

Spatially Localized Distortions of Event Time

Alan Johnston,^{1,2,3,*} Derek H. Arnold,^{1,3,5} and Shinya Nishida⁴

¹Department of Psychology

²CoMPLEX

³Institute of Cognitive Neuroscience

University College London

London WC1E 6BT

United Kingdom

⁴NTT Communication Science Laboratories

Nippon Telegraph & Telephone Corporation

Atsugi Kanagawa, 243-0198

Japan

Summary

A fundamental question about the perception of time is whether the neural mechanisms underlying temporal judgements are universal and centralized in the brain or modality specific and distributed [1–3]. Time perception has traditionally been thought to be entirely dissociated from spatial vision. Here we show that the apparent duration of a dynamic stimulus can be manipulated in a local region of visual space by adapting to oscillatory motion or flicker. This implicates spatially localized temporal mechanisms in duration perception. We do not see concomitant changes in the time of onset or offset of the test patterns, demonstrating a direct local effect on duration perception rather than an indirect effect on the time course of neural processing. The effects of adaptation on duration perception can also be dissociated from motion or flicker perception per se. Although 20 Hz adaptation reduces both the apparent temporal frequency and duration of a 10 Hz test stimulus, 5 Hz adaptation increases apparent temporal frequency but has little effect on duration perception. We conclude that there is a peripheral, spatially localized, essentially visual component involved in sensing the duration of visual events.

Results and Discussion

Adaptation-Induced Changes in Apparent Duration Are Spatially Localized

We hypothesized that the temporal scaling of visual experience and the temporal tuning properties of visual neurones [4–8] may be linked. Visual temporal mechanisms are differentiated as early as in the retina [9] and neurones in the retino-striate pathway have relatively small receptive fields—the majority of foveal V1 receptive fields cover less than half a degree of visual angle [10, 11]. If these mechanisms play a role in temporal analysis, then the effects of adapting these mechanisms

can be expected to be spatially localized. Since we know temporal channels in human vision [12–14] are subject to temporal frequency adaptation [15], we thought that temporal frequency adaptation might also influence duration perception.

We presented subjects with a central fixation spot and an adapting stimulus, placed right or left of fixation, consisting of a drifting sine grating (1 c/deg) that alternated in direction once every 2 s in order to adapt temporal channels without generating a directional motion after-effect (Figure 1A). After a period of adaptation, drifting gratings, with direction chosen at random, appeared sequentially on the adapted and unadapted sides. The order of presentation was randomized on a trial-by-trial basis. Subjects were asked to indicate which stimulus appeared to last longer. The duration of the standard stimulus, shown on the adapted side of fixation, was fixed at 600 ms. The duration of the stimulus on the unadapted side was varied systematically to generate a psychometric function, and the 50% point on the psychometric function provided an estimate of the perceived duration of the standard stimulus after adaptation. Note that since the standard and comparison gratings are presented in different spatial locations, any difference in apparent duration indicates a spatially localized adaptation effect. The perceived duration of the standard (10°/s; 10 Hz) was measured for both higher and lower adaptation temporal frequencies. We found that adaptation to a drift frequency of 20 Hz *reduced* perceived duration, whereas 5 Hz adaptation had relatively little effect (Figure 1B and Supplemental Data available with this article online).

Prior presentation of a rapid series of tones [16, 17] or a rapidly flickering visual stimulus [16, 18] has been observed to *increase* the apparent duration of temporal intervals. This phenomenon, which has been ascribed to the effect of increased arousal on the rate of a centralized universal neural clock, may appear similar to the duration aftereffect described here—but our result is a reversal of the standard finding. Also, the adapting pattern is a smoothly moving grating; therefore, it does not appear to flicker, and the crossmodal nature of the classical effect is in marked contrast to the spatial specificity of the duration aftereffect observed here. Although attention is known to increase apparent duration [19], the lack of an effect of 5 Hz adaptation shows that the duration aftereffect is not a delayed consequence of distracting attention from the adapted region.

The Duration Effect Is Not the Result of Changes in Apparent Onset or Offset

To dissociate the effects on duration perception from any manipulation of the time course of sensory processing, we separately measured the perceptual latency of the onset and offset of the standard pattern with and without adaptation. We paired either the onsets or offsets of the test with an auditory noise burst. Subjects were asked which occurred first. By varying the relative

*Correspondence: a.johnston@ucl.ac.uk

⁵Present address: School of Psychology, McElwain Building, The University of Queensland, St. Lucia, Queensland 4072, Australia.

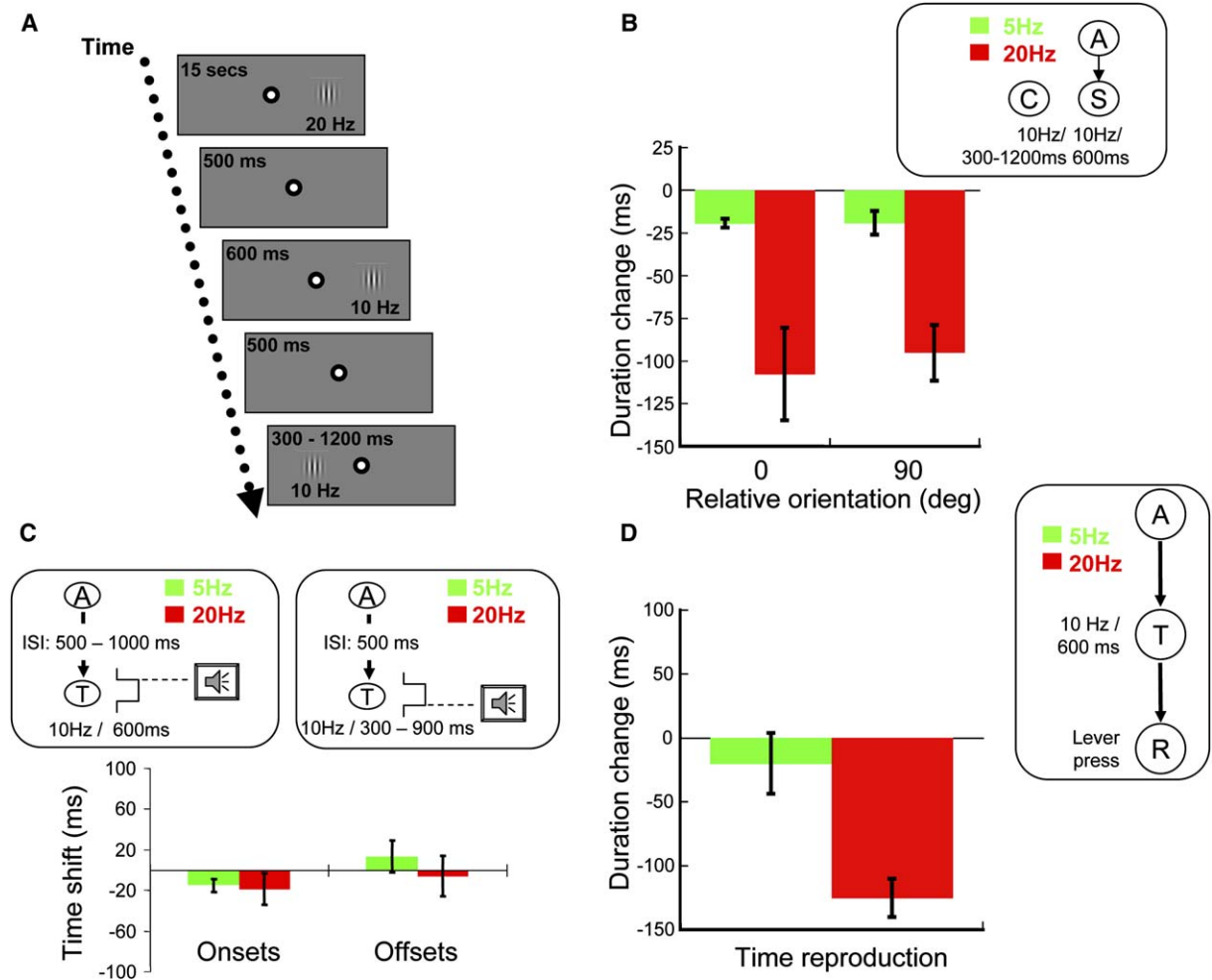


Figure 1. The Adaptation Duration Effect

(A) Time course of the binary choice experiments showing an adaptation period containing an oscillating grating followed by two test intervals containing a moving grating. The subject's task was to report which test interval appeared to last longer or (in a later experiment) which had the higher temporal frequency.

(B) Perceived duration of a 600 ms drifting grating after adaptation to 5 Hz and 20 Hz drift. The test grating was either of the same orientation or orthogonal to the adapt orientation.

(C) Perceived time of onset or offset of drifting gratings after adaptation measured relative to an auditory noise burst.

(D) Perceived duration assessed by a behavioral measure. Each point is the average measurement over four subjects (360 trials per subject). Error bars show ± 1 SE (A, adaptation; S, standard; C, comparison; T, test; R, response).

timing of the pair, we could generate a psychometric function for this crossmodal temporal order judgement. Figure 1C shows little effect of adaptation on the apparent timing of onsets or offsets. These data show that changes in apparent duration after adaptation cannot be attributed to changes in latency at onset relative to offset, which otherwise might have allowed a peripheral sensory account based on the time of activation of a population of visual neurones [20]. This indicates a requirement for an explicit process of duration encoding rather than an implicit process of time perception based on inspecting the time at which neural or perceptual systems become active [21, 22].

To ensure that adaptation to temporal frequency rather than motion was the key manipulation, we also measured apparent duration with gratings rotated 90° with respect to the adapting direction (Figure 1B and Supplemental Data). The strength of the duration after-

effect was similar, showing that the duration reduction is not confined to orientation- or direction-specific mechanisms. In a further experiment, we asked subjects to make a manual response to indicate the apparent duration of the test (Figure 1D). This task ensures that subjects have to explicitly encode the duration of the event. Again, the strength of the duration effect was similar, showing that apparent duration per se rather than some other apparent stimulus property was driving responses in the preceding forced-choice experiments.

The Duration Effect Does Not Result from a Temporal Frequency Shift

To investigate the relationship between apparent duration and apparent temporal frequency (or speed), we measured the apparent drift frequency of a 10 Hz standard after adaptation by using a similar binary choice task and found that 20 Hz adaptation reduced apparent

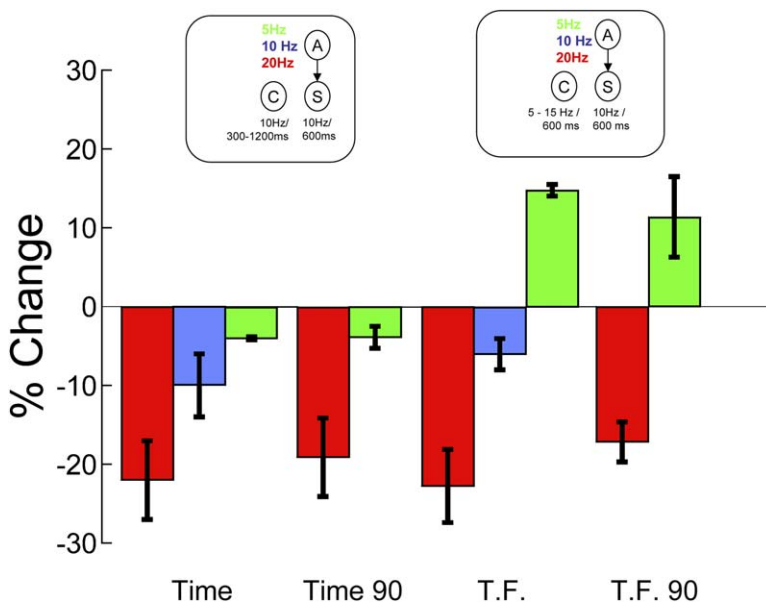


Figure 2. Duration and Temporal Frequency Adaptation

The data in Figure 1B expressed a proportion of the standard duration with additional data for adaptation to a 10 Hz drift rate. This is plotted alongside the perceived change in drift rate of a 600 ms, 1 cycle/deg sine grating with a drift frequency of 10 Hz after adaptation to 5, 10, or 20 Hz drift for test gratings that are parallel to the adapting grating. The effects of adaptation to 5 Hz and 20 Hz on the perceived duration and apparent temporal frequency are also shown for a 90° shift between adapt and test orientation. Each point is the average measurement over four subjects (360 trials per subject). Error bars show ± 1 SE.

drift rate while 5 Hz adaptation raised it (Figure 2). This result is shown beside the data from Figure 1B expressed as a percentage change for comparison. We also measured the effects of 10 Hz adaptation on a 10 Hz test pattern (Figure 2). We found a reduction in perceived duration (60 ± 24 ms) combined with a relatively minor reduction in perceived frequency (0.6 ± 0.23 Hz). These results provide two responses to possible concerns that changes in duration perception may be driven by changes in apparent temporal frequency. First, perceptual consistency would require that a reduction in duration (temporal compression) should be matched by a corresponding increase in frequency. However, 20 Hz adaptation reduced both duration and frequency. As is often the case in spatial vision or motion perception, the effects of adaptation can appear paradoxical, generally because adaptation affects mechanisms specialized for encoding separate attributes of the visual stimulus. For example, the motion aftereffect gives the impression of movement without a concomitant change in position [23]. Here the effects of adaptation on duration and temporal frequency are dissociable. Second, apparent duration may increase with increasing apparent speed as it does with increasing physical speed [24]. This hypothesis, however, cannot account for why 5 Hz adaptation increases apparent frequency, but not apparent duration (nor the results of the apparent-frequency-matching experiment described in the next section). These different patterns of the effects of adaptation indicate that different neural mechanisms are involved in expressing duration and temporal frequency.

Adaptation to Flicker Is Sufficient to Elicit a Duration Effect

To confirm that temporal frequency rather than motion adaptation was the critical factor, we repeated the adaptation experiments with Gaussian patches that simply varied in brightness sinusoidally over time. We also increased the range of durations tested. Figure 3A shows data for three subjects and three durations. Again, adaptation to 20 Hz reduces apparent duration

whereas 5 Hz adaptation has little effect. The effect size tends to increase with standard duration, indicating an approximate proportionality that is not consistent with adaptation effects at just onset or offset. There are no systematic effects of adaptation on Weber fractions (Figure 3B), indicating that psychometric functions are shifted in duration with duration discrimination remaining constant. Weber fractions are approximately constant as a function of standard duration reflecting the classic Weber Law for duration discrimination [17].

We conducted a more detailed investigation of whether the effects on temporal duration are mediated by changes in apparent temporal frequency by using the Gaussian flickering stimulus. We first measured the effect of flicker adaptation on perceived temporal frequency and the effect of varying temporal frequency on perceived duration per se. We then measured the consequence of temporal adaptation on perceived duration again, this time with the standard matched in terms of perceived temporal frequency. We found that adaptation at 20 Hz reduced the perceived temporal frequency of the 10 Hz test and adaptation at 5 Hz increased it by around 3 Hz in each case (Figure 4A). It has been reported that an interval appears to last longer if it contains high-temporal frequency pulses rather than low-temporal frequency pulses [25]. The same is true of visual flicker [26]. We asked subjects to make a manual response, thereby copying the apparent duration of the flickering test. There was a reduction of apparent duration for 5 Hz flicker and an increase for 20 Hz flicker (Figure 4B), but there was relatively little effect of temporal frequency in the 7–13 Hz range. Therefore, a reduction in perceived temporal frequency is unlikely to have contributed to the reduction in perceived duration of the 10 Hz test after 20 Hz adaptation. Nevertheless, to determine whether the difference in appearance of the standard and comparison after adaptation might have contributed to the duration effect, we measured the effects of flicker adaptation on duration again, but with the comparison adjusted to match the standard in perceived temporal frequency. The reduction in perceived

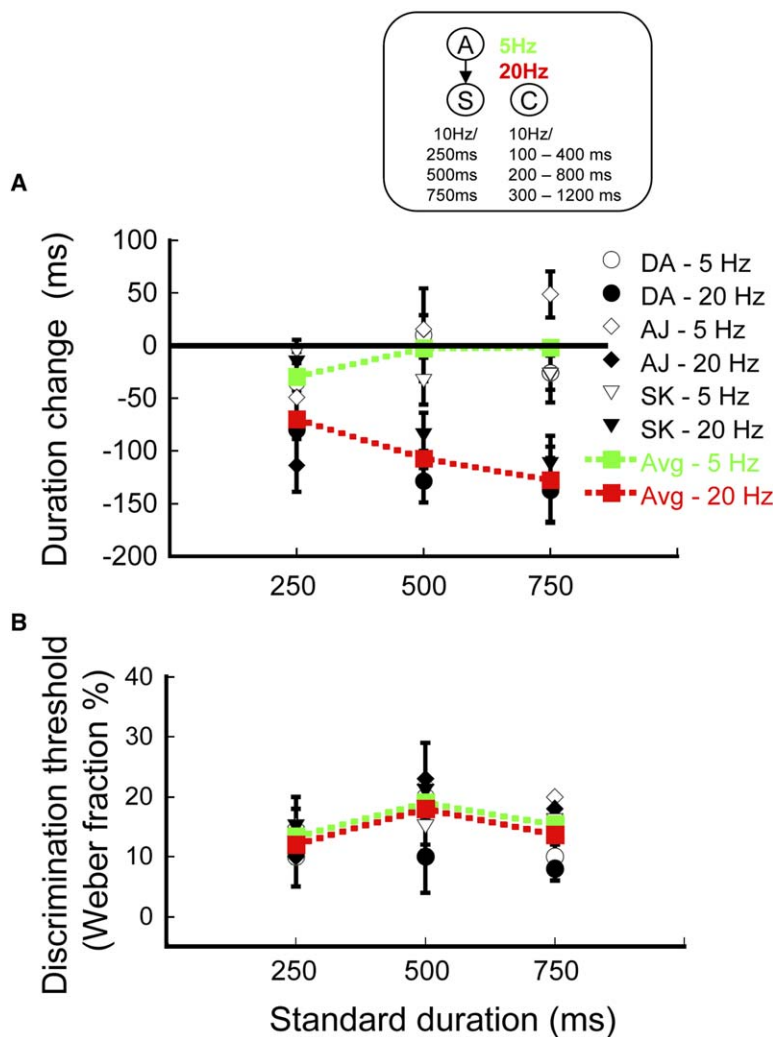


Figure 3. Duration Effect for Temporally Modulated Gaussian Patches
(A) Perceived duration of an interval of 10 Hz flicker of a Gaussian luminance patch after adaptation to 5 Hz and 20 Hz flicker.
(B) Duration discrimination threshold, plotted as a Weber fraction, as a function of standard duration. Each point is the average of four determinations, each based on 360 trials. Error bars show ± 1 SE.

duration after 20 Hz adaptation remained (Figure 4C), confirming the relative lack of influence of changes in apparent temporal frequency on duration perception after adaptation.

The Duration Effect Occurs for Spatial Locations in the Same Hemisphere

Time is often considered to be encoded with reference to a central internal clock [1, 27]. The spatial specificity of the duration effect implicates localized temporal mechanisms rather than a single neural timing mechanism. However, many cortical structures are duplicated, one for each visual hemisphere. To test whether the spatial specificity we see is a consequence of manipulating hemisphere-specific generic clocks, we repeated the adaptation experiment (matched apparent temporal frequency at test) with the adapted and unadapted regions presented at the same visual eccentricity but located in the upper and lower quadrants of the same hemifield. The spatial specificity of the temporal adaptation effect was essentially the same as in the original configuration (Figure 4D). There was no evidence that adaptation influenced temporal judgements across one whole adapted hemifield.

Conclusions

Temporal intervals can range from microseconds to days and weeks. Therefore, the issue of temporal scale needs to be kept in mind when considering the kinds of neural mechanisms that might be involved in time judgements [1, 2]. In particular, we would want to distinguish between temporal duration perception investigated here, which we would associate with the subsecond range, from time estimation that might operate on intervals of seconds and minutes.

Encoding the distance between two points or the duration of an event first requires us to select and mark the endpoints of the interval to obviate the combinatorial problem that would be inherent in trying to simultaneously encode all intervals. This attention-demanding procedure must operate on some underlying spatial or temporal representation. If space and time were encoded implicitly as in a dynamically updated map, we could simply measure distance in the map or time the temporal stream of neural events. The problem with this strategy is that distance in a cortical map is not directly related to visual angle [28] or spatial extent, and neural latencies appear too variable across and within cortical areas [29] to provide a reliable representation of the temporal properties of events [22].

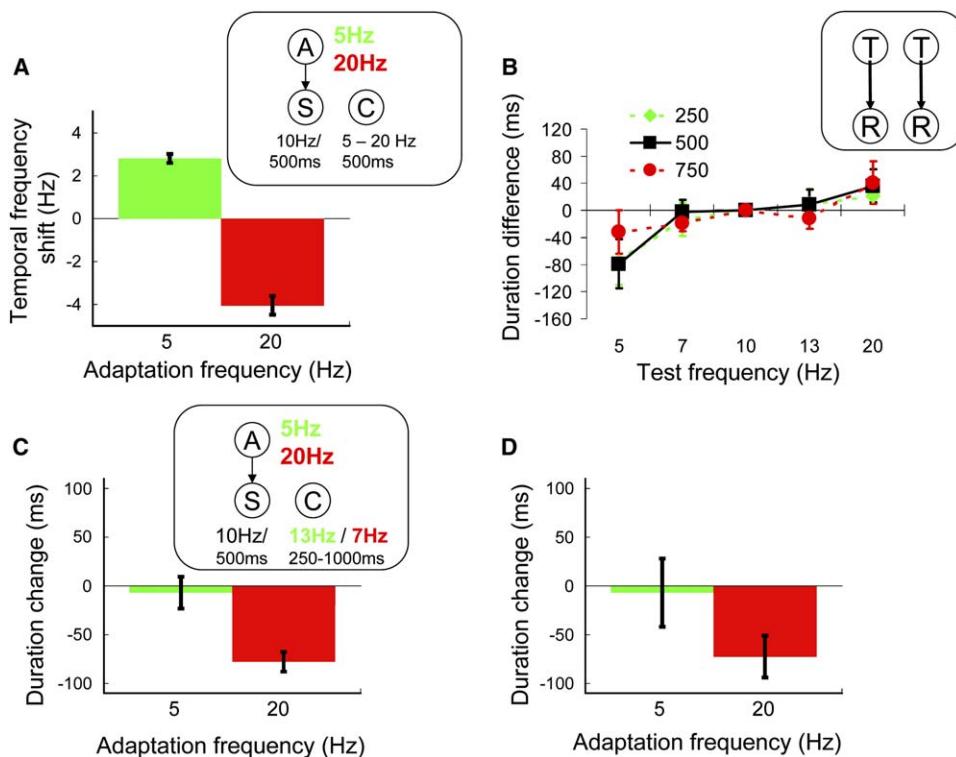


Figure 4. The Role of Temporal Frequency Adaptation

- (A) The perceived temporal frequency of a 10 Hz flickering Gaussian patch for two adapting temporal frequencies.
 (B) Perceived duration of a 500 ms flickering Gaussian luminance patch as a function of flicker temporal frequency measured via interval reproduction.
 (C) Perceived duration of a 500 ms interval of flicker as a function of the temporal frequency of prior adaptation with the comparison temporal frequency in the adapted region adjusted (13 Hz or 7 Hz) to have the same apparent frequency as the 10 Hz standard after adaptation.
 (D) As in (C) but with the standard and test in the same visual hemifield. Each point is the average measurement over four subjects (360 trials per subject). Error bars show ± 1 SE.

Recent brain-imaging studies of temporal interval and duration perception have implicated a complex network of brain areas in duration discrimination tasks [30]. Motor areas such as the SMA (supplementary motor area), left sensorimotor cortex, right cerebellum, and lateral premotor area have been associated with analysis of durations in the millisecond range [30]. Attention to duration has been shown to modulate a cortical striatal network including primarily the preSMA and the right frontal operculum [31]. Some recent single-cell [32, 33] and psychophysical [34] studies have also implicated area LIP (lateral intraparietal area). However, a recent split-brain study proposes that temporal representations are derived subcortically, perhaps in the basal ganglia or cerebellum, and project bilaterally to cortex [35]. Nobre [3] has suggested that the recruitment of areas for which time perception appears not to be the primary function may suggest a more distributed form of neural organization for duration perception. The number of brain regions implicated in timing judgments is indicative of the complexity of the duration judgment task. Some of these areas might be involved in selecting and marking the starting and finishing points for interval judgements and may not directly encode event duration. Both the stimulus modality and the nature of the timing task may be critical to which brain areas are recruited. Adaptation might influence the timing mechanism at

a number of levels. The spatial specificity of the temporal frequency adaptation effect described here, however, suggests that we are targeting an early component of the decision network.

In the classical internal clock model [1, 27], a pacemaker generates impulses at a set rate. The duration of an interval is determined by gating the impulses to an accumulator. The readout from the accumulator once the gate is shut determines the perceived duration of the interval. In this model, scaling between real and perceived time is accomplished by a change in pacemaker rate. Distortions in duration result from the comparison of a physical interval against a centralized, rate-adjusted clock. However, if visual flicker were to drive a central pacemaker, the spatial location of the flicker should not matter. A spatially localized effect of temporal flicker on perceived duration would indicate a distributed mechanism with a peripheral, modifiable, component.

Our control experiments show that the present adaptation effect cannot be ascribed to previously known modulators of apparent duration such as neural signal persistence [36], attention [19], and the density of stimulus changes [24–26, 37]. Note also that the changes in apparent duration we see are the result of adapting to temporal frequency and not the result of adapting duration channels per se (cf. [38, 39]). This precludes matched template- or channel- [1, 40] based explanations of the

phenomenon. Mauk and Buonomano in a recent review [2] argue for a more distributed view of temporal processing based on state-dependent changes in network dynamics. However, whatever the mechanism, since the effects of temporal frequency adaptation on temporal frequency and duration perception are dissociated, adaptation must have separate influences on the neural mechanisms encoding each of these stimulus properties.

It has been proposed that temporal frequency can be calculated as the ratio of bandpass to lowpass temporal filter outputs [15, 41]. According to this perspective, reducing the sensitivity of the bandpass filter will reduce apparent frequency, whereas reducing the sensitivity of the lowpass filter will increase apparent temporal frequency. Thus, adaptation-induced changes in the relative sensitivity of temporal filters could account for the temporal frequency shift. However, changes to the sensitivity or gain of a temporal filter can not alter the duration of a signal. Similarly, the process of neural transmission might introduce an overall delay in an extended signal, but it is not clear how processing considerations could explain temporal compression or dilation. To account for changes in perceived duration, we need a scaling mechanism to regulate the relationship between physical time and perceived time.

We propose that when an object is selected for duration encoding, a timing routine integrates and scales a temporal rate signal from the selected region of space. We think that adaptation to high-frequency flicker reduces the scale factor locally such that when temporal rate signals are integrated, a subsequent stimulus appears to be present for a shorter period relative to a physically identical stimulus that is presented in an unadapted region of visual space. It is not clear at present how the timing or scaling signals would be represented physiologically, but two possibilities suggest themselves. First, the change in the local temporal scale may be related to a change in the temporal scale of the impulse response (sharpening) that has been reported to occur after temporal frequency adaptation in the directionally selective cells of the nucleus of the optic tract in the wallaby [42–44]. Second, the specificity of the duration effect to high-temporal frequency adaptation suggests the locus of change is within the magnocellular pathway.

A similar distortion of duration perception has recently been demonstrated around the time of a saccadic eye movement [34, 45]. This eye movement-related distortion of apparent duration is similar to the distortion reported here in that both are specific to the visual modality. However, making a saccade can also deliver an apparent reversal of temporal order [34]. Because of this, it is not clear whether these temporal phenomena share a common cause. Eye movement-dependent changes in duration perception [34] and spatial distortion [46] have been related to predictive remapping of receptive fields in LIP [47]. We do not believe that the duration distortion reported here is related to eye movements or to receptive field remapping. Another process associated with saccades is the suppression of magnocellular activity [46, 48]. Since the duration effect was specific to high-temporal frequency adaptors that would be expected to reduce the sensitivity of magno cells, it

remains a possibility that distortions in duration perception after adaptation and around the time of saccades are both related to magnocellular suppression.

The view that time judgements are made by inspecting the temporal stream of events in the world or in the brain is difficult to sustain [21, 22]. An alternative is that there are explicit mechanisms for the encoding of time and duration. An estimate of duration seems to require some type of integration over time. The spatial specificity of the adaptation effect argues against a single universal internal clock. Instead, we propose that a temporal rate signal, which is local to a particular visual position, is integrated and scaled to deliver duration. One of the implications of a distributed mechanism is that the various elements need to be calibrated to provide a spatially uniform response. As we can expect the temporal statistics of environmental events to be spatially stationary, local adaptation to stimulus temporal frequency would provide an effective calibration strategy. The localization of temporal duration effects to the adapted region of the visual field demonstrates that peripheral, spatially localized and essentially visual sensory processes are involved in the encoding of duration.

Experimental Procedures

Stimuli were displayed, in a darkened room, on a 19-inch Sony Trinitron Multiscan 400PS monitor, with a refresh rate of 100 Hz, driven by a VSG 2/5 visual stimulus generator (Cambridge Research Systems).

In the first experiment (Figure 1B), subjects compared the duration of a moving, Gaussian windowed, sinusoidal grating (1 c/deg) against a standard (Figure 1A). An adapting grating was displayed in a circular aperture (diameter 7° of visual angle) on one side of fixation (centered 9.2° to the left or right of a central fixation point) for 15 s with 5 s top-ups between trials. In the adapt phase, the grating was vertical and drifted at a velocity of 5°/s or 20°/s. The adapting grating oscillated to avoid direction-specific motion adaptation. Drift direction reversed with a temporal frequency of 0.25 Hz. After the adapt phase, there was a 500 ms blank interval before the test phase. During the test phase, a grating drifting at 10°/s appeared sequentially on the adapted and unadapted sides. The order of presentation was randomized on a trial-by-trial basis and the test gratings drifted in opposite directions. The duration of one of the two gratings (the standard, shown on the adapted side) was fixed (600 ms). The duration of the other grating (the comparison, shown on the unadapted side) was varied between ± 1 octave of the standard duration (300–1200 ms). Both stimuli were presented in a Gaussian temporal window (amplitude 1.0; standard: SD = 100 ms; comparison: SD = comparison duration/6). In any run of trials, the orientations of the comparison and standard gratings were randomly set to vertical or horizontal. Each point on the psychometric function was based on 10 trials and each data point was the average of 4 trial runs. Psychometric functions were fitted by the Weibull function. The 50% point on the psychometric function provided a measure of the perceived duration of the comparison required to match the duration of the standard after adaptation.

In the temporal order experiments (Figure 1C), subjects compared the onset (or offset) of the standard or comparison against the onset of a 30 ms square wave white noise burst constructed by a TDT Basic Psychoacoustic Workstation (Tucker-Davis Technologies) and delivered binaurally by Sennheiser HD 265 linear headphones at 80 db. The subject reported which occurred first. The time at which the noise was presented was varied from trial to trial to generate a psychometric function, and the 50% point provided a measure of the apparent time of onset (or offset) of the visual stimuli.

The interval generation experiment (Figure 1D) was similar to the binary choice experiment; however, on any one trial, either the standard or the comparison grating was shown in isolation (for equal periods of time—600 ms). Observers attempted to generate an interval

that matched the stimulus duration by pressing a lever for the appropriate length of time.

We measured perceived temporal frequency after adaptation to oscillatory movement (Figure 2) in a way that was procedurally the same as the binary choice experiment (Figure 1B) except that subjects compared the temporal frequency of a moving grating after adaptation to 5 Hz and 20 Hz drift against a 10 Hz, 600 ms standard. Since spatial frequency was fixed, this was equivalent to judging perceived speed. The comparison was always presented on the unadapted side, and the temporal frequency of the comparison was varied (range 2–18 Hz) from trial to trial to determine a psychometric function.

In the next set of experiments (Figures 3 and 4), subjects compared the duration or temporal frequency of a flickering Gaussian comparison pattern ($SD = 1.15^\circ$ of visual angle) against a standard. For the standard and comparison stimuli, the Michelson contrast of the Gaussian varied according to a sinusoidal function with a modulation depth of 1. Thus, the center of the Gaussian patch alternated between light and dark relative to the gray surround, which had the same mean luminance as the Gaussian (39.6 cd/m^2). The modulation depth of the adapting stimuli was set to 0.5, half the contrast of the test stimuli, so that the visibility of the standard and comparison stimuli were not compromised [49]. Stimulus onset and offset were instantaneous rather than gradual and the onset phase was chosen at random.

Subjects reported which of two intervals contained the longer stimulus. Standard and comparison were allocated at random to the first or second interval on each trial. The duration of the comparison, which was always on the unadapted side, was varied from trial to trial (range 200–800 ms for a 500 ms standard) to determine a psychometric function indicating the likelihood of reporting the comparison was longer. The 50% point on the psychometric function provided a measure of the perceived duration of the standard after adaptation. Discrimination thresholds (Figure 3B) were calculated as the difference between the 50% and 75% points on the psychometric function and are expressed as Weber fractions. We compared the duration of comparison patterns (10 Hz; ranges 100–400; 200–800; 300–1200) for three standard (10 Hz) durations (250, 500, 750 milliseconds) after adaptation to 5 Hz or 20 Hz flicker.

We investigated perceived duration as a function of flicker temporal frequency (Figure 4B) by using the interval generation method described above (Figure 1D).

We measured perceived temporal frequency of a flickering Gaussian patch after adaptation to flicker (Figure 4A) in a way that was procedurally the same as the duration experiment (Figure 3A), except that subjects compared the temporal frequency of a flickering 10 Hz, 500 ms standard stimulus after adaptation to 5 Hz and 20 Hz flicker against a comparison. The comparison was always presented on the unadapted side, and its temporal frequency was varied (range 2–18 Hz) from trial to trial to determine a psychometric function.

To measure perceived duration with matched apparent temporal frequency after adaptation, the comparison was set at 7 Hz for the 20 Hz adaptation and 13 Hz after 5 Hz adaptation conditions (Figure 4C). To check whether the duration effect relied on a cross hemisphere comparison, patches were located 9.2° from the fovea in the upper and lower visual fields (Figure 4D). The stimulated hemifield varied randomly from trial to trial.

Supplemental Data

The supplemental figure can be found with this article online at <http://www.current-biology.com/cgi/content/full/16/5/472/DC1/>.

Acknowledgments

The authors thank the Human Frontiers Research Programme and NNT Communication Science Laboratories for support.

Received: November 21, 2005

Revised: January 6, 2006

Accepted: January 6, 2006

Published: March 6, 2006

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