The spatial tuning of adaptation-based time compression

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Temporal processing is traditionally dissociated from spatial vision. Recent evidence, however, has shown that adaptation to high temporal frequency (D. Burr, A.Tozzi, & M. C. Morrone, 2007; A. Johnston, D. H. Arnold, & S. Nishida, 2006; A. Johnston et al., 2008) induces spatially specific reductions in the apparent duration of subsecond intervals containing medium frequency drift or flicker. Here we examine the spatial tuning of these temporal adaptation effects. Our results show that duration compression is tightly tuned to the spatial location of the adaptor and can be induced by very narrow adaptors. We also demonstrate that the effects of adaptation on perceived duration are dissociable from those on apparent temporal frequency, which suggests early but separate influences of temporal frequency adaptation on time and speed perception.

Introduction

Whereas our sense of space can be traced to the orderly spatial arrangement of neurons in the retina, there is no equivalent arrangement of neurons to support our sense of time and duration. The lack of an isomorphic representation for duration shrouds the neural bases of time perception in mystery. Prevailing models of event time focus on the notion of an internal clock (Creelman, 1962; Treisman, 1963; Treisman, Faulkner, Naish, & Brogan, 1990), which assumes that timing is centralized and the same neural circuitry serves all modalities. Recent studies, however, have revealed that the apparent duration of brief intervals can be manipulated in a local region of visual space (Burr, Tozzi, & Morrone, 2007; Johnston, Arnold, & Nishida, 2006; Johnston et al., 2008). Thus, temporal processing has a spatial component. Johnston et al. (2006) showed a reduction in the apparent duration of a sub-second 10-Hz drifting grating following high temporal frequency motion adaptation. The magnitude of temporal compression is independent of the relative orientation of adaptor and test patterns, consistent with a pre-cortical

locus. Additional support for an early locus comes from evidence of apparent duration compression after adaptation to invisible flicker (Johnston et al., 2008) and the finding that intermediate high-temporal contrast intervals are apparently compressed after a 1.5-s dynamic high contrast interval (Bruno & Johnston, 2007). These manipulations are thought to modify, adapt, or suppress transient (magnocellular) mechanisms.

Although Johnston et al. (2006) demonstrated that adaptation-based reductions in apparent duration were space specific, the adapted and unadapted test regions were separated by at least a quadrant of the visual field. The extent of the spatial influence of temporal frequency adaptation remains unknown. The spatial tuning of these adaptation effects can provide a clue to the site of adaptation, since the average size of receptive fields increases systematically from the retina through the lateral geniculate nucleus (Lee, Kremers, & Yeh, 1998; Xu et al., 2001) and primary visual cortex to extrastriate areas (Smith, Singh, Williams, & Greenlee, 2001; Zeki, 1978). In the Johnston et al. (2006) study, the stimuli are viewed in the near periphery. At 5 degrees of visual eccentricity mean receptive field diameter in macaque V1 is around 0.4 degrees (Dow,

Snyder, Vautin, & Bauer, 1981; Johnston, 1989) and it increases systematically toward higher level areas of the brain such as LIP, a suggested locus of temporal distortions around the time of saccadic eye movements (Morrone, Ross, & Burr, 2005), where receptive field size reaches 12 degrees at 5 degrees of eccentricity (Blatt, Andersen, & Stoner, 1990).

Here we examine the spatial tuning functions of temporal adaptation. Since the apparent duration of a moving stimulus depends to some extent upon its temporal frequency (Kanai, Paffen, Hogendoorn, & Verstraten, 2006), we first eliminated the influence of temporal frequency adaptation on apparent temporal frequency. We then measured adaptation-induced changes in apparent duration for test patterns in the adapted and surrounding regions. We found that temporal compression is tightly tuned to the location of the adaptor. The spatial tuning of shifts in apparent temporal frequency was similar to that of adaptation-based duration compression perhaps indicating that they share common components. There was some evidence of a long-range duration expansion effect but this effect was considerably weaker than the duration compression effect. We also showed that even narrow adapting gratings could induce strong temporal compression. These results suggest that the effects of adaptation on perceived duration in the millisecond range can be attributed to levels of the visual pathway where the receptive fields of the neurons remain relatively small.

General methods

Observers

Six adults participated (one female, five males), three of which were naïve to the purpose of the experiment. Two of the authors participated in all experiments; in addition there was one naïve observer in Experiments 4 and 5 and three naïve observers in Experiment 6. Visual acuity was normal or corrected-to-normal for all subjects.

Apparatus

Observers were seated 57 cm from a 19-inch Sony Trinitron Multiscan 500PS monitor, with a refresh rate of 100 Hz, driven by a VSG 2/5 visual stimulus generator (Cambridge Research Systems). The resolution of the monitor was 800×600 pixels. At this distance, the monitor subtended 40×30 degrees.

Procedure

In all experiments, subjects were presented with a central fixation spot and an adaptor (1 cycle/deg sine grating; 50% Michelson contrast). The duration of the adaptation phase was 32 s with 8 s top-ups between trials. The direction of motion of the adaptor reversed every 1 s to avoid the build up of a directional motion after effect. After the adaptation phase, the test stimuli, drifting sinusoidal gratings with a spatial frequency of 1 cycle/deg, were displayed sequentially on the adapted (standard) and unadapted (comparison) side of the fixation point. The order of presentation of the standard and comparison was randomized from trial to trial to control for time order effects (Jamieson & Petrusic, 1975). Subjects were asked to determine which of the test stimuli drifted faster (in perceived temporal frequency experiments) or for longer (in perceived duration experiments). Details of the stimuli in each experiment can be found in the methods of the relevant section. Whereas the duration or temporal frequency of the standard stimulus was fixed across trials, the values of the comparison stimulus varied in 7 steps to generate a psychometric function indicating the percentage of trials in which the comparison was judged as longer or faster 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 or temporal frequency of the standard.

The temporal frequency shift

The apparent duration of a moving stimulus increases with temporal frequency for low to mid-range frequencies (Kanai et al., 2006). Burr et al. (2007) have reported that adaptation-induced duration compression disappears when the apparent speed of the two tests are matched. Johnston et al. (2006) had previously shown that reductions in perceived duration induced by a 20-Hz dynamic adaptor persist even after matching for perceived temporal frequency, indicating that temporal compression is not mediated by changes in apparent temporal frequency. Here, we introduce a new procedure designed to eliminate any possible influence of temporal frequency adaptation on speed judgments. We varied the duty cycle of interleaved 5 and 20 Hz adaptors to find, for each subject, a critical ratio of 5 and 20 Hz adaptation for which no change occurs in the perceived speed of a 10-Hz test pattern. 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.

Method

In Experiment 1, observers compared the temporal frequency or speed of a drifting, Gaussian windowed, sinusoidal grating against a standard following a period of

adaptation (Figure 1A). The adaptor was a vertical 1 cycle/deg grating displayed in a circular aperture (diameter 5° of visual angle) centered 5° to the right of a central fixation point. In the adaptation phase, the gratings drifted with a temporal frequency of either 5 or 20 Hz. The two adaptors were interleaved on the basis of one of 5 different duty cycles: 0% 5 Hz–100% 20 Hz, 25% 5 Hz–75% 20 Hz, 50% 5 Hz–50% 20 Hz, 75% 5 Hz–25% 20 Hz, 100% 5 Hz–0% 20 Hz. The duty cycle determined the proportion of time for which the two adapting temporal frequencies were displayed. Each cycle typically lasted 4 s during the initial adaptation and 2 s during the top-ups. After the adaptation phase, the test stimuli (sinusoidal gratings with a spatial frequency of 1 cycle/deg drifting for 600 ms) were displayed sequentially on the adapted and unadapted side of the fixation point. Since the spatial frequency was always 1 cycle/deg, the speed and drift frequency had the same numerical value. 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 (10 Hz). The temporal frequency of the comparison stimulus, which was displayed in an unadapted spatial position (centered 5° to left of the central fixation point), was varied between 2 and 18 Hz in 7 steps (2, 4.67, 7.33, 10, 12.67, 15.33, and 18 Hz). The luminance contrast of test stimuli was 100% (Michelson), and both were presented in a Gaussian temporal window (amplitude 1.0; Standard: standard deviation = 100 ms; Comparison: standard deviation = comparison duration/6 ms). Observers reported which of the tests appeared to drift faster.

Results

Since the adaptors reversed direction at regular intervals, we were able to adapt temporal channels without generating a directional motion aftereffect. For each subject, the duty cycle of the two interleaved adaptors (5 and 20 Hz) that had no effect on the perceived temporal frequency of a subsequently displayed drifting stimulus can be read from Figure 1B. 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 20-Hz adaptors. The straight lines are the linear fits to these data points for each subject. For two subjects, the critical proportion of 5-Hz adaptation was around 0.25, for one subject it was around 0.66 and for the remaining three it was around 0.50.
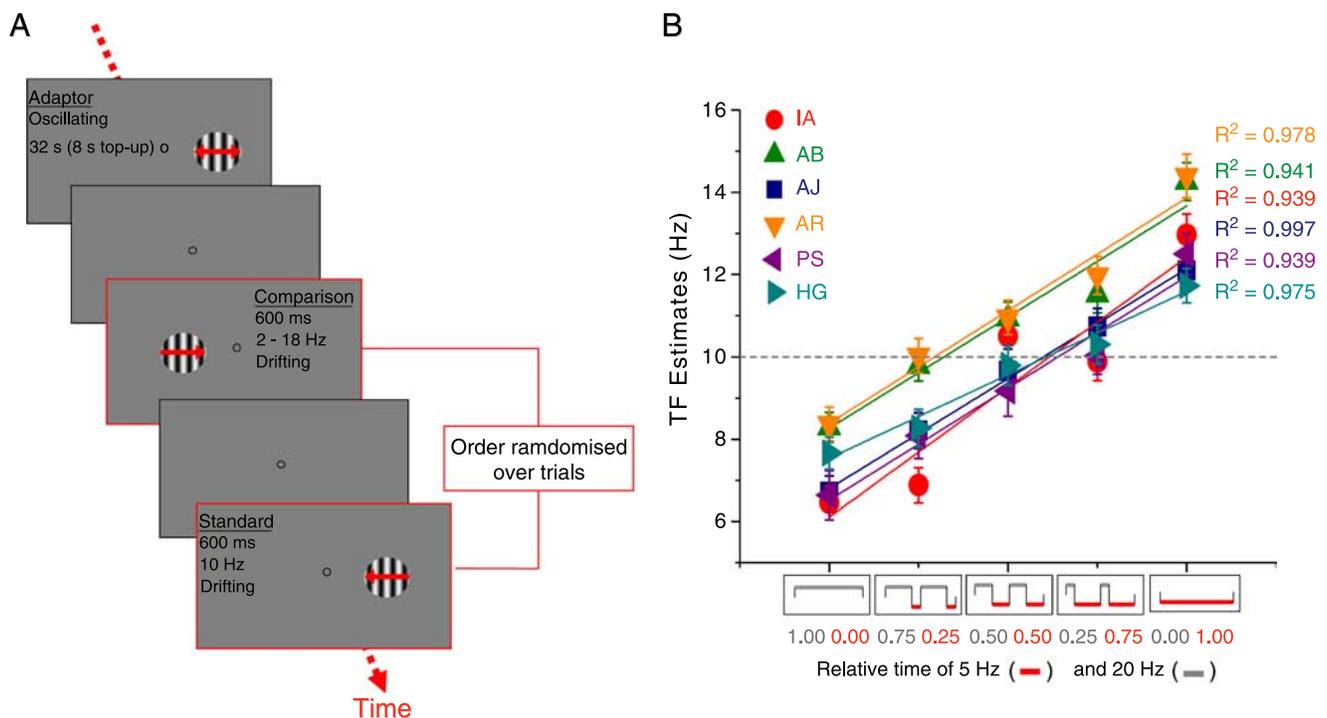

Figure 1. Eliminating the influence of temporal frequency adaptation on speed judgments. (A) Time course of the binary choice experiments in which subjects made a speed judgment between two vertically oriented drifting gratings displayed in succession following adaptation to an oscillating grating. (B) Results of the temporal frequency experiment for 6 different subjects (three authors and three naïves). 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 20-Hz adaptors. The straight lines are the linear fit of these data points for each subject. The adjusted coefficient of determination R^2 is reported for each subject separately. Error bars show ± 1 *SE*. Each point is derived from 140 trials.

Spatial tuning of duration compression

Local adaptation to high temporal frequency (20 Hz) oscillatory motion or flicker reduces the apparent duration of a subsequently displayed 10 Hz dynamic stimulus (Johnston et al., 2006) in the same region of the visual field but the spatial tuning of this temporal aftereffect is unknown. In our earlier study, both the adaptor and test had a diameter of 9° and their locations differed by approximately 18° (across hemispheres) or approximately 13° (within a hemisphere). Here we designed our stimuli to cover a range of separations and sizes of adaptor and test. The greatest separation was 11°, which was close to the previously used separation and the largest aperture used was 5°, which was around half the size of the original aperture. To study spatial specificity, we varied the spatial separation of adaptor and test. In one experiment, we adapted along the horizontal midline and then positioned the standard above and below to measure a spatial tuning function. In the other experiments, we presented the test patterns on the horizontal midline and positioned the adaptor above and below. These procedures generated similar spatial tuning functions.

Method

The temporal sequence of the adaptor and test patterns is shown in Figure 2A. In Experiment 2, subjects were presented with a central fixation spot and the adaptor, which was always displayed at the same position (5° to right of a central fixation point) in a 5° diameter circular patch. After the adaptation phase, the test stimuli (sinusoidal gratings with a spatial frequency of 1 cycle/deg) drifting with a temporal frequency of 10 Hz were displayed sequentially on the adapted and unadapted side of the fixation point. The standard appeared at the same position, half overlapping (2.5°) or completely (5°) above and below the adaptation location, while the comparison appeared at the vertically symmetrical position on the unadapted side. The duration of the standard stimulus was fixed across trials (600 ms). The duration of the comparison stimulus was varied between 300 and 1200 ms in 7 steps (300, 400, 500, 600, 800, 1000, and 1200 ms). The luminance contrast of both test stimuli was 100%. Observers reported which of the tests appeared to last longer. We compared the effects of adaptation against a control condition in which observers made temporal judgments between comparison and standard drifting gratings in the absence of adaptation. In this experiment, trials for the various positions of the standard were blocked.

The procedure in the third and fourth experiment was similar to the procedure we used in Experiment 2 except that the adaptor and the test stimuli were sinusoidal gratings displayed within different sized rectangular or square patches, 3.7° × 5° for the medium stimulus and 5° × 5° for the larger stimulus. In this case there was no physical overlap between the standard and the adaptor. Observers also made temporal judgments between comparison and standard drifting gratings in the absence of adaptation. Since the standard location was fixed in different adaptor locations, one baseline value was applied to all conditions for each subject.

In the fifth experiment we used narrow windows (0.75° × 5°). The procedure was similar to that used in the previous experiments except that in half of the trials the adaptor was displayed on the right of the fixation point and in half of the trials it was displayed to the left of the fixation point. This refinement allowed us to eliminate any possible hemispheric differences in duration judgments.

Figure 2. Effects of temporal frequency adaptation on duration judgments as a function of the vertical displacement of the standard or adaptor in the absence of temporal frequency shifts. The shape and the size of the stimuli relative to the monitor height are shown on the upper right corner of each graph. Filled red lines indicate the position of the adaptor and dotted lines indicate the position of the test patterns. (A) Time course of the binary choice experiments in which subjects made a duration judgment between two vertically oriented drifting gratings displayed in succession following adaptation to an oscillating grating. (B) Spatial tuning functions for temporal compression for two subjects. Apparent durations relative to the baseline conditions are plotted as a function of the vertical displacement of the standard grating relative to the position of the adaptor. Results are obtained following an adaptation phase consisted of the combination of 5 and 20 Hz that elicited no change in temporal frequency (Figure 1B). Error bars show ±1 SE. Each point is derived from 140 adaptation trials and 140 control trials. (C) Spatial tuning functions for medium scale with the stimuli dimensions of 3.7° × 5° for 2 subjects (2 authors; included in Figure 1B). The individual duration judgments comparative to the baseline conditions are plotted as a function of the vertical displacement of the standard grating relative to the position of the adaptor. Error bars show ±1 SE. Each point is derived from 140 adaptation trials and 140 control trials. (D) Spatial tuning functions for large scale with the stimuli dimensions of 5° × 5° for 4 subjects (3 authors and 1 naïve; included in Figure 1B). The mean duration judgment comparative to the baseline conditions is plotted as a function of the vertical displacement of the adapting field relative to the position of the standard. Error bars show ±1 SE of individuals and ±1 SE of the mean. Each point is derived from 140 adaptation trials and 140 control trials. (E) Results for narrow adaptors for 3 subjects. Mean duration judgment comparative to the baseline conditions is plotted as a function of the vertical displacement of the adapting field relative to the position of the standard. Error bars show ±1 SE of individuals and ±1 SE of the mean. Each point is derived from 140 adaptation trials and 280 control trials. (F) The narrow black line shows the Gaussian function fit to the mean data. Error bars show ±1 SE of the mean. Each point is derived from 140 adaptation trials and 280 control trials.
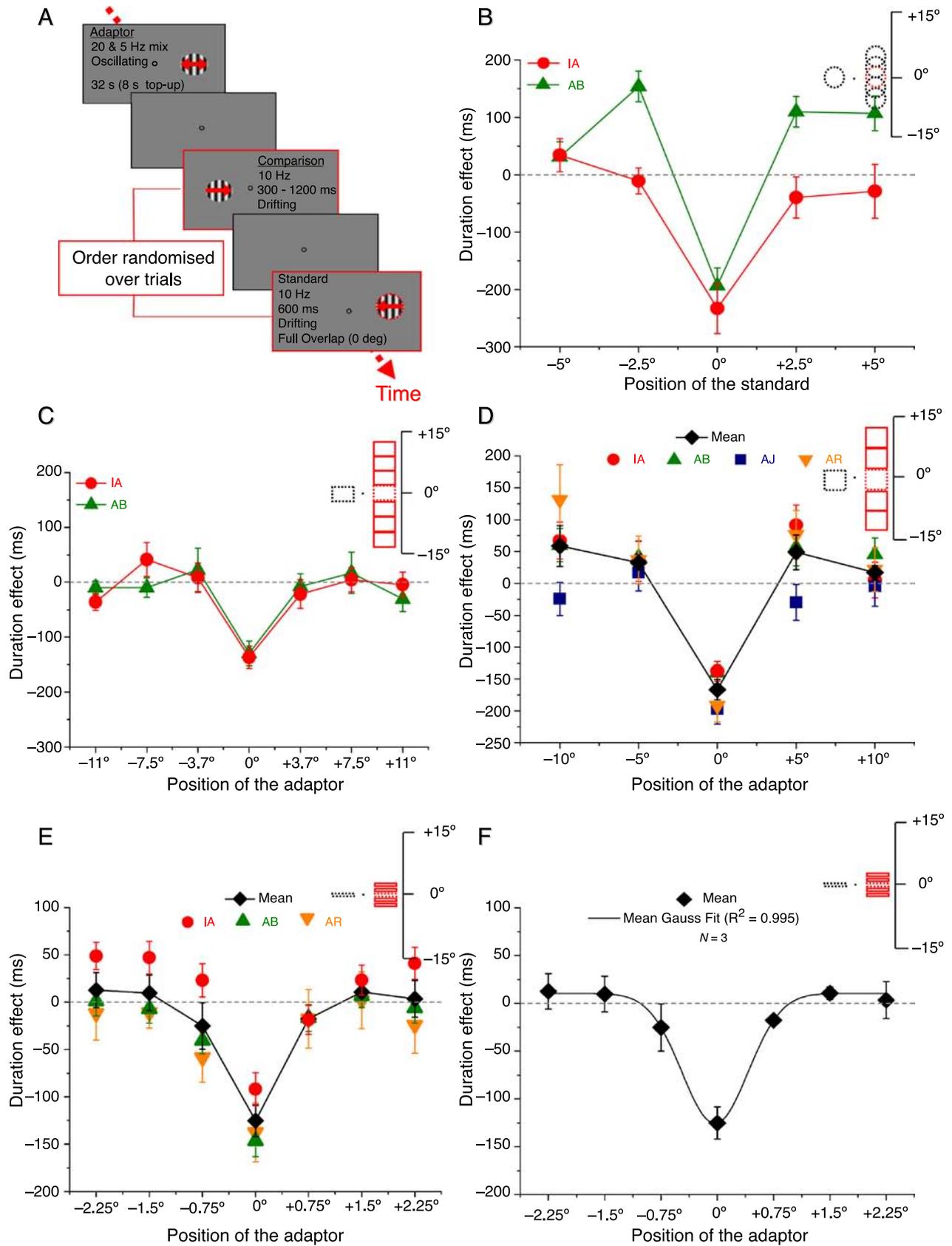
Results

In Experiments 2–4 (Figures 2B–2D), compression relative to the baseline conditions is highly spatially localized, appearing only in the full overlapping condition. In Experiment 2 (Figure 2B), the two subjects, however, differed in the direction of the effect of temporal frequency adaptation on apparent duration for the half overlap conditions. One subject AB shows evidence of temporal expansion for overlapping and one of the eccentric locations. One might have expected the magnitude of temporal compression in the half overlap condition to be somewhat less than half that in the full overlap condition. However, the data show no compression effect or expansion. There may be a number of ways adapted and non-adapted regions may combine. The presence of a lateral expansion effect (subject AB) suggests that a null result in the partial overlap condition may reflect a balance between compression in the adapted region and expansion in an adjacent unadapted region. The differences in the shape of the functions for the two subjects may reflect individual differences in this balance.

In the Experiments 3–5, we changed the location of the adaptor rather than the standard. Now the control position is the same for all adaptor positions. In this case, unlike Experiment 2, the relative shape of the function is independent of the baseline measurement. There were no partial overlap conditions. As in Experiment 2, we observed a very significant reduction in perceived duration for the full overlap position. For positions adjacent to the adaptor, apparent duration recovered sharply to approach baseline conditions. The results were qualitatively similar for the medium (Figure 2C) and large (Figure 2D) stimulus windows. Interestingly there was some evidence of an apparent duration expansion in the large-scale ($5° \times 5°$) experiment. However, this expansion effect was only observed in some conditions and some subjects. Figure 2E shows the perceived duration relative to the baseline conditions as a function of the adaptor locations for narrow ($0.75°$) windows. Analysis at this finer scale provided a better estimate of the shape and extent of the spatial tuning. The standard deviation of the best fitting Gaussian (Figure 2F) provided an estimate of the spatial extent of the spatial tuning of the duration compression effect ($SD = 0.59$ degrees of visual angle, adjusted $R^2 = 0.995$).

Taken together, the results show that temporal duration compression occurs in the absence of changes in temporal frequency or speed and is highly specific to the location of the adaptor.

Lateral expansion

There was some indication of an apparent expansion of duration at lateral spatial positions for large windows in Experiment 2. In this stimulus configuration, adaptation in a central location induced an apparent expansion in peripheral test grating duration. This configuration induced the strongest duration expansion, although this was only seen in one of our subjects (AB). There is little evidence for expansion for narrow windows. The data suggest a long-range expansive surround in combination with a short-range compressive mechanism. In Experiment 6, we attempted to investigate this lateral effect using a center-surround spatial arrangement.

Method

In this experiment, the adapting grating was displayed in a circular aperture and the test stimuli were displayed in surrounding annular patches. For the first experiment, we kept the diameter of the adaptor and the inner circle of the annuli test constant at $5°$. We changed the outer diameter of the annuli to $6°$, $7.5°$, and $9°$ in different conditions. In the second experiment, we kept the diameter of the outer circle of the annular test constant at $9°$ and adjusted the diameter of the adaptor and the inner circle of the annuli tests to $2°$, $5°$, and $8°$. The experimental procedure was similar to the procedure we used in the previous experiments. The comparison was always presented on the unadapted side and the duration of the comparison was varied (range 350–850 ms) from trial to trial to determine a psychometric function. In the baseline conditions, observers made temporal judgments in the absence of the adaptor for each size of test stimulus in different conditions. Trials for the various sizes of the tests were blocked.

Results

The results of Experiment 6 can be seen in Figures 3A and 3B. We found that while the adaptor produces a reduction in the perceived duration in narrow surrounding regions, this effect disappears when the surrounding region is wider. That the duration compression is only observed in narrow surrounding regions is consistent with the earlier experiments showing tight spatial tuning for temporal compression. The lack of compression for large annuli provides indirect evidence of a lateral expansion effect since an expansion further from the adaptor may be expected to null the compression close to the adaptor.

Spatial tuning of the temporal frequency shift

Our working hypothesis is that the time pathway and the motion pathway share some components. If this is the case, the spatial tuning of the temporal frequency shift should be similar to the spatial tuning of apparent duration
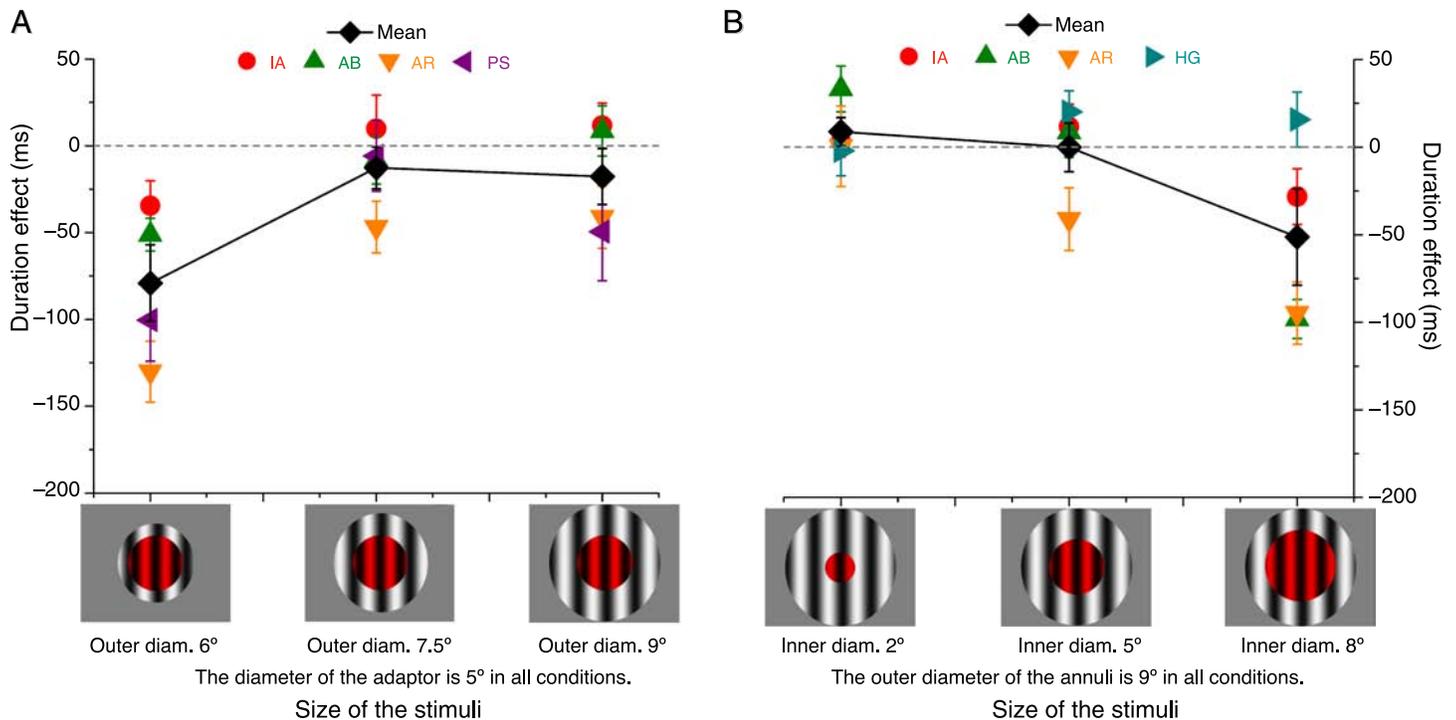
Figure 3. Effects of temporal adaptation on duration judgments in the surrounding areas as a function of the relative size of the adaptor. Colored gratings indicate the adaptor locations. (A) Results of the surround effects experiment for four subjects (2 authors and 2 naïves; included in Figure 1B). The mean duration judgments comparative to the baseline conditions are plotted as a function of the outer diameter of the surrounding area. Error bars show ±1 SE of individuals and ±1 SE of the mean. In this experiment, the diameter of the adaptor and the inner circle of the annuli are fixed at 5°. Each point is derived from 140 adaptation trials and 280 control trials. (B) Results of the surround effects experiment for four subjects (2 authors and 2 naïves; included in Figure 1B). As in Figure 3A except in this experiment, the outer diameter of the annuli is fixed at 9°. Each point is derived from 140 adaptation trials and 280 control trials.

compression. To test this, we investigated the spatial tuning of perceived temporal frequency following 5 and 20 Hz adaptation using narrow windows (0.75° × 5°).

Method

In Experiment 7, subjects compared the perceived temporal frequency of two drifting test gratings (0.75° × 5°) displayed sequentially on the adapted and unadapted side of the fixation point following an adaptation phase. In half of the trials, the adaptor was displayed on the right of the fixation point and in half of the trials it was displayed to the left of the fixation point. The temporal frequency of the standard grating was fixed across trials (10 Hz). The temporal frequency of the comparison stimulus was varied between 2 and 18 Hz in 7 steps. Observers reported which of the tests appeared to drift faster.

Results

As expected, 5-Hz adaptation induced an increase and 20-Hz adaptation induced a decrease in perceived temporal frequency when the adaptor was presented at the same location as the standard grating (Figure 4A). The spatial tuning is very similar to the tuning of duration compression (Figures 2E and 2F). For comparison, the results of the perceived temporal frequency experiment are plotted together with the Gaussian fit for the mean duration effect in Figure 4B. Similar spatial tuning of duration and temporal frequency effects following temporal frequency adaptation provides evidence that the time pathway and the motion pathway may share some components. However, given that we controlled for the perceived temporal frequency changes in duration tasks and still found changes in apparent duration, we conclude that the effects of adaptation on perceived duration are dissociable from those on temporal frequency. Adaptation can have more than one effect on temporal mechanisms, e.g., a change in sensitivity and a change in temporal tuning. We suggest that these separate adaptations selectively influence apparent temporal frequency and apparent duration respectively.

Window size

The size of the duration compression effect does not appear to depend upon window size (Figure 2). This raises
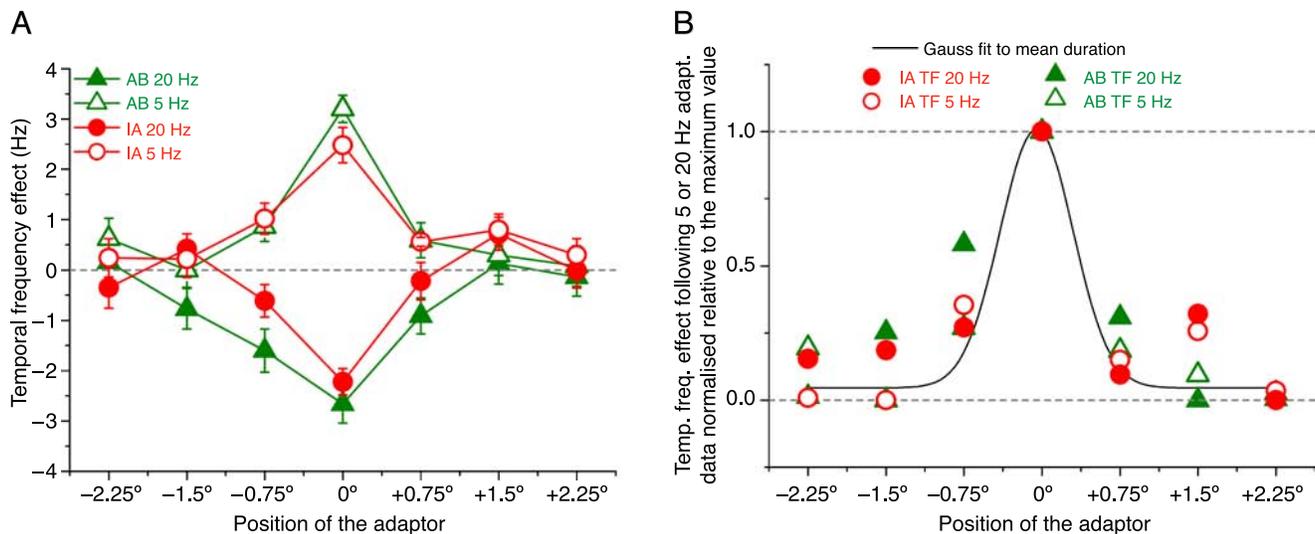
Figure 4. Effects of temporal frequency adaptation on perceived temporal frequency as a function of the vertical displacement of the adaptor relative to the location of the standard grating. (A) Perceived temporal frequency following 5- or 20-Hz adaptation. The individual temporal frequency judgments relative to baseline conditions are plotted as a function of the vertical displacement of the adapting field relative to the position of the standard. Error bars show ±1 *SE* over individuals. In this experiment, the dimensions of the stimuli and the locations of the adaptor were similar to those in Figures 2E and 2F. Each point is derived from 140 adaptation trials and 140 control trials. (B) Individual results of the perceived temporal frequency experiment replotted together with the Gaussian fit to the mean duration effect. Note that all data points are normalized relative to the maximum value.

the question of whether there is a lower spatial limit on adaptation-based temporal compression.

Method

We varied the height of the adaptor in four steps (0.05°, 0.25°, 0.50°, and 1.5°, with a constant width of 5°) and then measured the strength of the duration distortion. The duration of the standard, which was always displayed on the adapted side of the visual field, was fixed at 600 ms. The duration of the comparison, which was displayed on the unadapted side of the visual field, was varied (range 350–850 ms) from trial to trial to determine a psychometric function. As a control, observers made temporal judgments in the absence of the adaptor for each size of test stimulus in different conditions. Trials for the various heights of the adaptor and tests were blocked.

Results

As can be seen in Figure 5A, we found that the compression effect was not reduced even when the adaptors were very narrow. Indeed if we compare with the results of Experiments 3–5 for the same subjects, we can see that the size of the adaptor does not affect the strength of the duration compression across the range of window size tested (Figure 5B). The result indicates

localized adaptation is sufficient to induce adaption however small stimuli can activate large receptive fields. The spatial tuning function shown in Figures 2E and 2F provides a better estimate of the spatial extent of the influence of temporal frequency adaptation.

Discussion

Traditional brain timing models tend to dissociate temporal processing from spatial vision. Recent studies, however, have presented evidence of spatially localized time distortions in the visual domain after high temporal frequency adaptation (Burr et al., 2007; Johnston et al., 2006, 2008). Here we investigated the spatial tuning functions of temporal aftereffects during visual fixation. Our results demonstrate that:

1. Compression in the apparent duration of a dynamic stimulus is specific to the location of the adaptor and adjacent areas.
2. Even narrow adaptors can produce significant duration compression in the adapted region.
3. The width of the spatial tuning function for narrow adaptors is around 1 degree of visual angle.
4. There is some direct and some implicit evidence of duration expansion surrounding the location of the adaptor.
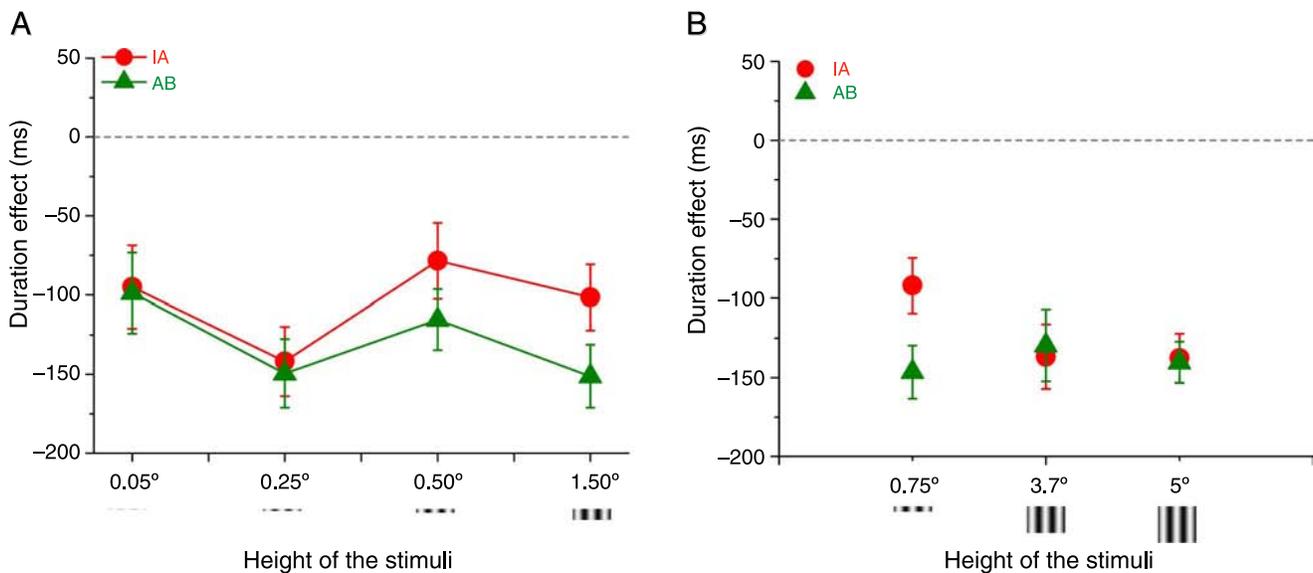
Figure 5. Compression in apparent duration following temporal adaptation as a function of the height of the adaptor. The relative dimensions of the stimuli are shown below the abscissa. (A) Results of the adaptor size experiment for two subjects (included in Figure 1B). The individual duration judgments comparative to the baseline conditions are plotted as a function of the height of the adapting area. Error bars show ±1 *SE*. Each point is derived from 140 adaptation trials and 140 control trials. (B) The results of the lateral interaction experiment in small, medium, and large scales (Experiments 3–5) are redrawn for two subjects for the condition in which the standard and the adaptor gratings fully overlap. Error bars show ±1 *SE*.

5. The effects of adaptation on perceived duration are dissociable from those on temporal frequency although the spatial tuning of these effects is similar.

The spatial specificity of the effects of temporal frequency adaptation on apparent duration argues against a supramodal centralized clock model (Creelman, 1962; Treisman, 1963; Treisman et al., 1990). Rather, the local distortions of apparent duration suggest a modality specific mechanism that shares some components with the motion pathway.

It has been suggested that time might be encoded by a population of metaneurons that are sensitive to the time course of neural processing in the brain (Buonomano & Merzenich, 1995; Eagleman et al., 2005; Karmarkar & Buonomano, 2007). This distributed neural account of timing posits the translation of a temporal code into a place code, with separate duration tuned units. An interval can then be encoded by reading out the distribution of activity over this population. The population response to a stimulus can be biased in a direction opposite to an adaptor after prolonged viewing of a stimulus that is slightly different to the test along the relevant stimulus dimension. However, rather than adapting to intervals of a particular duration, participants adapted to flicker of a particular temporal frequency. Since participants are not adapted to duration *per se*, it is not clear how the changes in perceived duration we see after temporal frequency adaptation could be explained on a duration-tuned population model. We therefore have to consider in more detail how temporal frequency adaptation alters the visual system.

The narrow spatial tuning of both the temporal frequency shift and apparent duration compression suggests an early locus in the visual pathway. The standard deviation of spatial tuning for narrow windows was 0.59 degrees at 5 degree of visual eccentricity. Closer to the mean receptive field diameter of macaque V1 at around 0.4 degrees (Dow et al., 1981; Johnston, 1989) than to higher level cortical areas such as LIP, where receptive field size reaches 12 degrees at 5 degrees of visual eccentricity (Blatt et al., 1990). Thus, the spatial tuning of duration compression is more compatible with an early than late location in the visual pathway. A possible candidate for the site of the adaptation is the magnocellular pathway through the lateral geniculate nucleus (Johnston et al., 2006, 2008). Magnocellular neurones are known to be sensitive to low spatial frequency achromatic stimuli (Benardete & Kaplan, 1999). They are also responsive to high frequency (60 Hz) adaptors, which are invisible to cortical cells (Hawken, Shapley, & Grosof, 1996) but which can still induce duration compression (Johnston et al., 2008). Solomon, Peirce, Dhruv, and Lennie (2004) have shown that magnocellular (M) cells in the LGN show slow adaptation at high temporal frequencies (45 Hz) but not at low temporal frequencies (1 Hz). M cells, but not P cells, are also subject to a fast adaptation phase referred to as contrast gain control which results in a sharpening of temporal tuning as a consequence of a loss of gain at low temporal frequencies (Shapley & Victor, 1978). Recently Bruno and Johnston (2007) have demonstrated a reduction in perceived duration for intervals following a high contrast

context relative to a low contrast context, providing evidence that reductions in perceive duration may be mediated by a compression of the temporal impulse response in M cells, in this case following contrast gain.

There is some evidence for duration expansion at locations some distance from the adaptor. This suggests that adaption can have a local effect in the region of the adaptor and an opposite but weaker effect at a distance. This spatial pattern of adaptation could explain why the compression effect is eliminated as test patterns extend beyond the spatial location of the adaptor (Experiment 6) as if the duration percept resulted from the spatial summation of a compression and expansion effect.

Changes in apparent temporal frequency after temporal frequency adaption can be dissociated from changes in apparent duration. Temporal frequency shifts are bidirectional, whereas a 10-Hz interval appears compressed after 5-, 10-, and 20-Hz adaptation (Johnston et al., 2006), a difference we exploit in the current paper. Changes in apparent duration can also occur in the absence of any change in apparent temporal frequency, as reported above. Dyslexics show normal temporal frequency shifts but do not show any duration compression after adaption to invisible flicker (Johnston et al., 2008). We therefore need to identify separate mechanisms for changes in apparent temporal frequency and changes in apparent duration. We will first consider the change in apparent frequency.

The available evidence is that there are only two or three temporal frequency channels in the human visual system (Fredericksen & Hess, 1998; Hess & Snowden, 1992; Johnston & Clifford, 1995) and each filter has a different shape as well as a different pass-band. 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. Therefore, the available evidence does not support the idea that temporal frequency is encoded in terms of the peak response of a set of identical narrow band filters. However, 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 the shift in apparent temporal frequency of a 10-Hz test pattern after high temporal frequency 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 following adaptation. An increased ratio of low to band-pass channel activity signifies a lower temporal frequency. The opposite shift arises after adaption to a low (e.g., 5 Hz) frequency.

Since changes in perceived duration can be dissociated from changes in perceived temporal frequency, a different mechanism is required to explain changes in apparent

duration. In addition to changes in sensitivity, adaptation to high temporal frequency also sharpens band-pass temporal filters (Ibbotson, 2005), which as a consequence introduces a forward shift in the band-pass response. We may use this adaptation to explain the apparent duration compression. Johnston (in press) has proposed a content-dependent clock. In this clock a forward model of the visual signal is generated from the visual input. The new visual input is then continuously compared to the prediction. When there is a match the system can tell the preset interval has elapsed, the clock ticks and the cumulated ticks are a measure of the duration of the interval. This forward prediction needs to know the rate of change of image brightness and therefore relies on band-pass differentiating temporal filters (magnocellular neurones). The current brightness signal can be provided by a low-pass channel, which does not adapt to the same degree (parvocellular neurones). After adaptation, the phase advance in the magnocellular signal shifts the prediction forward in time, increasing the time to reset and thereby producing the psychophysically observed time compression. Therefore, we propose changes in responsivity of the M cells relative to P cells explain changes in apparent temporal frequency, whereas sharpening of the M cell temporal impulse response explains apparent time compression (Johnston et al., 2006).

In summary, adaptation-based apparent duration compression was found to be tightly tuned to the location of the adaptor. For large adaptors compression extended to a small region beyond the location of the adaptor. For small adaptors the spatial extent of compression was around 1 degree. For larger adaptors, compression was eliminated and in some cases replaced by expansion, indicating a region of apparent temporal expansion beyond the duration compression zone. These local distortions in apparent duration elicited by temporal frequency adaptation in the absence of changes in perceived speed or perceived temporal frequency leads us to conclude that temporal channels in human vision mediate duration perception, as well as temporal frequency coding and motion perception.

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