *SE*. Each point is derived from 140 trials. (B) Mean results of the temporal frequency experiment for isoluminance (Iso) and luminance modulation (Lum) conditions for 5 different subjects (two authors and four naïve subjects). The dashed line indicates the temporal frequency of the standard grating. Data points show the mean PSEs plotted as a function of the relative duration of the 5- and 10-Hz adaptors. The straight lines are the linear fit of these data points. The slope (*m*) is reported for each condition separately. Error bars show ±1 *SE* of the mean.

reduction in the perceived speed of the test, $t(5) = -4.16$, $p < 0.01$, and low temporal frequency induced a significant increase in the perceived speed, $t(5) = 2.70$, $p = 0.043$. A paired-samples t-test, however, showed that the reduction of perceived speed following high temporal frequency adaptation in the isoluminance condition was significantly smaller than that in the luminance modulation condition, $t(5) = -2.816$, $p = 0.037$, but a similar increase was observed following low temporal frequency adaptation, $t(5) = 0.378$, $p > 0.1$. As can be seen in Figure 1B, the slope in the isoluminance condition is shallower than in the luminance modulation condition, $t(5) = 2.237$, $p = 0.038$, confirming the reduction in the temporal frequency shift. One might think that the difference in the adaptation-induced temporal frequency effects in two conditions might be explained by the difference in effective contrasts as the isoluminant gratings had much lower contrast than the luminance-modulated stimuli. However, this is not necessarily the case, as Keck, Palella, and Pantle (1976) found that the duration and initial speed of the motion aftereffect was not greatly affected by increasing the adapting contrast of a 5-Hz adapting grating over 3% contrast. Similarly, Wright and Johnston (1985) found little change in the speed of the MAE for contrasts between 10% and 100% for 7-Hz adaptors, although adaptation declined with contrast at high temporal frequencies as the adapting stimulus became less visible. Therefore, although it is possible that the difference in slope in the temporal frequency (or speed) function reflects differences in effective contrast, it may rather reflect real differences in the adaptability of luminance and chromatic mechanisms.

In sum, we have determined the individual ratios of 5- and 10-Hz adaptation, which had no effect on the perceived temporal frequency of a subsequently presented test stimulus. We can use these ratios to design adapting stimuli for the following duration experiments to ensure that any aftereffect we observe cannot be attributed to changes in apparent temporal frequency. Temporal frequency adaptation induced perceived temporal frequency shifts for both luminance and isoluminance conditions, though the shift following high temporal frequency adaptation in the isoluminance condition was significantly smaller than that in the luminance condition.

Experiment 2: The role of the luminance signal on duration compression

In Experiment 2, we investigated the role of the luminance signal on duration compression using stimuli defined in the cone contrast space. We used the individual critical ratios of 5- and 10-Hz adaptation, which we obtained from the previous experiment in order to control for the changes in perceived temporal frequency on the adapted position. We systematically reduced the luminance contrast over three levels.

Methods

A standard grating (600 ms, 0.5 c/deg) was always displayed at the adapted location (in half of the trials 5° above and in the other half 5° below the fixation point) and a comparison (0.5 c/deg), presented at the unadapted side, had variable duration across trials (300–1200 ms) to generate a psychometric function. The PSE provided a measure of perceived duration. Both test and adaptor were either isoluminant or luminance modulated across different conditions. The RMS cone contrasts of the isoluminant stimuli were 5% for the adaptor and 7% for the test. For the medium luminance modulation condition, the chromatic contrast of the adaptor and test was set to 3% and 4%, with a Michelson contrast of 27% and 36%. For the large luminance modulation condition, the Michelson luminance contrast was doubled to 54% and 72% for the adaptor and test with a decrease in chromatic contrast to 1.5% and 2%. These ratios generated 45 cd/m^2 (adaptor) and 60 cd/m^2 (test) and 90 cd/m^2 (adaptor) and 120 cd/m^2 (test) luminance differences between the two phases (magenta being darker) for the medium and large luminance-modulated stimuli, respectively.

Since it is known that the sensitivity to flicker for chromatic contrast is low at high temporal frequencies (De Lange, 1958; Kelly & Van Norren, 1977; Swanson, Ueno, Smith, & Pokorny, 1987), we used low and mid-temporal frequencies for the adaptor (5 Hz and 10 Hz interleaved) and test (7 Hz) stimuli. We also used a high-contrast bull's-eye fixation target to encourage constant accommodation, which in turn would reduce the luminance artifact caused by chromatic aberration.

Results

The results for Experiment 2 are shown in Figure 2A. There was a mild apparent temporal compression that was not significantly different from zero at isoluminance $t(5) = -1.87$, $p > 0.1$. A paired-samples t-test showed that duration compression is significantly lower at isoluminance as compared to the effect obtained at high luminance modulation, $t(5) = 3.136$, $p = 0.013$. We also plotted the discrimination threshold, defined as the difference between the 50% and 84% point on the psychometric function, obtained in the baseline conditions as a function of the different luminance conditions (Figure 2B). The graph shows that the discrimination thresholds are similar in both isoluminance and luminance modulation conditions, implying that a potential increase in task difficulty
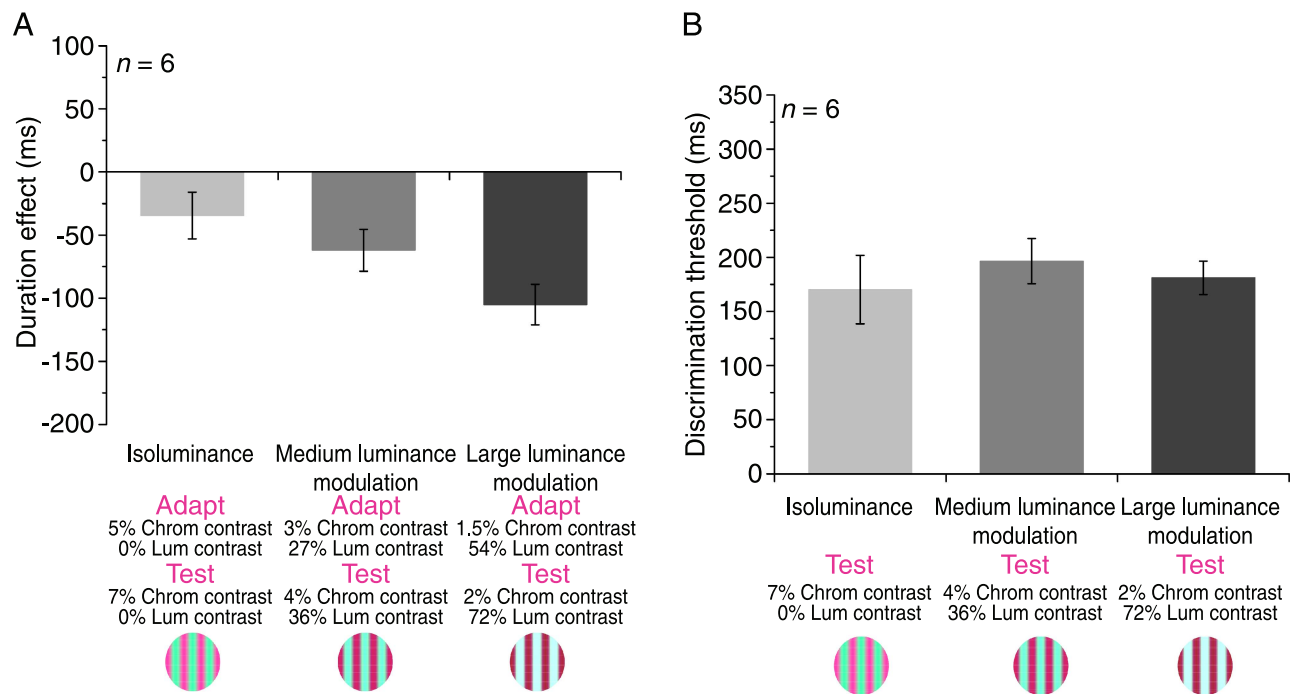
Figure 2. Effects of temporal frequency adaptation on duration judgments as a function of the luminance signal in the absence of temporal frequency shifts. The chromatic and luminance contrasts of the stimuli are shown on the bottom of each condition in the two graphs. (A) Effect of luminance signal on duration compression for 6 subjects (1 author and 5 naïve subjects, included in (B)). The mean duration judgments comparative to baseline conditions are plotted as a function of the luminance signal. Error bars show ±1 *SE* of the mean. Each point is derived from 140 adaptation trials and 280 control trials. (B) Discrimination thresholds are plotted for the baseline trials in the conditions shown in Figure 2A. Error bars show ±1 *SE* of the mean. Each point is derived from 280 trials.

at isoluminance cannot explain the difference in the two conditions. These results indicate that duration compression following adaptation is minimized in the isoluminant condition. That the compression persists even after controlling for the perceived temporal frequency changes on the adapted region suggests that the effects of adaptation on perceived duration are dissociable from those on temporal frequency.

Experiment 3: Visibility

It is known that chromatic stimuli are less visible than luminance stimuli (Cavanagh & Anstis, 1991). This raises the question of whether the decline of the duration effect in the isoluminance condition can be explained by reduced visibility. The fact that there was no difference in the discrimination threshold argues against a significant influence of visibility. Nevertheless, we decided to investigate this issue with an explicit test. We first found the direction discrimination thresholds for isoluminant and luminance-modulated stimuli. We then matched perceptual strength (visibility) for these two conditions in our duration experiment.

Methods

In Experiment 3, we first found the contrast threshold for 75% correct direction discrimination. Subjects judged the motion direction (left or right) of a drifting stimulus (isoluminant or luminance-modulated sinusoidal grating displayed within an 8° patch 5° below the central fixation point) as a function of different contrast levels assigned by the QUEST procedure (Watson & Pelli, 1983). We then used these direction discrimination-based contrast thresholds to match the visibility of luminance-modulated grating to that of the isoluminant condition for each subject separately by the following formula:

$$(\text{Contrast}_{\text{chrom}} \text{ in Exp. 2}/\text{Threshold}_{\text{iso}}) * \text{Threshold}_{\text{lum}}, \tag{8}$$

where $\text{Contrast}_{\text{chrom}}$ in Exp. 2 refers to the chromatic contrast of the isoluminant stimuli in Experiment 2, $\text{Threshold}_{\text{iso}}$ refers to the contrast threshold for the isoluminant stimuli, and $\text{Threshold}_{\text{lum}}$ refers to the contrast threshold for the luminance-modulated stimuli. Finally, we carried out the duration experiment using the obtained contrast values for the luminance-modulated stimuli.
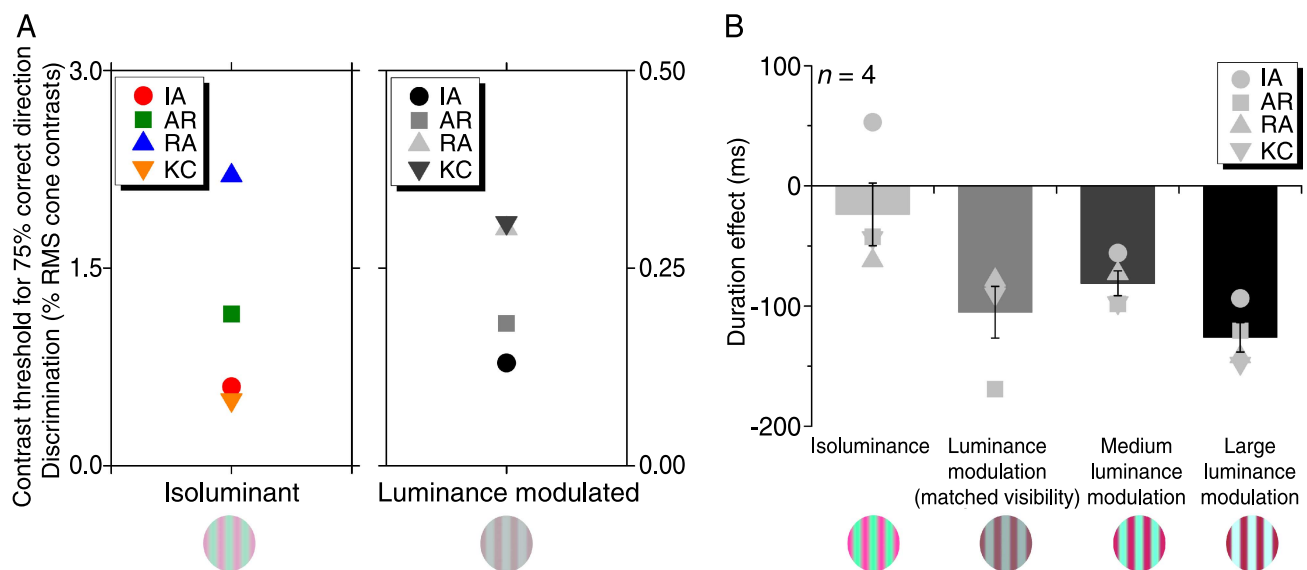
Figure 3. Effect of temporal frequency adaptation on duration judgments as a function of the luminance signal at matched visibility for isoluminant and luminance-modulated stimuli. (A) Direction discrimination contrast thresholds for isoluminant and luminance-modulated stimuli. Note that the contrast value for the luminance modulation condition includes both luminance and chromatic contrasts (see Results section for more details). Each point is derived from 192 trials. (B) Effect of the luminance signal on duration compression at matched visibility. The mean duration judgments compared to baseline conditions are plotted as a function of the luminance signal. The judgments at isoluminance, medium luminance modulation, and large luminance modulation conditions in Experiment 2 are redrawn for the 4 subjects (1 author and 3 naïve subjects, included in Figure 1A). Error bars show ±1 *SE* of the mean. Each point is derived from 140 adaptation trials and 280 control trials.

Results

As can be seen in Figure 3A, the contrast thresholds for 75% correct direction discrimination are much higher for isoluminant stimuli as compared to luminance-modulated stimuli, when compared in terms of our contrast definition. However, what is more important is that the duration compression is quite strong compared to baseline conditions, $t(3) = -4.89$, $p = 0.016$, for the luminance-modulated stimuli even after the perceptual strength is matched to the isoluminance condition (Figure 3B). This is consistent with the observation that adaptation-based compression can occur even for invisible adaptors (Johnston et al., 2008). Thus, the lack of apparent duration effect observed for isoluminant conditions cannot simply be ascribed to low visibility. We found that the mean chromatic and luminance contrasts of the luminance-modulated stimuli were 0.03% and 1.03% for the adaptor and 0.05% and 1.35% for the test at matched 5% (adaptor) and 7% (test) chromatic contrasts. The representations of adaptor and test stimuli (in the isoluminance and luminance condition with matched perceptual strength) in L- and M-cone contrast space for a naïve subject and the individual L- and M-cone contrasts, together with the RMS contrasts in both conditions, are given in Appendix A. That the RMS cone contrasts are higher for isoluminant than luminance-modulated gratings at matched perceptual strength implies that the duration compression observed

with the latter cannot be ascribed to the difference in the effective cone contrast of the two stimuli.

The luminance contrast in the luminance condition with matched visibility generated 1.67 cd/m^2 and 2.19 cd/m^2 luminance differences between the two phases of the gratings at adaptation and test, respectively. In Figure 3B, we also replot the data from the medium and large luminance modulation conditions for the same 4 subjects. As can be seen, the duration compression effect in the 3 luminance modulation conditions does not correlate with the magnitude of luminance contrast, $r = -0.272$, $p = 0.392$. Thus, apparent duration compression occurs for low luminance contrast but not for chromatic contrast.

Experiment 4: Background chromaticity

Flicker studies showed that background chromaticity induces phase lags between L- and M-cone contrast signals (Stromeyer, Chaparro, Tolias, & Kronauer, 1997; Swanson, Pokorny, & Smith, 1988) that can generate a luminance response to an isoluminant chromatic grating in motion. These delays are found only in the luminance system and not in the M- and L-cone opponent system, so they are likely to originate in the retinal magnocellular

cells (Smith, Lee, Pokorny, Martin, & Valberg, 1992). To investigate the effect of the phase shift on the duration compression effect, we used two background colors (orange and green) that were shown to produce the greatest temporal differences between the L- and M-cone contrast signals (Stromeyer et al., 1997). We then compared the duration compression obtained on those chromatic backgrounds to the duration compression obtained on a background with mean chromaticity (gray).

Methods

We carried out the duration experiments on the green and orange background colors with L/M stimulation ratios of 1 and 1.33, respectively. The procedure in this experiment was similar to the procedure we used in Experiment 3 except that there was an initial color adaptation phase in which the subjects were asked to look at the background color (either orange or green) for 3 min before the experiment began. We compared the duration compression following adaptation to baseline conditions in which no adaptor was presented.

Results

The results of Experiment 4 can be seen in Figure 4. We plot the duration effect as a function of the different background colors (orange, green, and gray) with the same mean luminance. We found that when the isoluminant stimuli previously presented on a gray background are displayed on orange and green backgrounds, the
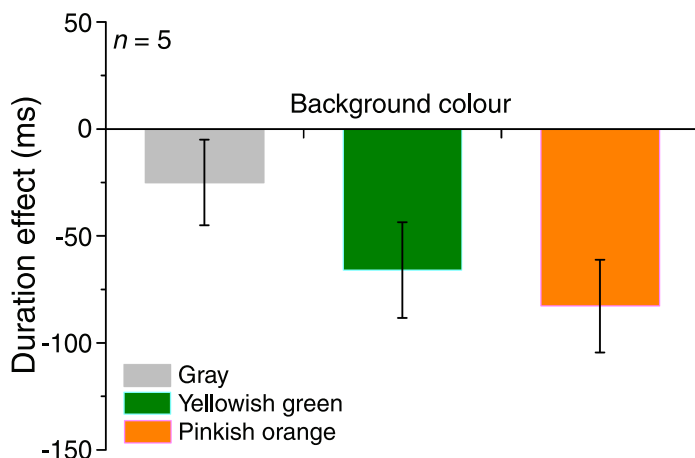

Figure 4. Effect of temporal frequency adaptation on duration judgments at isoluminance as a function of background chromaticity. The mean duration judgments comparative to baseline conditions are plotted for 5 subjects (2 authors and 3 naïve subjects, included in Figure 1A). Error bars show ±1 *SE* of the mean. Each point is derived from 140 adaptation trials and 280 control trials.

duration compression effect is restored and becomes significantly different from the baseline conditions (no adaptation), $t(4) = -3.84$, $p = 0.019$ and $t(4) = -2.95$, $p = 0.042$, respectively. We also observed a nonsignificant trend of stronger duration compression for the orange compared to the green background, $t(4) = 1.50$, $p > 0.1$. This is consistent with a previous report that shows that the phase shifts are bigger on orange adapting backgrounds and weakly reverse on green backgrounds (Swanson et al., 1988).

Discussion

As a test of the magnocellular hypothesis of time compression (Ayhan et al., 2009; Johnston et al., 2006, 2008), we investigated the role of the luminance signal and temporal frequency on adaptation-based temporal distortions. Our results demonstrate that:

1. The apparent duration compression following temporal frequency adaptation is specific to luminance-modulated stimuli and the effect disappears at isoluminance.
2. Visibility and task difficulty cannot explain the discrepancy between the strength of duration compression in the isoluminant and luminance-modulated conditions.
3. At isoluminance, duration compression can be recovered on orange and green backgrounds.
4. The effects of adaptation on perceived duration are dissociable from those on temporal frequency, although the speed aftereffect following high temporal frequency adaptation is also reduced at isoluminance.

It is well accepted that visual information such as color, motion, depth, or spatial pattern are implicit in the spatiotemporal patterns in the retinas. Time, on the other hand, has traditionally been treated as dissociated from other sensory attributes. The specificity of the adaptation-based duration compression to the luminance channel contradicts a supramodal centralized clock model (Creelman, 1962; Treisman, 1963; Treisman et al., 1990), which implies that time is coded by an abstract high-level cognitive mechanism. Rather, we suggest that temporal perception works in a similar way as other sensory attributes and we have low-level adaptable sensory mechanisms that encode the relative time of external events (Johnston & Nishida, 2001). There is strong physiological evidence that while the magnocellular pathway provides the physiological substrate of a luminance channel (De Valois et al., 1966; Kaiser, Lee, Martin, & Valberg, 1990; Kremers, Lee, & Kaiser, 1992; Lee, Martin, & Valberg, 1988), the parvocellular pathway is responsible for the detection of

chromatic modulation, at least at low temporal frequencies (Lee, Martin, & Valberg, 1989b; Lee, Pokorny, Smith, Martin, & Valberg, 1990). That the duration compression is specific to luminance-modulated stimuli suggests that the adaptation affects the magnocellular layers of the LGN.

The idea that the magnocellular pathway might be involved in time perception has been supported by an increasing number of observations. Johnston et al. (2006) have demonstrated that the adaptation-induced time compression is independent of the relative orientation of the adaptor and test. The adaptation-induced duration effect was also shown to exhibit no interocular transfer (Bruno et al., 2010), which together imply an early locus. As well as orientation independence, Johnston et al. (2006) have also shown that the adaptation is limited to high temporal frequencies, which preferentially stimulate cells in the magnocellular layers (Derrington & Lennie, 1984; Lee, Pokorny, Smith, & Kremers, 1994). Consistent with these findings, Johnston et al. (2008) have revealed that the duration compression is still present following adaptation to invisible flicker (~60 Hz), which is thought to stimulate the magnocellular layers of the LGN but not the primary visual cortex. Moreover, cortically invisible flicker produces duration compression in normal subjects but not in dyslexics for whom a magnocellular-related impairment has been proposed (Stein, 2001; Stein & Walsh, 1997). It is known that M cells are liable to a very fast adaptation referred to as *contrast gain control,* in which contrast gain at low temporal frequencies is reduced and which, in turn, delivers a more band-pass temporal frequency response. Bruno and Johnston (2010) have demonstrated that the perceived duration of an interval containing 50% luminance contrast is compressed when it follows a high (90%) contrast, implying a link between the contrast gain properties of M cells and the duration perception of brief intervals. There is also evidence that the duration of an interval is perceived as being compressed before the execution of a saccadic eye movement (Morrone, Ross, & Burr, 2005), during which the magnocellular pathway has been shown to be selectively suppressed (Burr, Morrone, & Ross, 1994). More recently, a similar duration compression effect was observed for intervals embedded within a sequence of high-frequency random dynamic luminance flicker, which was also considered to suppress the activity in the magnocellular pathway (Terao, Watanabe, Yagi, & Nishida, 2008).

We observed a recovery of the duration compression at isoluminance on chromatic backgrounds. Flicker studies in humans show that adapting to chromatic backgrounds can robustly influence the luminance mechanism. Swanson et al. (1988) revealed that orange (~500 nm) backgrounds induce a large phase lag of the L-cone contrast signal relative to the M-cone contrast signal and that the phase shift reverses on green (~600 nm) backgrounds. Stromeyer et al. (1997) also showed that orange and green backgrounds lead to relative phase shifts between the L- and M-cone contrast signals. Using single-cell recording,

Smith et al. (1992) demonstrated that the phase shifts arise at a post-receptor level, in the phasic retinal ganglion cells that provide input to the magnocellular pathway. On orange backgrounds, the phase at which M cells give minimal response to dynamic chromatic stimuli shifted to the *red-leads-green* quadrant. The authors explained the effect by a first harmonic response, which was pronounced at low temporal frequencies, including the range (5–10 Hz) we used in our chromatic background experiments (Experiment 4). The recovery of duration compression on orange and green backgrounds is possibly linked to this phase shift, which provides further evidence for the role of the magnocellular pathway in time perception.

There is a mild nonsignificant duration compression even with isoluminant stimuli viewed on a background with mean chromaticity. Our use of low spatial frequencies (0.5 and 1.5 c/deg) and a high-contrast bull's-eye fixation spot should exclude the possibility that this effect is due to luminance artifacts arising from chromatic aberration (Cavanagh & Anstis, 1991; Flitcroft, 1989; Logothetis, Schiller, Charles, & Hurlbert, 1990). Physiological studies have shown that although cells within the magnocellular pathway are generally not color opponent, they are not totally blind to chromatic stimuli. As well as the first harmonic response we mentioned above, a frequency-doubled signal in response to a grating or a uniform field sinusoidally modulated along the isoluminant red–green axis has also been reported in the phasic cells of the retina (Lee, Martin, & Valberg, 1989a) and the magnocellular cells of the LGN to which they project (Derrington et al., 1984; Lee & Sun, 2009). It has been suggested that both the first harmonic and the frequency-doubled response observed within the magnocellular pathway may contribute to psychophysical performance (Dobkins & Albright, 1993; Lee & Sun, 2009; Mullen, Yoshizawa, & Baker, 2003; Yoshizawa, Mullen, & Baker, 2003). The frequency-doubled response is present over a large temporal range (Lee et al., 1989a, 1989b), which makes it likely that the small compression effect present in our data at isoluminance might arise from this type of nonlinearity.

There is evidence that P cells might contribute to luminance detection and discrimination under some conditions (Lennie, Pokorny, & Smith, 1993; Wassle & Boycott, 1991). Gouras and Zrenner (1979) suggested that the color-opponent cells in the monkey retina respond better to spectral opponency at low temporal frequencies and better to luminance changes at high temporal frequencies. They explained this transformation from chromatic sensitivity by a delay of the color-opponent response produced by the surround mechanism such that the signal arrives at the site of center–surround combination in the same phase as the signal from the center. The authors recorded the flicker responses of color-opponent ganglion cells at three different temporal frequencies (low: 1.1 Hz, medium: 15–18 Hz, high: 33 Hz) and found synergistic responses at medium and high ranges. Our

adaptor oscillated at an interleaved frequency of 5 Hz and 10 Hz, which falls below the range within which P cells display such frequency-dependent phase shifts (Lee et al., 1988). The units of the parvocellular pathway have also been shown to respond to achromatic stimuli at high luminance contrast (Benardete & Kaplan, 1999a). In Experiment 3, however, we showed strong duration compression even at very low luminance contrasts, suggesting that the effect does not depend on the responses of P cells.

Temporal frequency adaptation can have dissociable effects on apparent temporal frequency and apparent duration. While low temporal frequency adaptation increases and high temporal frequency adaptation decreases the perceived speed of a mid-temporal frequency stimulus, distortions in perceived duration are unidirectional such that 5-, 10-, and 20-Hz adaptation all induce compression (Johnston et al., 2006). Changes in apparent duration can also occur in the absence of any change in perceived temporal frequency although the spatial tuning of these effects has been shown to be similar (Ayhan et al., 2009). Moreover, dyslexics show normal temporal frequency shifts for intermediate temporal frequencies but do not show any duration compression following adaptation to invisible flicker (Johnston et al., 2008). Here, we investigated the effect of the luminance signal on adaptation-induced duration and temporal frequency shifts. Despite the reduction of both temporal frequency (Experiment 1) and duration shifts (Experiment 2) following high temporal frequency adaptation at isoluminance, duration compression was present at luminance modulation even after the changes in perceived temporal frequency were eliminated. These results provide further support for separate mechanisms for changes in apparent temporal frequency and changes in apparent duration.

There is evidence that there are at least two, but possibly three, temporal frequency channels in the human visual system (Fredericksen & Hess, 1998; Hess & Snowden, 1992; Johnston & Clifford, 1995), each filter having a different shape and a different passband. Johnston and Clifford (1995) showed that the temporal filters measured by Hess and Snowden (1992) were well fitted by a Gaussian in log time and its first and second derivatives. While the zero-order filter has the low-pass temporal property characteristic of P cells, the derivative filters have the band-pass property associated with M cells. For sine functions, temporal frequency can be recovered from the relative activity of band-pass and low-pass filters (Smith & Edgar, 1994). On this model, changes in apparent temporal frequency are attributed to the changes in relative sensitivity of the filters. One might assume that the sensitivity of the band-pass filter, which is associated with M cells, is not affected following adaptation at isoluminance as much as it is following luminance modulation. This may explain why we observed a reduction in the temporal frequency shift following high temporal frequency adaptation with stimuli defined by

chromatic contrast. The sensitivity of the low-pass filter, however, should be affected by low temporal frequency chromatic adaptation, leading to an increase in the response of the band-pass channel. Indeed, no reduction was observed in temporal frequency shifts for low temporal frequency adaptation at isoluminance. These results are consistent with a previous report by Champion, Hammett, and Thompson (2005). In the same context, we also found that the temporal shifts following low temporal frequency adaptation with luminance modulation are smaller (~1 Hz) than the shifts following high temporal frequency adaptation.

Since changes in perceived duration can be dissociated from changes in perceived temporal frequency, we propose that the duration effects are linked to a different mechanism, possibly to the changes in the temporal tuning curve of M cells (Ayhan et al., 2009; Johnston et al., 2006). There is physiological evidence that high temporal frequency adaptation induces changes in the temporal frequency tuning of the band-pass cells of the nucleus of the optic tract (NOT) in wallaby, decreasing relative sensitivity to low temporal frequencies and sharpening the temporal impulse response (Clifford, Ibbotson, & Langley, 1997; Ibbotson, 2005; Ibbotson et al., 1998). We use this adaptation to explain the apparent duration compression in a content-dependent clock model (Johnston, 2010). In this model, the band-pass differentiating temporal filters (magnocellular units) set a prediction based on the current image brightness and the rate of change in image brightness. The current brightness level registered by a low-pass channel (parvocellular pathway) is then continuously compared to this forward prediction. When there is a match, the system can tell that the preset interval has elapsed so the clock ticks and the duration of an interval is indicated by the cumulated ticks. After adaptation, the phase advance in the magnocellular neurons shifts the prediction forward in time, delaying the match between the prediction and the current input, thereby introducing duration compression. Therefore, we attribute changes in temporal frequency to changes in relative sensitivity of M and P cells and attribute changes in apparent duration to the sharpening of the M cell temporal impulse response (Johnston et al., 2006).

In conclusion, the luminance signal is crucial for adaptation-based temporal compression. Visibility and task difficulty cannot explain the disappearance of the effect at isoluminance. Changing background chromaticity (orange and green) can restore the duration effect at isoluminance indicating the involvement of phasic cells in the retina and the magnocellular layers to which they project. High temporal frequencies generate stronger duration compression when the adaptor and test drift at the same temporal frequency. Finally, temporal frequency adaptation has dissociable effects on perceived duration and perceived temporal frequency. These results provide further evidence that temporal channels in human vision mediate duration perception, as well as temporal frequency coding and motion perception.
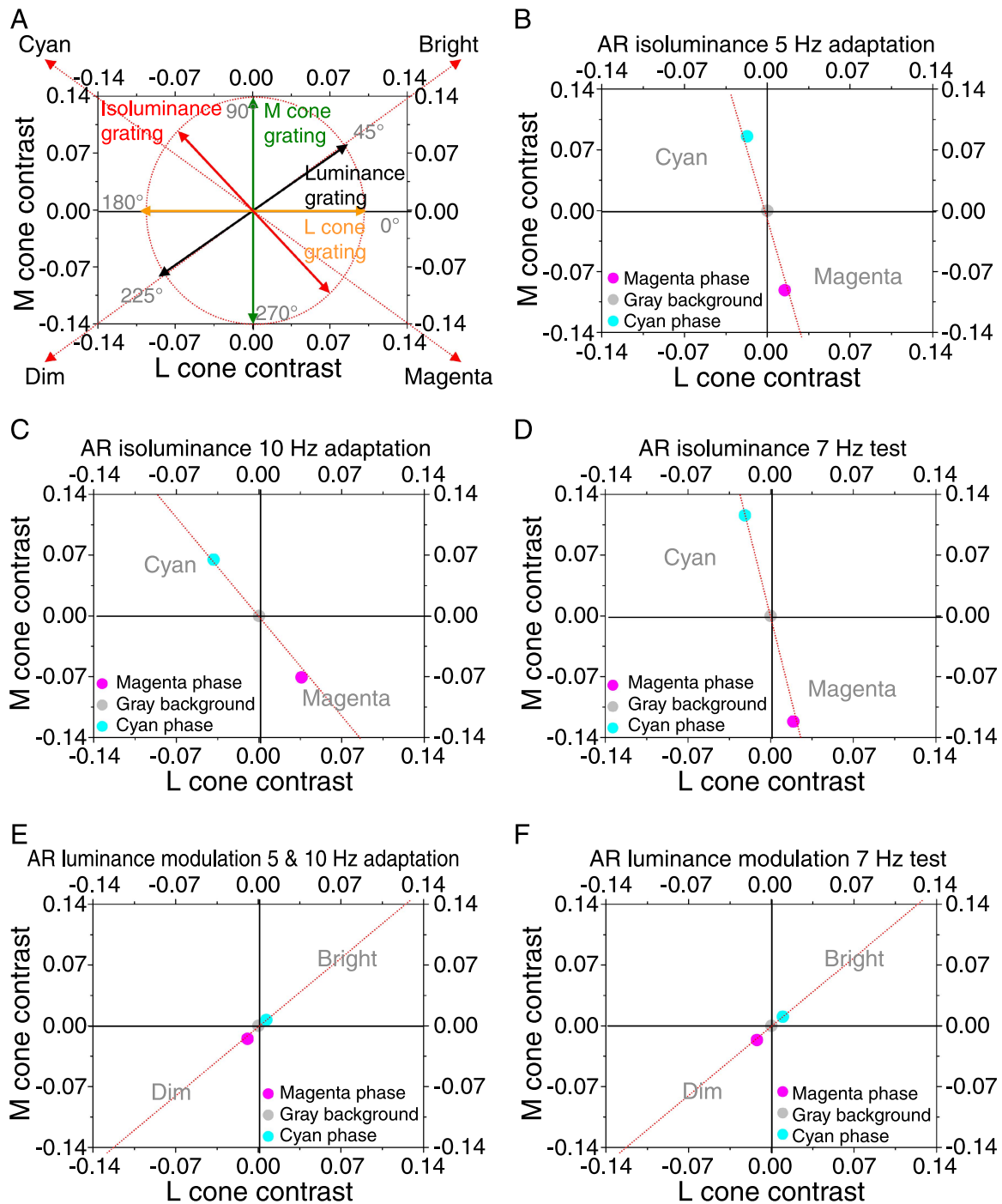
Figure A1. Graphical representation of the stimuli in L- and M-cone contrast space. The background field color is drawn in the origin. While the background direction represents the mechanisms and the color of the stimuli, the vector length represents the stimulus contrast. (A) Representation of the modulations, which isolate different mechanisms. The points on black arrow specify the L- and M-cone contrasts that isolate the luminance mechanism. The red arrow represents the L- and M-cone contrasts that isolate the isoluminance (L–M) mechanism. (B) L- and M-cone contrasts generated by the magenta and cyan phases of the gratings in the isoluminance 5-Hz adaptation phase for a naïve subject (AR). (C) L- and M-cone contrasts generated by the magenta and cyan phases of the gratings in the isoluminant 10-Hz adaptation phase for the same subject. (D) L- and M-cone contrasts generated by the magenta and cyan phases of the gratings in the isoluminant 7-Hz test phase for subject AR. (E) L- and M-cone contrasts generated by the magenta and cyan phases of the gratings in the low luminance 5- and 10-Hz adaptation phases for subject AR. (F) L- and M-cone contrasts generated by the magenta and cyan phases of the gratings in the low luminance 7-Hz test phase for subject AR.

	Magenta phase		Cyan phase		Root-mean-square contrast
	L-cone contrast	M-cone contrast	L-cone contrast	M-cone contrast	
IA Iso 5-Hz adapt	0.015	−0.092	−0.017	0.086	6.4%
IA Iso 10-Hz adapt	0.029	−0.078	−0.031	0.072	5.7%
IA Iso 7-Hz test	−0.001	−0.142	−0.002	0.136	9.8%
IA Lum 5- and 10-Hz adapt	−0.007	−0.010	0.005	0.004	0.6%
IA Lum 7-Hz test	−0.008	−0.012	0.006	0.006	0.8%
KC Iso 5-Hz adapt	0.021	−0.085	−0.023	0.080	6.1%
KC Iso 10-Hz adapt	0.007	−0.099	−0.009	0.094	6.9%
KC Iso 7-Hz test	−0.011	−0.152	−0.008	0.146	10.6%
KC Lum 5- and 10-Hz adapt	−0.036	−0.045	0.034	0.039	3.9%
KC Lum 7-Hz test	−0.047	−0.059	0.045	0.053	5.1%
RA Iso 5-Hz adapt	0.007	−0.099	−0.009	0.094	6.9%
RA Iso 10-Hz adapt	0.075	−0.032	−0.077	0.026	5.7%
RA Iso 7-Hz test	0.019	−0.122	−0.022	0.116	8.5%
RA Lum 5- and 10-Hz adapt	−0.009	−0.015	0.007	0.007	0.9%
RA Lum 7-Hz test	−0.012	−0.016	0.010	0.010	1.2%
AR Iso 5-Hz adapt	0.015	−0.092	−0.017	0.086	6.4%
AR Iso 10-Hz adapt	0.036	−0.071	−0.038	0.065	5.5%
AR Iso 7-Hz test	0.019	−0.122	−0.022	0.116	8.5%
AR Lum 5- and 10-Hz adapt	−0.009	−0.015	0.007	0.007	0.9%
AR Lum 7-Hz test	−0.012	−0.016	0.010	0.010	1.2%

Table A1. The first four columns of the table show the individual L- and M-cone contrasts generated by the magenta and cyan phases of the stimuli in different conditions. The individual RMS cone contrast values are also listed in the final column.

Appendix A

Supplementary materials

In Figures A1B–A1F, we drew the representations of adaptor and test stimuli (in the isoluminance and luminance condition with matched perceptual strength) in L- and M-cone contrast space for a naïve subject (AR). As can be seen in Figure A1A, the 45°–225° direction (black arrow) is the luminance axis along which the amplitudes of L- and M-cone contrasts are equal and in phase. A slight rotation above or below this axis means that the amplitudes of L- and M-cone contrasts are imbalanced; thus, the stimulus is chromatic as well as luminance modulated (Figures A1E and A1F). The vector direction of 133°–313° represents the isoluminant axis (red arrow), which corresponds to the direction of $\tan^{-1}(-x)$, where x refers to the ratio of L- and M-cone excitations of the adapting field. As the point of subjective isoluminance was measured individually for each subject and for different contrast and temporal frequencies, individual axes in different conditions (Figures A1B–A1D) differed from the photometrically isoluminant axis in Figure A1A (see General methods section for further details).

At threshold, we found that sensitivity to discriminate motion direction of isoluminant stimuli (mean = 90) at mid-temporal frequency (7 Hz) is lower than that of luminance-modulated stimuli (mean = 443) when both thresholds are expressed in cone contrast consistent with previous studies (Gegenfurtner & Hawken, 1996a, 1996b). Thus, for all subjects, the RMS cone contrasts of the isoluminant stimuli were higher than the RMS cone contrasts of the luminance-modulated stimuli matched in visibility (Table A1).

Acknowledgments

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