

Motion-direction specificity for adaptation-induced duration compression depends on temporal frequency

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Adapting to a 20 Hz oscillating grating reduces the apparent duration of a 10 Hz drifting grating displayed subsequently in the same location as the adaptor. The effect is orientation-independent as it remains once the adaptor is rotated 90° relative to the tests (Johnston, Arnold, & Nishida, 2006). However, it was shown that, for random dots moving at 3°/s, duration compression follows adaptation only when the adaptor and test drift in the same direction, and it disappears when they drift in opposite directions (Curran & Benton, 2012). Here, we explored the relationship between the relative motion direction of adaptor and test and the strength of duration compression for a wider range of speeds and for narrow-band stimuli (temporal frequencies between 3 and 18 Hz). We first measured perceived temporal frequency for the same stimuli after adaptation, and we used these estimates to match the apparent rate of the adapted and unadapted tests in the duration task. We found that, whereas at 3 Hz the effect of adaptation in the opposite direction on duration is marginal, at higher frequencies there is substantial duration compression in the opposite direction. These results indicate that there may be two contributions to apparent duration compression: a cortical contribution sensitive to orientation and motion direction at a wide range of temporal frequencies and a direction-independent subcortical contribution, which is revealed at higher frequencies. However, while direction specificity implies cortical involvement, subcortical orientation dependency and the influence of feedback to subcortical areas should not be ignored.

Introduction

Our judgments of the duration of a brief interval containing a visual stimulus can be biased by visual adaptation. In the subsecond range, adaptation to high temporal-frequency visual motion (Ayhan, Bruno, Nishida, & Johnston, 2009; Burr, Tozzi, & Morrone, 2007; Johnston et al., 2006), contrast (Bruno & Johnston, 2010), or reduced illumination (Bruno, Ayhan, & Johnston, 2011) can all induce changes in perceived duration. Johnston et al. (2006) asked their participants to adapt to a 20 Hz drifting grating or flickering Gaussian blob and observed a strong reduction in apparent duration only for test stimuli (drifting or flickering at 10 Hz) that were displayed in the same spatial position as the adaptor. A 5 Hz adaptor did not substantially affect duration estimates.

The question of where, in the visual system, this kind of adaptation might take place has been subject to debate in the past few years. Initial evidence from our group suggested an early locus for apparent duration compression. When Johnston et al. (2006) rotated the adaptor 90° relative to the tests, they found a comparable duration compression, implying that the effect is orientation-independent and therefore pointing to a pre-V1 site at which visual neurons are not selective for stimulus orientation. The spatial tuning of adaptation-induced time compression was found to be tightly tuned (less than a degree of visual angle) to the spatial location of the adaptor and to be robust even for very narrow adaptors (Ayhan et al., 2009). These results are more compatible with brain regions with small rather than large receptive fields, and we know

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that the average size of receptive fields increases systematically along the visual pathway from the retina to extrastriate areas (Lee, Kremers, & Yeh, 1998; A. T. Smith, Singh, Williams, & Greenlee, 2001; Xu et al., 2001; Zeki, 1978). We also know that precortical regions respond to higher temporal frequencies than cortical ones (Hawken, Shapley, & Grosf, 1996). Adaptors with temporal frequencies above the flicker fusion threshold (and, therefore, likely to be invisible to the visual cortex) still caused substantial duration compression (Johnston et al., 2008).

However, other studies suggest that adaptation might take place later in the visual pathway. In a follow-up to the study by Johnston et al. (2006), Burr et al. (2007) interposed a saccadic eye movement between the adaptation and test phases in order to investigate the frame of reference of the duration effect. They found strong compression after spatiotopic but not retinotopic adaptation although this finding has proved controversial (Bruno, Ayhan, & Johnston, 2010; Burr, Cicchini, Arrighi, & Morrone, 2011; Johnston, Bruno, & Ayhan, 2011). They suggested that this kind of adaptation might occur higher up in the visual pathway (post-V1), where the visual stimuli are coded in space- or world-centric rather than retino-centric coordinates.

Using translating random dot kinematograms (RDKs), Curran and Benton (2012) showed that, for dots drifting at 3°/s, duration compression follows adaptation only when the adaptor and test move in the same direction with no compression when they move in opposite directions. These results might imply that adaptation takes place when neuronal response is selective for a specific motion direction (typically, V1 or later) (Kohn & Movshon, 2004). However, this finding seems to be at odds with the orientation-independent effect observed by Johnston et al. (2006) for a 10 Hz drifting grating after adaptation to 20 Hz.

In this study, we explored the direction dependence of the adaptation-induced duration compression for drifting gratings for a wider range of temporal frequencies (3–18 Hz; 1 c/°). Because perceived temporal frequency can influence perceived duration (Kanai, Paffen, Hogendoorn, & Verstraten, 2006), we first measured the effect of adaptation on perceived temporal frequency, and then we used these estimates to minimize the difference in perceived rate between adapted and unadapted tests. We found that, whereas adapting and testing at the same temporal frequency does not induce substantial changes in apparent temporal frequency, regardless of motion direction, duration was perceptually compressed when the adaptor and adapted test drifted in the same but not in the opposite direction at only 3 Hz. Adaptation to higher temporal frequencies induced compression for both directions. Finally, we measured the direction tuning of duration compression. This confirmed orientation

tuning for test patterns moving in the same general direction as the adaptor, but there was no tuning for test patterns drifting in the opposite general direction.

General methods

Observers

Five observers participated in the perceived temporal frequency (Experiment 1) and perceived duration (Experiment 2) experiments (one author and four naïves) whereas four subjects (a different author and three different naïves) participated in the direction-tuning experiment (Experiment 3). All of them had normal or corrected-to-normal vision.

Apparatus

Stimuli were displayed, in a darkened room, on a gamma-corrected CRT monitor (Mitsubishi Diamond Plus 230SB) with a refresh rate of 100 Hz. The stimuli were generated in Matlab using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). Stimuli were viewed from a distance of 57 cm.

Procedure

All the experiments were composed of an adaptation phase followed by a test phase (Figure 1). Continuous fixation on a central spot was required for the whole duration of the experiment. All stimuli were drifting luminance sinusoidal gratings (or Gabors, in the direction-tuning experiment) displayed at a distance of 5° of visual angle from the center of the screen. As their spatial frequency was 1 c/°, the temporal frequency and speed were numerically the same. The diameter of the stimulus window was 5° of visual angle, and the Michelson contrast was 50% for the adaptor and 80% for the tests (to avoid changes in apparent contrast in the tests). All test stimulus waveforms were amplitude-modulated by a temporal Gaussian envelope ($\sigma = \text{standard duration}/6$) to avoid sudden signal onset or offset effects. In the adaptation phase, subjects were exposed to an eccentric adaptor (displayed on the left-hand side of the screen, 5° from the monitor center) that drifted unidirectionally, initially for 30 s (8 s for the following trials). When the adaptor disappeared, it was replaced by a blank page of mean luminance for 500 ms, which preceded the test phase. In the test phase, two test stimuli were sequentially displayed: one in the same spatial location as the adaptor and the other in the opposite position relative to the fixation

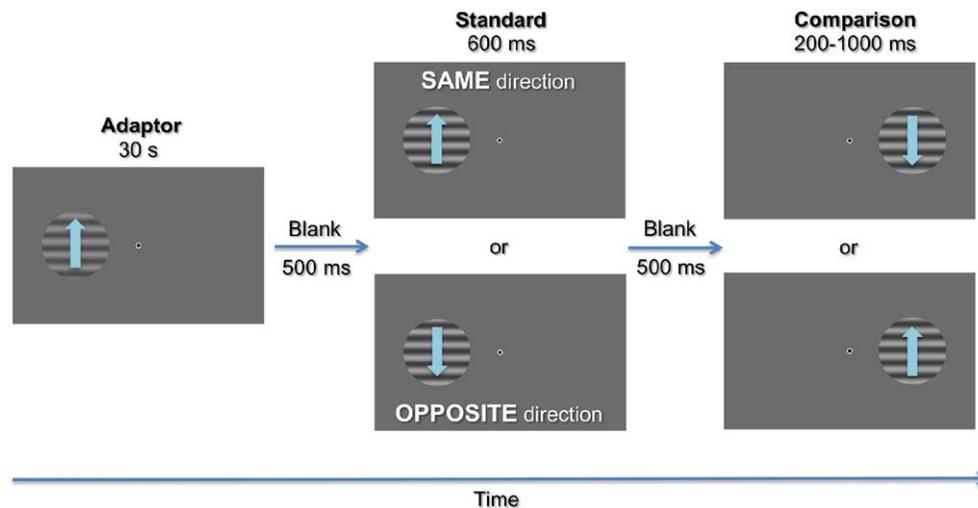


Figure 1. Schematic representations of the stimuli and the task. For the perceived temporal frequency and perceived duration experiments, stimuli were luminance-modulated sinusoidal gratings whereas for the direction-tuning experiment stimuli were luminance Gabor stimuli with the same spatial frequency, size, and position. In the adaptation phase, subjects had to keep fixation on the middle of the screen while an adaptor was displayed on the left side of the fixation spot. In the test phase, two stimuli (the standard, fixed temporal frequency in Experiment 1 or the fixed duration in Experiments 2 and 3 and the comparison with variable temporal frequency in Experiment 1 or variable duration in Experiments 2 and 3 across trials) were sequentially displayed on either side of the fixation spot. The presentation order of standard and comparison was randomized on a trial-by-trial basis. At the end of each trial, subjects had to report which stimulus appeared to drift at a higher rate (in the perceived temporal frequency experiment) or to stay on for a longer duration (in the perceived duration and direction-tuning experiments).

spot. The presentation order was randomized, and the two test intervals were separated by a 500-ms uniform mean luminance page. After the disappearance of the second test, subjects were required to report the relative temporal frequency (Experiment 1) or the relative duration (Experiments 2 and 3) of the two tests (see Methods section for each experiment of more details).

Experiment 1: Effect of unidirectional motion adaptation on perceived temporal frequency

The apparent temporal frequency of a visual pattern can be altered by adaptation. For example, adapting to a higher or to a lower temporal frequency will have opposite effects on the perceived rate of a 10 Hz flicker or drift (an underestimation and an overestimation, respectively) (Ayhan et al., 2009; Johnston et al., 2006). Our ability to judge the duration of a dynamic stimulus has been shown to be influenced by its temporal frequency (Kanai et al., 2006) or speed (Kaneko & Murakami, 2009). Stimuli that change at a higher rate are perceived as lasting longer than static stimuli or stimuli with a lower rate although this effect saturates for temporal frequencies greater than around 6 Hz. Therefore, when we measured the effect of temporal

frequency adaptation on apparent duration, we first had to make sure that we minimized the effect of adaptation on the perceived rate of our stimuli. In order to do so, in Experiment 1, we measured apparent temporal frequency after adapting to frequencies ranging from 3 to 18 Hz. Once we determined the apparent temporal frequency of the stimulus displayed in the adapted position, we could then use this estimate to match the apparent temporal frequency of the two tests when we measured apparent duration (Experiment 2).

Methods

In the adaptation phase, participants were exposed to a horizontally oriented eccentric adaptor that drifted upward initially for 30 s with 8-s top-ups. The temporal frequency of the adaptor was 3, 8, 13, or 18 Hz in different sessions. After a blank interval of 500 ms, two tests (also horizontally oriented) were sequentially displayed (600 ms separated by a 500-ms blank interval), one in the adapted position (the standard stimulus at the fixed adaptor temporal frequency) and the other on the opposite side of the monitor (the comparison stimulus, which varied in temporal frequency across trials in seven steps in order to generate a psychometric function). Both tests drifted in opposite directions relative to each other. Across trials, we

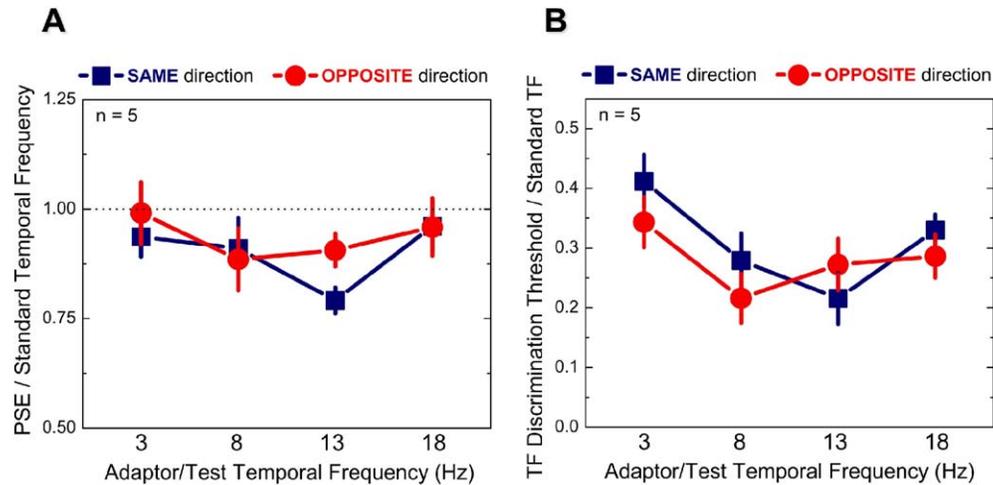


Figure 2. Effect of motion direction on apparent temporal frequency and discrimination thresholds. (A) Mean perceived temporal frequency (calculated as the 50% point on the psychometric function, PSE, divided by the actual temporal frequency, indicated by the dashed line) across five subjects for four temporal frequencies and two directions of motion (*same* indicates that adaptor and standard drifted in the same direction and *opposite* that they drifted in opposite directions). Error bars indicate ± 1 SEM. (B) Average discrimination thresholds (defined as the difference between the 50% and 84% points on the psychometric function/the stimulus temporal frequency) for the same subjects and conditions as in 2A. Error bars indicate ± 1 SEM.

randomly varied the presentation order of the tests and, more importantly, the congruency between the adaptor's direction of motion and that of the standard stimulus that was displayed in the same spatial location as the adaptor. We interleaved trials in which they had the same direction (both moving upward) with trials in which they moved in opposite directions (the adaptor upward and the standard downward). Participants were asked to pay attention to their relative temporal frequency and report which test moved at a higher rate by pressing a button on a computer keyboard. The point of subjective equality (PSE) provided a measure of perceived temporal frequency. The discrimination threshold was defined as the spread of the error distribution σ . The value of σ is equivalent to the difference in stimulus level corresponding to the 50% and 84% points on the psychometric function.

Results

Figure 2 shows the main results for Experiment 1. The effects of adaptation on perceived temporal frequency and temporal frequency discriminability are presented as averages across five subjects. Because we used a wide range of temporal frequencies, we transformed the data in order to explore and compare the effects of adapting to the same or to the opposite direction of motion on apparent temporal frequency and discriminability. We divided the PSEs by the corresponding standard temporal frequency. The values we obtained described the proportion of temporal frequency change relative to the standard temporal

frequency: Values bigger than one indicate overestimation, values smaller than one underestimation, whereas one indicates no change in perceived temporal frequency (Figure 2A). The discrimination thresholds were divided by the correspondent standard temporal frequencies to give Weber fractions (Figure 2B).

Although a mild underestimation of the standard temporal frequency can be observed, the difference between perceived and actual temporal frequency (investigated with one-sample t tests on the ratios against 1) was significant for only one of the eight tested conditions, 13 Hz *same* direction, $t(4) = -7.051$, $p < 0.005$. More generally, repeated measures ANOVA revealed no significant main effect of temporal frequency or motion direction. The interaction between these two factors was also not significant. Moreover, perceived temporal frequency between the *same* and *opposite* directions did not differ significantly at any of the tested frequencies (as revealed by paired-sample t tests). For frequency discrimination thresholds (Weber fractions, Figure 2B), a significant main effect was observed for temporal frequency, $F(3, 12) = 5.905$, $p = 0.01$, but not for motion direction. Discriminability was clearly lower for 3 Hz; it then increased for 8 Hz, remained similar at 13 Hz, and decreased again at 18 Hz, a significant quadratic trend, $F(1, 4) = 26.66$, $p < 0.01$. The interaction between temporal frequency and motion direction was also significant, $F(3, 12) = 4.736$, $p < 0.05$, with the *same* direction condition showing lower thresholds than the *opposite* direction condition at 3, 8, and 18 Hz and with the opposite pattern observable at 13 Hz. Paired-sample t tests revealed a

significant difference between the *same* and *opposite* conditions only at 13 and 18 Hz (both $p < 0.05$).

Experiment 2: Effect of unidirectional motion adaptation on perceived duration

Johnston et al. (2006) showed that a substantial duration compression for a 10 Hz drifting pattern followed adaptation to a 20 Hz adaptor but not for a 5 Hz adaptor and that the effect was still observable when the adaptor was rotated 90° relative to the tests. However, Curran and Benton (2012) reported a direction-specific effect of adaptation to motion on apparent duration for random dots moving at 3°/s: Compression occurred when the adaptor and the test displayed in the adapted position moved in the same direction but not when they moved in opposite directions. In Experiment 2, we aimed to investigate whether this direction dependency still held at high temporal frequencies when the duration compression after adaptation was originally reported to be maximal.

Methods

The paradigm used in Experiment 2 was identical to that in Experiment 1 with the following exceptions. The temporal frequency estimates obtained in Experiment 1 were used in the duration task to minimize the differences in apparent temporal frequency between the two tests. In fact, adaptor and standard had the same temporal frequency (3, 8, 13, or 18 Hz) whereas the temporal frequency of the comparison was adjusted to match the apparent frequency of the standard as determined individually in Experiment 1. We varied the duration of the comparison across trials (also in seven steps) whereas the standard had a fixed duration (600 ms). Participants had to report which of the tests appeared to last longer. In this case, the PSE provided a measure of perceived duration.

Results

Although in Experiment 1 we did not observe any substantial difference in apparent temporal frequency between the two tested directions of motion, we nevertheless used the temporal frequency estimates obtained individually to match the perceived temporal frequency of the two tests after adaptation in the perceived duration task. The temporal frequency of the comparison stimulus (displayed in an unadapted

position) was varied to minimize the adaptation-induced perceptual differences with the standard. In Experiment 2, we did not have to transform the data as the standard duration was the same (600 ms) for all the tested temporal frequencies. Generally, adaptation induced a compression of apparent duration for all the tested conditions (Figure 3A). However, the amount of compression depended on the temporal frequency of the adaptor and the standard, ANOVA repeated measures, main effect for temporal frequency, $F(3, 12) = 3.912$, $p < 0.05$. In particular, the duration underestimation became more substantial at higher temporal frequencies. At 3 Hz, the compression was in the range ~80–200 ms whereas at 18 Hz it was in the range ~180–300 ms. A significant main effect was also present for the direction of motion, $F(1, 4) = 12.773$, $p < 0.05$. Duration compression was stronger when the adaptor and standard drifted in the same direction (range ~200–300 ms) relative to when they moved in opposite directions (range ~80–180 ms). The interaction between temporal frequency and direction of motion did not reach statistical significance. However, paired-sample t tests conducted to investigate the comparisons between the *same* and *opposite* directions for each temporal frequency independently revealed a statistically significant difference only at 3 Hz, $t(4) = -4.071$, $p < 0.05$, and at 8 Hz, $t(4) = -5.156$, $p < 0.01$. At 13 Hz, $t(4) = -2.497$, $p = 0.067$, *partial eta squared* = 0.609, and at 18 Hz, $t(4) = -1.878$, $p = 0.134$, *partial eta squared* = 0.469, the difference was too small to reach statistical significance. As in Curran and Benton (2012), the difference between perceived duration and 600 ms at 3 Hz (3°/s) was statistically significant only when the standard drifted in the same direction as the comparison, one-sample t test, $t(4) = -9.188$, $p = 0.001$. However, for all the other tested frequencies, apparent duration was lower than 600 ms for both the *same* and *opposite* directions (one-sample t tests, all $p < 0.05$). No significant differences between direction conditions or across temporal frequencies were observed for the discrimination thresholds (Figure 3B). For this reason, we did not report the discrimination thresholds for Experiment 3.

Experiment 3: Direction tuning of adaption-induced duration compression

We showed in Experiment 2 that the effect of direction-specific adaptation was different at high relative to low temporal frequencies. Replicating the results of Curran and Benton (2012), at 3°/s, we observed duration compression only when the adaptor

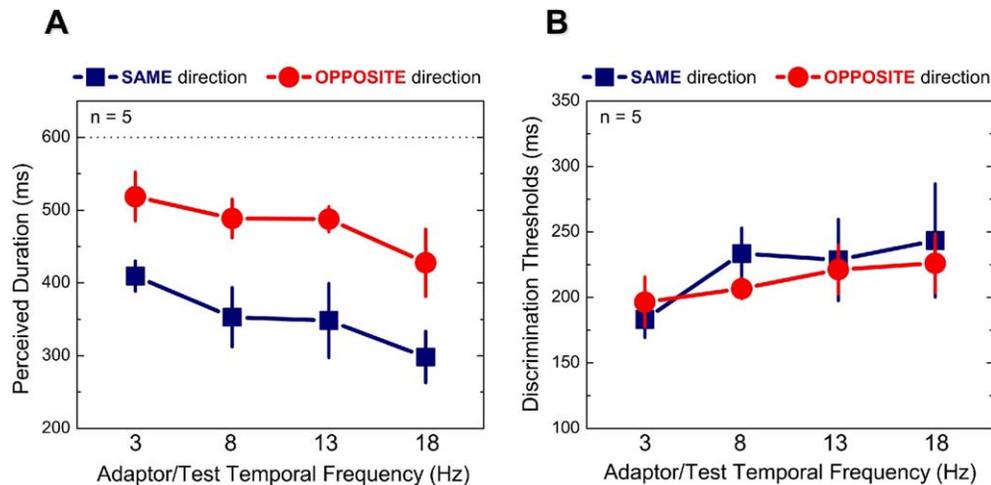


Figure 3. Effect of motion direction on apparent duration and discrimination thresholds. (A) Duration estimates (PSE) averaged across five subjects for five temporal frequencies and two directions of motion (different symbols and colors). The dashed line represents the standard duration. Error bars indicate ± 1 SEM. (B) Mean discrimination thresholds for the same subjects and conditions as in 3A.

and standard test drifted in the same direction. However, at higher speeds, adapting to the opposite direction of motion also induced substantial reduction in apparent duration, suggesting the existence of two components: one sensitive to motion direction, which induced compression at both high and low temporal frequencies, and the other, more direction-independent, which compressed apparent duration preferentially at high temporal frequencies. In order to further investigate this hypothesis, in Experiment 3, we measured the direction tuning of adaptation-induced duration compression by changing the orientation of the adaptor relative to the tests.

Methods

The test phase of the direction-tuning experiment was identical to that of Experiment 2. In the adaptation phase, we varied the orientation (and, consequently, the direction of motion) of the adaptor, in different sessions, from -90° to $+90^\circ$ relative to the orientation of the test stimuli (which were horizontally oriented). We measured perceived duration at 3 and 18 Hz. A baseline condition with no adaptation phase was also run.

Results

In Experiment 3, we tested our subjects at the lowest (3 Hz) and highest (18 Hz) temporal frequencies used in the previous experiments as they showed distinctively different compression patterns. The orientation of the adaptor varied between -90° and $+90^\circ$ relative to the standard orientation in five steps (Figure 4, 0° corresponds to the same orientation as the standard). A

baseline condition without any adaptation was also run. In Figure 4, we plotted the duration change, defined as the difference between the adaptation conditions and the baseline, as a function of the adaptor orientation. Negative values corresponded to apparent duration compression, positive values to apparent duration expansion, and zero corresponded to no difference between adaptation and baseline conditions.

Manipulating the relative orientation of adaptor and standard had an effect on duration estimates as

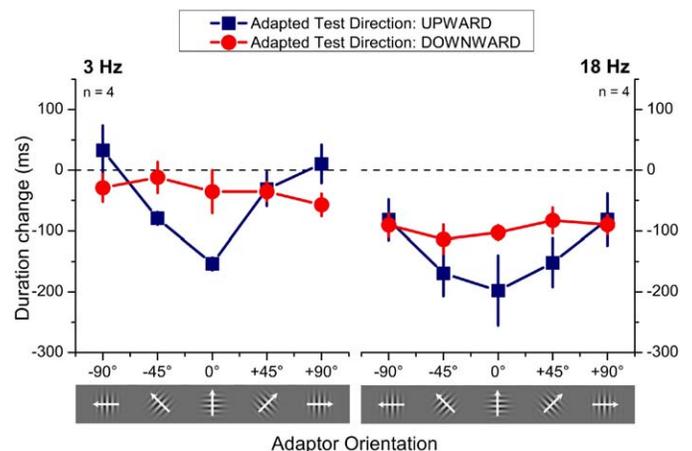


Figure 4. Direction tuning of the adaptation-induced duration compression. Duration change (expressed as the difference between the PSE obtained in the adaptation conditions and that obtained in the baseline, no-adaptation condition) averaged across three subjects for two temporal frequencies and two directions of motion (different symbols and colors). Dashed line represents no difference between baseline and adaptation conditions. The Gabor stimuli at the bottom indicate the orientation and drifting direction of the adaptor in the different conditions. The error bars indicate ± 1 SEM.

revealed by ANOVA repeated measures, main effect of orientation, $F(4, 12) = 14.807$, $p < 0.001$, and this effect depended on the direction of motion of the standard stimulus, interaction orientation \times direction, $F(4, 12) = 8.518$, $p < 0.005$. Also, the amount of duration compression after adaptation is significantly stronger at 18 Hz than at 3 Hz, main effect of temporal frequency, $F(1, 3) = 17.018$, $p < 0.05$, as can be noticed by the downward shift of both curves in Figure 4. As in the first duration experiment, when the adaptor and standard had the same orientation (0° condition) and drifted in the opposite direction (adaptor upward, standard downward, red circles in Figure 4), a significant duration compression is observable at 18 Hz, one-sample t test against 0, $t(3) = -18.666$, $p < 0.001$, but not at 3 Hz. At 3 Hz, as the difference between the adaptor and standard orientations becomes more pronounced, the duration compression does not increase for the *downward* standard direction (none of the one-sample t tests reaches statistical significance). However, at 18 Hz, the compression for the same condition (*downward*) seemed to be fairly constant across adaptor orientations (one-sample t tests revealed statistically significant differences from 0 for all the tested orientations; all $p < 0.05$). As far as the *upward* standard direction is concerned (Figure 4, blue squares), at both 3 and 18 Hz the compression was maximal for the condition in which the adaptor and standard had the same orientation and drifted in the same direction (0°), and then it progressively decreased as the adaptor was rotated away from the standard orientation. At 3 Hz, only -45° and 0° were significantly different from 0 whereas at 18 Hz compression for the -45° , 0° , and $+45^\circ$ adaptors were statistically significant (all $p < 0.05$). We conducted four separate one-way ANOVAs to verify the existence of a quadratic trend for the two directions of motions separately at both temporal frequencies. For the *upward* direction of motion, a quadratic trend was found to be significant both at 3 Hz, $F(1, 15) = 24.885$, $p < 0.001$, and at 18 Hz, $F(1, 15) = 5.906$, $p < 0.05$. However, no quadratic trend emerged for the *downward* direction for either temporal frequency.

Discussion

We investigated the effect of direction-specific adaptation on perceived temporal frequency and apparent duration of visual intervals over a wide range of temporal frequencies (3–18 Hz) for a 600 ms standard duration. We found that:

- A mild temporal frequency underestimation followed unidirectional adaptation for all the tested

frequencies regardless of whether the adaptor and test drifted in the same or opposite direction.

- Temporal frequency discrimination thresholds were affected by the adaptor's (and the standard's) temporal frequency: Precision for intermediate frequencies was higher than for high and low frequencies. The effect depended on motion direction. However, motion direction per se did not differentially affect discrimination thresholds.
- As in Curran and Benton (2012), at 3 Hz ($3^\circ/\text{s}$) duration compression (after minimizing changes in perceived temporal frequency between the two tests) followed adaptation only when the adaptor drifted in the same direction as the standard (displayed in the adapted position).
- For higher temporal frequencies (≥ 8 Hz), the amount of compression observed after adaptation to the opposite motion direction also became significantly different from zero.
- The magnitude of compression was larger after adapting to the same rather than the opposite motion direction only for the two lowest temporal frequencies we tested (3 and 8 Hz).
- No substantial difference in duration discriminability was observed either across temporal frequencies or across motion directions.
- The compressive effect of adaptation on apparent duration was maximal when the adaptor and standard had the same orientation and direction of motion and then decreased as we increased the difference in orientation between the two, both at 3 and 18 Hz.
- When the adaptor and standard drifted in opposite directions (but with the same orientation), compression was observed at 18 Hz but not at 3 Hz. This pattern remained constant when the orientation of the adaptor was rotated away from that of the standard both at 3 Hz and at 18 Hz.

Adaptation-induced duration compression has been shown to be orientation-independent (Johnston et al., 2006) and to be very tightly tuned to the adapted location (Ayhan et al., 2009) and does not show interocular transfer (Bruno et al., 2010). Furthermore, compression also followed adaptation to a temporal frequency (60 Hz) that exceeded the flicker fusion threshold (Johnston et al., 2008). Taken together, all these results point to an early, probably precortical, locus in the visual system at which adaptation has its effect on time perception. However, using RDKs, Curran and Benton (2012) found that adapting to $3^\circ/\text{s}$ translational motion reduced the apparent duration of an interval containing the same type of motion with the same speed only when the adaptor and the test displayed in the adapted position moved in the same direction, implying that adaptation takes place at a cortical level at which we can find direction-selective

cells. The results of the present study go some way toward a resolution of this apparent inconsistency.

We were able to replicate Curran and Benton's (2012) result at 3 Hz ($3^\circ/\text{s}$) using drifting sinusoidal gratings. In fact, after matching the two tests for apparent temporal frequency, duration estimates revealed a significant compression only for the condition in which both adaptor and standard (the adapted test) were drifting in the same direction: upward (Figure 3A). Johnston et al. (2006) did not find a substantial reduction in the amount of duration compression after adaptation when they rotated the adaptor 90° relative to the tests. Also, in their study, substantial compression was only observed after a 20 Hz adaptation but not after adapting to 5 Hz. Curran and Benton suggested that "...sub-second modality-specific clocks [...] are influenced by activity at multiple levels of the relevant processing pathway" (p. 256). The results presented in Figure 4 seem to support this view. Experiment 3 provided evidence for the existence of two components with different direction tuning and compression profiles at low and high temporal frequencies. When the standard drifted upward, tight tuning was found at both 3 and 18 Hz: Maximum compression was observed when adaptor and standard drifted in the same direction (0° , Figure 4) whereas compression progressively decreased when the adaptor was rotated away. However, when the standard drifted downward, the amount of duration change observed after adaptation did not depend on the adaptor orientation (and, therefore, on its direction), but it did depend on temporal frequency. At 3 Hz, the amount of compression was negligible across orientation whereas at 18 Hz all adaptor orientations induced significant duration reduction. Curran and Benton focus on the effect of direction-selective adaptation. However, our previous evidence showing that compression also followed adaptation to nondirectional stimuli, specifically flickering Gaussian blobs (Johnston et al., 2006), indicates a significant role for nondirectional adaptation.

A few differences between the two paradigms should be considered. First, in Curran and Benton (2012) and in our duration experiment, adaptor and standard had the same speed. In Johnston et al. (2006), the tests always drifted or flickered at 10 Hz whereas the temporal frequency of the adaptor changed in different conditions (5, 10, or 20 Hz). Note that apparent duration compression was reported for adaptors and tests that had the same speeds but at the higher temporal frequency of 10 Hz. In Ayhan, Bruno, Nishida, and Johnston (2011), we found duration compression for 7 Hz tests and 5 Hz and 10 Hz interleaved adaptors. Second, in Curran and Benton's experiment and in our duration experiment (Figure 3), participants adapted to unidirectional motion whereas

in Johnston et al. the adaptor changed direction every 250 ms "...to avoid direction-specific motion adaptation" (p. 477). It is not clear to what extent the implicit presence of a direction motion aftereffect in the direction of the test pattern might account for the direction-specific duration effect. It is unlikely the apparent slowing of the test pattern might have had a direct effect as we controlled for the speed of the test. Finally, as previously reported, the type of stimuli used was different: RDKs in Curran and Benton, drifting gratings or flickering Gaussian blobs in Johnston et al. RDKs are broadband stimuli both spatially and temporally, and so they will include a broad range of temporal frequencies. In the present study, we also used drifting gratings, but in other respects, our paradigm is more similar to Curran and Benton.

We showed that when we increased the adapting temporal frequency, we also observed duration compression for the condition in which the adaptor and standard drifted in opposite directions (Experiment 2). This result seems to be in line with a number of studies suggesting different mechanisms for duration perception at low and high temporal frequencies. The effect of contrast context on apparent duration also depends on the temporal frequency of the stimuli. Duration compression in a high-contrast context was observed only for temporal frequencies higher than 5 Hz (Bruno & Johnston, 2010).

Curran and Benton (2012) observed duration compression after adaptation to global motion (but not after adaptation to transparent motion), implying that this kind of adaptation might take place in the human homologue of area MT or later. Neurophysiological recordings in direction-selective cells in V1 in the monkey have shown a larger decrease in responsiveness after adaptation to the optimal direction than that observed after adapting to the opposite (antipreferred) direction when the adaptor and test drifted at the same rate (Kohn & Movshon, 2004). However, Kohn and Movshon also found that adaptation has different effects in areas MT and V1. In MT, a larger decrease in cell responsiveness is observed for adaptation to directions nearby the preferred one as compared to adaptation in the preferred direction. Although it has to be noted that Kohn and Movshon's observations are from single-cell recordings whereas the adaptation-induced effects described in this study are likely to result from neuronal population activity. Similarly, in the speed domain, Krekelberg, van Wezel, and Albright (2006) found that in area MT of the monkey adaptation induced a larger reduction in responsiveness when the adapted speed was different from the preferred speed. The link between responsiveness and perceived duration is not clear; however, if there is a dependency, one would predict stronger duration

compression after adapting to nearby directions rather than to the preferred one.

It is traditionally assumed that orientation and direction selectivity emerge in the primary visual cortex. However, neurons that show some degree of selectivity for orientation or direction (or sometimes both) have been found in the lateral geniculate nucleus (LGN) of the mouse (Marshel, Kaye, Nauhaus, & Callaway, 2012; Piscopo, El-Danaf, Huberman, & Niell, 2013) and the cat (Shou & Leventhal, 1989) and also in the LGN of primates (Lee, Creutzfeldt, & Elepfandt, 1979; E. L. Smith, Chino, Ridder, Kitagawa, & Langston, 1990; Xu, Ichida, Shostak, Bonds, & Casagrande, 2002). In particular, two subgroups of cells belonging to the koniocellular pathway have been identified and studied in the LGN of the marmoset monkey in relation to their orientation and direction response biases. The K-o (koniocellular-orientation) neurons showed orientation selectivity comparable to that observed in V1 (Cheong, Tailby, Solomon, & Martin, 2013). The K-bon (koniocellular-blue-on) cells selectively responded to a preferred motion direction for achromatic gratings drifting at ~4–5 Hz (Tailby et al., 2010). It is not clear what function these cells might have. According to the authors, it is unlikely that they contribute to motion extraction as their direction selectivity varies with stimulus chromaticity, spatial frequency, and temporal frequency. A very recent study employed functional MRI and multivariate pattern analysis to study orientation selectivity in the human LGN for spiral and linear gratings (Ling, Pratte, & Tong, 2013). They found that stimulus orientation could be reliably decoded from the recorded LGN activity. It is also possible that cortical feedback from V1 plays a role in all these types of orientation and direction selectivities (Sillito, Cudeiro, & Murphy, 1993; Wang, Jones, Andolina, Salt, & Sillito, 2006).

The spatial tuning of the duration compression that follows high temporal–frequency adaptation was shown to be very tightly tuned to the adaptor location (Ayhan et al., 2009), arguing for a precortical locus for this effect to occur as the receptive fields are much smaller than in the cortex. An analysis of the differences in the spatial specificity of the two components of the adaptation-induced reduction in apparent duration highlighted in this study could potentially help disambiguate at which stage in the visual pathway they operate. Our present results cannot shed much light on this particular issue as adaptor and adapted test were always in the same spatial location. Further experiments are needed to investigate the effects of adapting to the same or opposite motion direction on spatial tuning.

We proposed elsewhere (Johnston, 2010) that duration compression following temporal frequency adaptation might be caused by changes in the temporal

impulse response function. We hypothesized that in order to determine the duration of a visual stimulus our brain makes a prediction (carried by a band-pass signal) about the world's appearance forward in time, and then it continuously compares this prediction with a low-pass signal carrying the current world's appearance. When the two representations match, we know that a duration has passed, a tick is stored in an accumulator-type of mechanism, and the prediction is reset. If we assume that only the band-pass temporal mechanism is affected by adaptation and that, in particular, adaptation induces a phase-advance in the signal (Ibbotson, 2005), then the prediction would be shifted further forward in time, and the match would be delayed. Therefore, there would be fewer ticks in the accumulator, indicating duration compression. As we previously noted, duration compression after adaptation was observed for nondirectional stimuli, like flickering Gaussian blobs (Johnston et al., 2006; Johnston et al., 2008). Whether direction-specific adaptation might differentially alter temporal tuning of band-pass mechanisms remains open, and it certainly requires further investigation.

In conclusion, we provided evidence for the existence of two components of the mechanism that underlies adaptation-induced duration compression. One component, likely to be cortical or operating in the LGN through cortical feedback, is direction-selective and compresses apparent duration both at high and at low temporal frequencies. The other component, likely subcortical, induces duration reduction regardless of the adapting direction at high but not at low temporal frequency.

Keywords: perceived duration, temporal frequency adaptation, motion direction specificity, psychophysics

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