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Flicker adaptation of low-level cortical visual neurons contributes to temporal dilation

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Abstract

Several seconds of adaptation to a flickered stimulus causes a subsequent brief static stimulus to appear longer in duration. Non-sensory factors such as increased arousal and attention have been thought to mediate this flicker-based temporal-dilation aftereffect. Here we provide evidence that adaptation of low-level cortical visual neurons contributes to this aftereffect. The aftereffect was significantly reduced by a 45° change in Gabor orientation between adaptation and test. Because orientation-tuning bandwidths are smaller in lower-level cortical visual areas and are approximately 45° in human V1, the result suggests that flicker adaptation of orientation-tuned V1 neurons contributes to the temporal-dilation aftereffect. The aftereffect was abolished when the adaptor and test stimuli were presented to different eyes. Because eye preferences are strong in V1 but diminish in higher-level visual areas, the eye specificity of the aftereffect corroborates the involvement of low-level cortical visual neurons. Our results thus suggest that flicker adaptation of low-level cortical visual neurons contributes to expanding visual duration. Furthermore, this temporal-dilation aftereffect dissociates from the previously reported temporal-constriction aftereffect on the basis of the differences in their orientation and flicker-frequency selectivity, suggesting that the visual system possesses at least two distinct and potentially complementary mechanisms for adaptively coding perceived duration.

Introduction

Duration estimation can occur in several ways. Cognitive strategies such as counting can be used to estimate durations on the order of seconds or longer (e.g., Grondin, Meilleur-Wells, & Lachance, 1999). However, durations shorter than a second are unlikely to rely on such a mechanism. They are perceptually processed, and are important for motor behavior as well as for perception of motion, rhythm, and speech (see Mauk & Buonomano, 2004, for a review). Whether or not perception of brief durations is mediated by a centralized clock (e.g., Creelman, 1962; Treisman, 1963; Treisman, Faulkner, Naish & Brogan, 1990; Treisman, & Brogan, 1992) or by temporal processes that are distributed across sensory modalities is debated.

Recent results on temporal adaptation suggest that magno cells in the LGN contribute to visual time perception. Specifically, when an observer adapts to a flickered (e.g., 20 Hz) visual stimulus, a subsequently presented stimulus flickered at a different frequency (e.g., 10 Hz) appears shorter in duration (e.g., Johnston, Arnold, & Nishida, 2006; Bruno, Ayhan, & Johnston, 2010). This temporal-*constriction* aftereffect is strongly position specific (abolished even by a 1° shift of the test stimulus relative to the adaptor stimulus; Ayhan,

Bruno, Nishida, & Johnston, 2009), is eye specific (abolished when the test and adaptor stimuli are presented to different eyes; Bruno et al., 2010), is orientation independent (unaffected by a 90° stimulus rotation between adaptation and test, the maximum difference for linear grating stimuli; Johnston et al., 2006), is disrupted by dyslexia (believed to involve deficits in the magno-cellular pathway; Johnston, Bruno, Watanabe, Quansah, Patel, Dakin, & Nishida, 2008), is absent for equiluminant stimuli (that do not effectively stimulate magno cells; Ayhan, Bruno, Nishida, & Johnston, 2011), and occurs with flicker too fast (50-60 Hz) for conscious resolution (Johnston et al., 2008). These characteristics of the temporal-constriction aftereffect are consistent with the response characteristics of LGN magno cells (Bruno et al., 2010), suggesting that magno cells contribute to time perception (though there is controversy associated with this interpretation; Burr, Cicchini, Arrighi, & Morrone, 2011; Johnston, Bruno, & Ayhan, 2011).

In addition to this temporal-constriction aftereffect that a flickered adaptor produces on a *flickered* test stimulus, a flickered adaptor produces an opposite, temporal-*dilation* aftereffect, on a *static* test stimulus (e.g. Droit-Volet, & Wearden, 2002). It is possible that, unlike the temporal-constriction aftereffect, this temporal-dilation aftereffect might be mediated by adaptive changes in a centralized clock, for example, by increasing attention and/or arousal, a hypothesis suggested by Treisman & Brogan (1992). It is also possible that the temporal-dilation aftereffect is mediated by the same mechanisms as the temporal-constriction aftereffect, potentially involving LGN magno cells; however, it is unclear exactly which changes in experimental parameters would reverse the direction of an aftereffect mediated by a single mechanism. Alternatively, the visual system might possess at least two distinct mechanisms that differentially contribute to duration perception. To test these possibilities, we investigated orientation selectivity, eye specificity, and frequency dependence of the temporal-dilation aftereffect.

If low-level cortical visual neurons play a role in the temporal-dilation aftereffect, it should be sensitive to small changes in orientation between adaptation and test because orientation-tuning bandwidths are narrow for low-level cortical visual neurons. For example, in monkeys the tuning bandwidths are 25-45° in V1-V2, 35-75° in V4, and ~70 in IT (e.g., Hubel & Wiesel, 1968; Schiller, Finlay, & Volman, 1976; Desimone & Schein, 1987; Levitt, Kiper, & Movshon, 1994; Geisler & Albrecht, 1997; McAdams & Maunsell, 1999; Vogels & Orban, 1991, 1994; Sato, Katsuyama, Tamura, Hata, & Tsumoto, 1996; Ringach, Shapley, & Hawken, 2002). In humans, the orientation-tuning bandwidth has been shown to be approximately 45° in V1 (e.g., Jakobsson, 1985; Tootell, et al., 1998; Haynes & Rees, 2005a; Fang, Murray, Kersten & He, 2005; Yacoub, Harel, & Ugurbil, 2008; Sapountzis, Schluppeck, Bowtell, & Peirce, 2010), and broader in higher-level visual areas (e.g., Kamitani & Tong, 2005; Sapountzis et al., 2010). Thus, if V1 neurons play a role in the temporal-dilation aftereffect, a 45° change in orientation between adaptation and test should substantially reduce the aftereffect. An effect of orientation would also suggest that the temporal-dilation aftereffect is mediated by a different mechanism than the orientation-independent mechanism proposed by Johnston and colleagues for the temporal-constriction aftereffect (Johnston et al., 2006).

If low-level cortical visual neurons mediate the temporal-dilation aftereffect, the aftereffect should also be eye specific because eye preferences are strong for low-level cortical visual neurons but weak for higher-level visual neurons in monkeys (e.g., Hubel & Wiesel, 1968; Schiller et al., 1976; Gross, Rocha-Miranda, & Bender, 1972) and in humans (e.g., Menon, Ogawa, Strupp & Ugurbil, 1997; Dechent & Frahm, 2000; Haynes & Rees, 2005b, Adams, Sincich & Horton, 2007).

Finally, the temporal-constriction aftereffect has been shown to be selective for high flicker frequencies; a 20 Hz (or higher-frequency) adaptation produces a strong temporal-constriction aftereffect, but a 5 Hz adaptation produces little aftereffect, consistent with a role of LGN magno cells (Johnston et al., 2006; 2008). In contrast, if the temporal-dilation aftereffect is mediated by V1 neurons, a 5 Hz adaptation should be just as effective as (or potentially more effective than) a 20 Hz adaptation in producing the aftereffect because the average optimum temporal frequency to drive V1 neurons is approximately 10 Hz, based on a monkey study (Hawken, Shapley, & Grosof, 1996).

Thus, by examining the orientation-, eye-, and frequency-specificity of the temporal-dilation aftereffect, we determined whether the temporal-dilation aftereffect is mediated by adaptation of low-level cortical visual neurons, and whether the temporal-dilation aftereffect is distinct from the temporal-constriction aftereffect. Specifically, if the temporal-dilation aftereffect is mediated by an adaptation of a centralized clock, changes in stimulus orientation and the eye to which the stimulus is presented should have no effect. If the aftereffect is mediated by the same LGN magno mechanism proposed to mediate the temporal-constriction aftereffect, the temporal-dilation aftereffect should also be eye specific and frequency dependent, but orientation independent. Alternatively, if the temporal-dilation aftereffect is mediated by an adaptation of low-level cortical visual neurons, it should be orientation dependent as well as eye specific, and equivalent for 5 Hz and 20 Hz adaptation frequencies.

Experiments 1A, 1B, and 1C: Orientation dependence of the temporal-dilation aftereffect

Because the temporal-constriction aftereffect was shown to be undiminished by a 90° stimulus rotation between adaptation and test (Johnston et al., 2006), we first tested the effect of a 90° rotation on the temporal-dilation aftereffect (Experiment 1A), with a control experiment to rule out potential effects of attention (Experiment 1B). We then tested whether the temporal-dilation aftereffect is sensitive to a 45° rotation comparable to the orientation-tuning bandwidth in the human primary visual cortex (Experiment 1C).

Experiment 1A: The effect of 90° rotation between adaptation and test

Method

Participants—Participants in all experiments were undergraduate students at Northwestern University, who gave informed consent to participate for course credit, had normal or corrected-to-normal visual acuity, and were tested individually in a quiet and normally lit room. Twenty students (14 women) participated in this experiment.

Apparatus—Visual stimuli were displayed on a 19" color CRT monitor (75 Hz, 1152 by 870 resolution). The experiment was controlled with Apple MacBook Pro (2Ghz Intel Core 2 Duo, 2GB RAM) running OS 10.5, using MATLAB (Version R2008a) with the Psychophysics Toolbox extensions Version 3.0.8 (Brainard, 1997; Pelli, 1997; Kleiner, Brainard & Pelli, 2007).

Stimuli—The adaptor and test stimuli were both Gabors (4.32 cycles/degree, SD = 1.97°) known to resemble the spatial weighting functions of V1 simple cells (Watson, Barlow, & Robson, 1983), viewed from 116 cm. The adaptor had a Michelson contrast of 0.14 and the test stimulus had a contrast of 0.22 (with a mean luminance of 21.4 cd/m²). The adaptor was tinted blue (CIE[.282, .307]) so that it was clearly distinguishable from the subsequently presented achromatic test stimulus. The adaptor and test stimuli were presented at the center

of the screen against a gray background (21.4 cd/m²; CIE[.316, .368]). The adaptor was either static or on-off flickered (5 Hz, frequency within the range known to produce temporal-dilation aftereffects; Droit-Volet & Wearden, 2002, Kanai, Paffen, Hogendoorn, & Verstraten, 2006; Treisman, & Brogan, 1992), whereas the test stimulus was always static. The stimuli were either horizontally or vertically oriented. There were three adaptation conditions, a flicker adaptor followed by a test stimulus of the same orientation (the flicker same-orientation condition), a flicker adaptor followed by a 90°-rotated test stimulus (the flicker 90°-rotated condition), and a static adaptor followed by a test stimulus of the same orientation (the static same-orientation condition).

The adaptor was always presented for 5 sec. The test stimulus was presented for 200, 300, 400, 500, 600, 700 or 800 ms. The minimum and maximum durations were the short and long reference durations.

Procedure—For half of the participants the static adaptor and the test stimulus were always vertical, whereas for the remaining participants they were always horizontal. For all participants, the flicker adaptor was horizontal or vertical with the two orientations randomly intermixed across trials.

Each block of trials consisted of a reference phase and a test phase. In the reference phase, a short or long reference test stimulus was alternately presented across six trials (Figure 1A). Each trial began with a display indicating which reference duration (short or long) would be presented, followed by a 5-sec presentation of a static adaptor, followed (after 500 ms of a gray screen) by the corresponding reference duration. After 150 ms, the display indicated the appropriate key to press, and the participant pressed the key. The next trial was initiated following a 1-sec inter-trial interval.

In the test phase the three adaptor conditions were randomly intermixed across trials. On each trial, the duration of the test stimulus was randomly selected from the seven durations including the reference durations. Each trial began with a 500 ms gray screen, followed by a 5-sec presentation of an adaptor, another 500 ms of gray screen, and then the selected test stimulus. After 150 ms of blank screen the participant was prompted to respond as to whether the test duration was closer to the short or long reference by pressing the corresponding key. The participant's response initiated the next trial (Figure 1B). This is a standard temporal-bisection task used to measure perceived duration and temporal resolution (e.g., Church & Deluty, 1977; Wearden, 1991).

In summary, each block consisted of six reference trials followed by 21 test trials (3 adaptation conditions × 7 test durations), and each participant ran 9 such blocks.

Data analysis—We obtained a temporal-bisection function, the proportion of “Long” responses as a function of the test duration, for each condition for each participant. A

logistic function of the form, $y = \frac{1}{1 + e^{-(x - PSE)/k}}$, is typically fit to a sigmoidal psychometric function to extract the point of subjective equality (*PSE*) and the *k* parameter (a measure of temporal sensitivity). Logistic functions produced good fits to individual participants' data across all experiments (mean $\omega^2 = 0.93$). The *PSE* (the test duration at which the bisection function crosses the 50% point) corresponds to the test duration that the participant judges to be equidistant from 200 ms and 800 ms; the *PSE* is therefore effectively the stimulus duration that the participant perceives to be equivalent to 500 ms. Thus, if the *PSE* is shorter following flicker adaptation than following static (control) adaptation, this would indicate that flicker adaptation causes temporal dilation because a shorter physical duration is judged to be 500 ms after flicker adaptation than after static adaptation. The *k* parameter is

inversely related to the slope of the bisection function and it approximately corresponds to the just noticeable difference (JND) around the PSE. The k parameter thus provides a measure of temporal sensitivity (with a smaller value indicating a smaller JND or higher sensitivity). We will not present “mean” temporal-bisection functions based on the proportions of “Long” responses averaged across observers because such averaging inevitably confounds PSE and slope.

Results

A mixed ANOVA on PSEs with the within-participant factor of adaptation condition and between-participant factor of test orientation yielded a significant effect of adaptation condition, $F(2, 57) = 19.41, p < 0.001$. Because there was no significant main effect of test orientation, $F(1, 18) = 0.28, n.s.$, nor did it interact with adaptation condition, $F(2, 57) = 0.36, n.s.$, we collapsed the data across the two test orientations in Figure 2A and in the follow-up analyses. As shown in Figure 2A, the PSEs are clearly shorter for the two flicker-adaptation conditions relative to the static-adaptation condition, $t(19) > 4.03, ps < 0.001$, replicating the temporal-dilation aftereffect (e.g., Droit-Volet & Wearden, 2002). Importantly, the PSE is shorter for the flicker same-orientation condition than for the flicker 90°-rotated condition, $t(19) = 2.61, p < 0.02$, indicating that the temporal-dilation aftereffect was reduced when the test stimulus was rotated 90° relative to the adaptor.

A similar mixed ANOVA on the k parameter (indicative of JND) yielded a significant effect of adaptation condition, $F(2, 57) = 4.57, p < 0.02$. We again collapsed the data across the horizontal and vertical test orientations because there was no significant main effect of test orientation, $F(1, 18) = 1.75, n.s.$, nor did it interact with adaptation condition, $F(2, 57) = 1.43, n.s.$. The k values were smaller for the two flicker-adaptation conditions (72 ms, $SEM^1 = 8$ ms for the flicker same-orientation condition, and 66 ms, $SEM = 6$ ms for the flicker 90°-rotated condition), than for the static-adaptation condition (84 ms, $SEM = 4$ ms), $t(19) > 2.40, ps < 0.03$, but were not statistically different between the two flicker-adaptation conditions, $t(19) = 1.02, n.s.$ Thus, flicker adaptation in general improved temporal JND, but the orientation-dependent aspect of the temporal-dilation aftereffect is not associated with changes in JND.

These results suggest that a portion of the temporal-dilation aftereffect is orientation specific and independent of changes in temporal JND. However, an alternative explanation is that the orientation change between adaptation and test per se had the effect of making the test stimulus appear shorter, thereby countering the effect of flicker adaptation.

Experiment 1B: A control for the effect of orientation change per se

We conducted a control experiment where the adaptor was always static but its orientation was either the same as or 90° rotated from the test stimulus. If an orientation change per se makes the test stimulus appear shorter in duration, the 90° orientation change should make the PSE longer.

Participants

Ten new students (8 women) participated.

¹All $SEMs$ including those presented in figures as error bars have been corrected for within-participant comparisons (i.e., the baseline variability across participants was removed prior to computing the $SEMs$).

Apparatus, Stimuli, and Procedure

All methods were the same as in Experiment 1A with the following exceptions. The test stimulus was always static and vertical but the adaptor was either vertical (the static same-orientation condition), or horizontal (the static 90°-rotated condition). These adaptation conditions were randomly intermixed across a block of 14 trials (2 adaptation conditions $\times$ 7 test durations). Each participant ran 9 such blocks.

Results

As is evident in Figure 2B, the PSEs are virtually identical for the static same-orientation and static 90°-rotated conditions, $t(9) = 0.06$, *n.s.* The k values are also virtually identical for the two conditions (66 ms, $SEM = 4$ ms for the static-same-orientation condition and 77 ms, $SEM = 4$ ms for the static 90°-rotated condition), $t(9) = 1.22$, *n.s.* Thus, a 90° orientation change between adaptation and test affects neither perceived duration nor JND. Thus, the orientation specificity of the temporal-dilation aftereffect we demonstrated in Experiment 1A is likely to implicate an adaptation of orientation-tuned visual processes in time perception.

Experiment 1C: The effect of 45° rotation between adaptation and test

Because the orientation tuning bandwidth in human V1 is approximately 45° (see above), if the temporal-dilation aftereffect is mediated by low-level cortical visual neurons, it should be substantially reduced by a 45° change in orientation between adaptation and test.

Methods

Participants—Twenty-two new students (16 women) participated.

Apparatus, Stimuli, and Procedure—All methods were the same as in Experiment 1A except that the adaptor and test stimuli were $\pm 22.5^\circ$ rotated from horizontal.

Results

The results are essentially the same as those for Experiment 1A. A mixed ANOVA on PSEs with the within-participant factor of adaptation condition and between-participant factor of test orientation yielded a significant effect of adaptation condition, $F(2, 63) = 20.15$, $p < 0.001$. Because there was no significant effect of test orientation, $F(1, 21) = 0.79$, *n.s.*, nor did it interact with adaptation condition, $F(2, 63) = 0.49$, *n.s.*, we averaged the data across the two test orientations in Figure 3 and in the follow-up analyses.

As shown in Figure 3, PSEs are shorter for the two flicker-adaptation conditions relative to the static-adaptation condition, $t(21) > 4.90$, $p < 0.001$. Importantly, the PSE is shorter for the flicker same-orientation condition than for the flicker 45°-rotated condition, $t(21) = 2.42$, $p < 0.03$.

A mixed ANOVA on the k parameter (57 ms, $SEM = 13$ ms for the flicker same-orientation condition, 80 ms, $SEM = 14$ ms for the flicker 45°-rotated condition, and 77 ms, $SEM = 12$ ms for the static-adaptation condition) yielded no significant main effect of adaptation ($F(2, 63) = 1.94$, *n.s.*), test orientation ($F(1, 21) = 0.05$, *n.s.*), or their interaction ($F(2, 63) = 1.68$, *n.s.*), suggesting that the temporal-dilation aftereffect is not associated with changes in temporal JND.

The 45° selectivity of the temporal-dilation aftereffect suggests that flicker adaptation of low-level cortical visual neurons contribute to perceived duration.

Experiment 2: The effect of switching eyes between adaptation and test

Lower-level cortical visual neurons respond with a greater degree of eye specificity than higher-level cortical visual neurons (see above). Thus, if the temporal-dilation aftereffect is mediated by an adaptation of low-level cortical visual neurons, the aftereffect should be strongly eye specific.

Methods

Participants—Fifteen new students (10 women) participated.

Apparatus—Visual stimuli were displayed on a 21" color CRT monitor (75 Hz, 1152 by 870 resolution). A stereoscope with four front-surface mirrors integrated with a headrest was used to present a different stimulus to each eye. The viewing distance was 110 cm.

Stimuli—We used a high-contrast (0.97) square-wave grating (1.74° by 1.74° and 5.17 cycles/deg, presented against a mid-gray background, 42.8 cd/m^2) as the adaptor and test stimuli, so that they were clearly visible (without fading) when presented monoptically. The grating was always vertically oriented, and was presented within a 4.99° -by- 4.99° binocular frame with random black (1.8 cd/m^2) lines to facilitate stable binocular fusion (Figure 4). An adaptor or test stimulus was presented to one eye while a blank frame was presented to the other eye. Other aspects of the stimuli were the same as in Experiment 1A.

Procedure—The temporal-bisection task was the same as in Experiment 1A except for the following. There were eight blocks of trials. In the reference phase of each block, a static adaptor and the test stimulus were always presented to the same eye, with the stimulus eye chosen randomly on each trial (with the constraint that each eye served equally often as the stimulus eye across the eight blocks). In the test phase, on flicker-adaptation trials, the adaptor and test stimuli were both randomly presented to the left or right eye (with the constraint that each of the four combinations, left-eye vs. right-eye adapt and left-eye vs. right-eye test, occurred equally often across the eight blocks). On static-adaptation trials, the adaptor was randomly presented to the left or right eye but the test grating was always presented to the same eye (with the constraint that a static adaptor was presented to each eye equally often across the eight blocks). Each combination of adaptation condition (flicker same-eye, flicker opposite-eye, and static same-eye) and test duration (the same seven durations used in Experiment 1A) was presented once per block, yielding 21 trials per block.

Results

A repeated-measures ANOVA on PSE yielded a significant effect of adaptation condition, $F(2, 43) = 4.28$, $p < 0.024$. As shown in Figure 5, the PSE is significantly shorter for the flicker same-eye condition than for both the flicker-opposite eye, $t(14) = 3.09$, $p < 0.01$ and the static same-eye, $t(14) = 2.54$, $p < 0.024$, conditions, but the PSEs are not significantly different for the flicker opposite-eye and the static same-eye conditions, $t(14) = 0.98$, *n.s.*

A repeated-measures ANOVA on the k parameter (73 ms, $SEM=9$ ms for the flicker same-eye condition, 94 ms, $SEM=5$ ms for the flicker opposite-eye condition, and 85 ms, $SEM=8$ ms for the static same-eye condition) yielded no significant effect of adaptation condition, $F(2, 43) = 1.28$, *n.s.*

Thus, the temporal-dilation aftereffect is eye specific, and it is not associated with changes in temporal JND. We note that because people are generally unaware of the eye to which a stimulus is presented, a demonstration of eye specificity of the temporal-dilation aftereffect also makes contributions of cognitive factors to the aftereffect unlikely.

Experiment 3: The effect of adaptation frequency

A 20 Hz (or higher-frequency) adaptation but not a 5 Hz adaptation produces a robust temporal-constriction aftereffect hypothesized to be mediated by LGN magno cells (Johnston et al., 2006; 2008). In contrast, adaptation to either frequency should produce an equivalently robust temporal-dilation aftereffect if it is mediated by low-level cortical visual neurons (see above).

Methods

Participants—Thirteen new students (7 women) participated.

Apparatus, Stimuli, and Procedure—All methods were the same as in Experiment 1A except for the following. Adaptors and test stimuli were vertical. An adaptor was either flickered at 5 Hz (the flicker-5 Hz condition), flickered at 20 Hz (the flicker-20 Hz condition), or static (the static condition).

Results

A repeated-measures ANOVA on PSE yielded a significant effect of adaptation condition, $F(2, 37) = 4.45$, $p < 0.022$. As shown in Figure 6, the PSEs were equivalent in the flicker-5 Hz and flicker-20 Hz conditions, $t[13] = 0.36$, *n.s.*, but were significantly shorter in these flicker conditions than in the static condition, $t[13] > 2.75$, $ps < 0.018$.

A repeated-measures ANOVA on the k parameter (94 ms, $SEM = 11$ ms for the flicker-5 Hz condition, 98 ms, $SEM = 8$ ms for the flicker-20 Hz condition, and 99 ms, $SEM = 9$ ms for the static condition) yielded no significant effect of adaptation condition, $F(2, 37) = 0.0001$, *n.s.*

Thus, the temporal dilation aftereffect is equivalent for an adaptation to 5 Hz or 20 Hz flicker, and it is not associated with changes in temporal JND.

Discussion

Is the perception of brief durations mediated by a centralized clock (e.g., Creelman, 1962; Treisman, 1963; Treisman et al., 1990; Treisman, & Brogan, 1992) or by temporal processes that are distributed across sensory modalities? Non-visual cortical areas such as the supplementary motor area (e.g., Macar, Coull, & Vidal, 2006), the right prefrontal and inferior parietal cortex (e.g., Harrington, Haaland, & Knight, 1998), the frontal cortex (e.g., Genovesio, Tsujimoto, & Wise, 2009) and the posterior parietal cortex (e.g., Buetti, Bahrami, & Walsh, 2008), subcortical structures such as the basal ganglia and cerebellum (e.g., Mangels, Ivry, & Shimizu, 1998; Handy, Gazzaniga, Ivry, 2003; Rao, Mayer, & Harrington), as well as high-level visual areas such as MT/V5 (e.g., Jantzen, Steinberg, & Kelso, 2005; Buetti, Walsh, Frith & Rees, 2008) have all been implicated in time perception based on brain imaging, transcranial magnetic stimulation, and neuropsychological results. Our psychophysical results suggest that adaptive responses of low-level cortical visual neurons also contribute to perception of temporal duration.

Adaptation to a flickered stimulus increases the perceived duration of a subsequently presented static test stimulus (e.g., Droit-Volet, & Wearden, 2002). The standard explanation for this temporal-*dilation* aftereffect is that adaptation to a flickered stimulus increases arousal, making a presumed central clock tick faster, thereby causing a test stimulus to appear longer in duration (e.g., Treisman, & Brogan, 1992; Ortega & Lopez, 2008). This hypothesis is consistent with crossmodal results that adapting to a train of auditory clicks increases the perceived duration of both auditory and visual stimuli (e.g.,

Treisman et al., 1990; Penton-Voak, Edwards, Percival, & Wearden, 1996; Wearden, Edwards, Fakhri, Percival, 1998; Wearden, Philpott, & Win, 1999).

Our results demonstrate that adaptation of low-level cortical visual mechanisms also contribute to the temporal-dilation aftereffect. Cortical visual neurons are more tightly tuned to their preferred orientation and are more strongly eye selective in lower-level visual areas, with the average orientation-tuning bandwidth of approximately 45° (in humans) and exclusive eye selectivity (identified in both monkeys and humans) present in V1 (see the introduction for details). Thus, our demonstration that either a 45° change in orientation or switching eyes between adaptation and test significantly reduces the temporal-dilation aftereffect suggests that low-level cortical visual neurons (likely in V1) contribute to adaptive coding of duration.

Although a 45° change in orientation significantly reduced the temporal-dilation aftereffect, it did not abolish the aftereffect. This may reflect the fact that orientation-tuned neurons respond even when the stimulus orientation deviates from the preferred orientation and that some neurons have orientation tuning bandwidths that are substantially broader than the average bandwidth in a given visual area (including V1; e.g., Schiller et al., 1976; Ringach et al., 2002). In contrast, switching eyes between adaptation and test resulted in a non-significant temporal-dilation aftereffect, suggesting that the aftereffect is mediated by strongly monocular neurons such as V1 simple cells (e.g., Hubel & Wiesel, 1968).

What might be the mechanism of the temporal-dilation aftereffect? One possibility is that flicker adaptation accelerates the rate of visual processing. If so, flicker adaptation should have increased temporal resolution as well as dilated perceived duration. Temporal resolution is reflected in the k parameter, a measure of the temporal JND. In Experiment 1A, flicker adaptation significantly reduced the k value irrespective of orientation change, potentially consistent with the idea that the orientation-non-specific component of the temporal-dilation aftereffect may be associated with an increased rate of visual processing. However, flicker adaptation had no significant effect on the k value in the rest of the experiments (Experiments 1C, 2, and 3). Although it is possible that a measure of temporal sensitivity more sensitive than the k parameter might reveal an effect of flicker adaptation on temporal resolution, our current results suggest that the temporal-dilation aftereffect reflects an adaptive calibration of visual duration rather than acceleration of visual processing.

Two outstanding questions remain. One is the relationship between the previously reported crossmodal temporal-dilation aftereffect induced by an adaptation to a train of auditory clicks (Penton-Voak, 1996; Wearden, et al., 1998; Wearden, Philpott, & Win, 1999), and the current demonstration of the visually specific temporal-dilation aftereffect. One possibility is that a train of auditory clicks might adapt low-level cortical visual neurons of all orientation selectivity and eye specificity. This scenario, however, is unlikely because low-level visual neurons are much more strongly driven by visual flicker than by auditory clicks; for example, although auditory clicks can modulate the perception of visual flashes (e.g., Shams, Kamitani, & Shimojo, 2000), they do not typically generate the perception of visual flashes. A more likely possibility is that the crossmodal and visual forms of temporal-dilation aftereffects are mediated by different mechanisms. For example, crossmodal temporal dilation might reflect an accelerated central clock, whereas visual temporal dilation might reflect an adaptive calibration of low-level cortical visual processes.

A second outstanding question is why flicker adaptation causes a temporal-*constriction* aftereffect in some paradigms (e.g., current results, Droit-Volet, & Wearden, 2002) and a temporal-*dilation* aftereffect in others (e.g., Johnston et al., 2006; 2008). The apparent

critical difference between these paradigms is whether the test stimulus is flickered or static. The temporal-constriction aftereffect occurs when the test stimulus is flickered, whereas the temporal-dilation aftereffect occurs when the test stimulus is static. It is difficult to speculate that a single temporal calibration mechanism produces opposite effects depending on whether the test stimulus is flickered or static. Rather, the specific parametric dependencies of the temporal-constriction and temporal-dilation aftereffects suggest that they are mediated by subcortical and cortical visual mechanisms, respectively. The temporal-constriction aftereffect is specific to eye, position, high temporal frequency (strong aftereffects with a 20 Hz flicker adaptation but no or minimal aftereffects with a 5 Hz flicker adaptation) and luminance signals (no aftereffect for equiluminant stimuli) but orientation independent, consistent with the response properties of LGN magno cells (see Bruno et al., 2010 for a review). In contrast, the temporal-dilation aftereffect is eye and orientation specific but equivalent for 20 Hz and 5 Hz flicker adaptation, consistent with the response properties of V1 neurons (see above). It is thus likely that the visual system implements separate temporal calibration mechanisms for processing dynamic and static stimuli.

In summary, the current results suggest that the visual system has at least two distinct mechanisms to adaptively encode duration, one potentially mediated by LGN magno cells (e.g., Bruno et al., 2010) and the other potentially mediated by cortical visual neurons in V1 (the current study). Future research is needed to determine how adaptation of these subcortical and cortical neural populations produce opposite and potentially complementary forms of temporal calibration, and what functional roles these peripheral duration mechanisms serve.

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Figure 1.

Illustration of a trial sequence for the reference phase (A) and the test phase (B), for Experiments 1A, 1B, 1C, and 3. (A) Reference phase (training for the short and long reference durations, and for the general experimental procedure). A prompt indicating the duration (short or long) of the upcoming reference stimulus was followed by a 5-sec static adaptor (always the same orientation as the reference stimulus), followed by a 500 ms blank screen and then by the corresponding reference stimulus. After a 150 ms blank screen a prompt instructed the observer to press the appropriate button. The next trial began after 1 sec. (B) Test phase. One of the three adaptors was presented for 5 sec, a flickered adaptor of the same orientation as the test stimulus (the flicker same-orientation condition), a flickered adaptor rotated 90° from the test stimulus (the flicker 90°-rotated condition), or a static adaptor of the same orientation as the test stimulus (the static same-orientation condition). The adaptor was followed by a 500 ms blank screen and then by the test stimulus of one of seven durations (200, 300, 400, 500, 600, 700, or 800 ms). After a 150 ms blank screen a prompt instructed the observer to respond as to whether the duration of the test stimulus was closer to the short or long reference. The next trial began after 1 second.

Figure 2.

Results of Experiments 1A and 1B. (A) Mean points of subjective equality (PSEs) based on the logistic-function fits to individual participants' data, for the three adaptation conditions: flicker same-orientation, flicker 90°-rotated, and static same-orientation (Experiment 1A). The test orientation was vertical (as shown in the figure) for half of the participants and horizontal for the remaining participants (the data have been averaged across the vertical and horizontal test orientations). (B) Mean PSEs for the two adaptation conditions: static same-orientation and static 90°-rotated (Experiment 1B). The test orientation was always vertical. All error bars represent ± 1 *SEM* adjusted for within-participant comparisons. * $p < 0.05$, *** $p < 0.001$

Figure 3.

Results of Experiment 1C. Mean points of subjective equality (PSEs) based on the logistic-function fits to individual participants' data, for the three adaptation conditions: flicker same-orientation, flicker 45°-rotated, and static same-orientation. The test orientation was 22.5° counterclockwise rotated from horizontal for half of the participants (as shown in the figure), and 22.5° clockwise rotated from horizontal for the remaining participants (the data have been averaged across the two test orientations). The error bars represent ± 1 SEM adjusted for within-participant comparisons. * $p < 0.05$, *** $p < 0.001$

Figure 4.

Illustration of the stimuli and trial sequence in Experiment 2. (A) Dichoptic presentation of the stimuli. A high-contrast square-wave grating was presented to one eye (either left or right) and the blank frame was presented to the other eye (using a stereoscope). The binocularly presented frame facilitated stable binocular fusion. (B) The appearance of the stimulus when viewed through the stereoscope. (C) A trial sequence for the test phase. One of the three adaptors was presented for 5 sec, a flickered adaptor presented to the same eye as the subsequent test stimulus (the flicker same-eye condition), a flickered adaptor presented to the opposite eye from the test stimulus (the flicker opposite-eye condition), or a static adaptor presented to the same eye as the test stimulus (the static same-eye condition). The adaptor was followed by a 500 ms blank screen and then by the test stimulus of one of seven durations (200, 300, 400, 500, 600, 700, or 800 ms). After a 150 ms blank screen a prompt instructed the participant to respond as to whether the duration of the test stimulus was closer to the short or long reference. The next trial began after 1 sec.

Figure 5.

Results of Experiment 2. Mean points of subjective equality (PSEs) based on the logistic-function fits to individual participants' data, for the three adaptation conditions: flicker same-eye, flicker opposite-eye, and static same-eye. The test stimulus was randomly presented either to the left or right eye (the data have been averaged across the two eyes). The error bars represent ± 1 SEM adjusted for within-participant comparisons. * $p < 0.05$, ** $p < 0.01$

Figure 6. Results of Experiment 3. Mean points of subjective equality (PSEs) based on the logistic-function fits to individual participants' data, for the three adaptation conditions: flicker-5 Hz, flicker-20 Hz, and static. The error bars represent ± 1 SEM adjusted for within-participant comparisons. * $p < 0.05$