Spatially localised distortions of perceived duration

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A fundamental question about the perception of time is whether the neural mechanisms underlying temporal judgements are universal and centralised in the brain or modality specific and distributed[1,2]. Although time perception is normally thought of as being completely dissociated from spatial vision here we report that adaptation to a 20Hz visual flicker can subsequently reduce the perceived duration of a 10Hz flickering test patch that is presented in the adapted region. This is not an indirect effect of an apparent reduction of test flicker rate, since the adaptation effect remained for test items matched in apparent temporal frequency in the adapted and unadapted regions. While a similar duration reduction was found after adaptation to a drifting sine grating, little influence of the relative orientation of the adapt and test sine gratings indicates temporal frequency as the critical dimension. These experiments demonstrate for the first time that perceived duration in the subsecond range can be manipulated by adapting the spatially localised temporal mechanisms of early visual processing.

Recent brain imaging studies of temporal interval and duration perception have uncovered a complex network of brain areas implicated in duration discrimination tasks[3]. Motor areas including the supplementary motor area (SMA), left sensorimotor cortex, right cerebellum and lateral premotor area (PMC) have been associated with analysis of durations in the subsecond range[3]. Attention to duration has been shown to modulate a cortical striatal network including primarily the preSMA and the right frontal operculum[4]. However a recent split-brain study proposes that temporal representations are derived subcortically and project bilaterally to cortex[5]. The recruitment of brain areas for which time perception appears not to be the primary function may suggest a distributed form of neural organisation for duration perception[2], for example, different brain areas may be involved in the registration and evaluation of an event.

We considered whether there might be a peripheral, sensory component to duration perception. Visual neurones vary in their response to temporal change and are therefore sensitive to the temporal properties of stimulation. These temporally tuned neural systems may also be implicated in duration encoding. Since we know temporal channels are subject to temporal frequency adaptation it is plausible that temporal adaptation might also influence duration perception.

Time is often considered to be encoded by means of an internal clock. In the classical internal clock model[1,6] 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 the conventional view distortions in duration result from the comparison of a physical interval against a centralised, rate-adjusted clock. If visual flicker were to drive a central pacemaker the spatial location of the flicker should not matter. A spatially localised effect of temporal flicker on perceived duration would indicate a distributed mechanism with a peripheral modifiable component.

Subjects were presented with a central fixation spot and an adapting stimulus, placed right or left of fixation, consisting of a Gaussian luminance pattern

sinusoidally modulating in contrast relative to a grey background (Figure 1a). Following a period of adaptation, contrast modulated Gaussian patches appeared sequentially on the adapted and unadapted sides. Subjects were asked to indicate which stimulus appeared to last longer. The duration of the stimulus on one side was varied systematically to generate a psychometric function and the 50% point on the psychometric function provided an estimate of the change in perceived duration. Since the test and comparison gratings are presented in different spatial locations any measured change in apparent duration indicates a spatially localised effect.

We measured perceived duration for the flickering test for both higher and lower adaptation flicker rates. We found adaptation to 20 Hz flicker *reduced* perceived duration at all test durations, whereas 5Hz flicker had relatively little effect (Figure 1b). Prior presentation of a rapid series of tones [7,8] or a rapid flickering visual stimulus[7,9] has been observed to *increase* the apparent duration of temporal intervals. This phenomenon, which has been ascribed to the effect of increased arousal on a centralised universal clock, appears similar to the duration after effect described here but our result is a reversal of the standard finding. In addition the cross-model nature of the classical effect is in marked contrast to the spatial specificity of the duration after effect. The decrease in duration appears to be approximately proportional to the standard duration (Figure 1b) rather than subtractive as might be predicted if adaptation simply masked the onset of the stimulus.

The relatively constant discrimination threshold when expressed as a Weber fraction (Figure 1c), an enduring feature of temporal interval judgement tasks[8], provides supporting evidence that subjects were judging temporal duration as requested. In addition the lack of a duration effect for the 5Hz condition shows that the duration aftereffect is not a delayed consequence of simply attending to the adapted region.

Temporal frequency adaptation will modify the sensitivity of sustained and transient temporal frequency channels, the properties of which are well known [10-17], and is likely to shift the perceived frequency of similar flickering patterns away from the adapting frequency, as is the case in the spatial frequency domain[18]. Temporal frequency could be encoded as the ratio of bandpass to lowpass temporal filter responses [12,19,20]. If so, the temporal frequency shift can readily be explained (Figure 4a) in terms of an alteration in the balance of these two systems following adaptation [21].

To investigate whether the effects on temporal duration may be mediated by changes in apparent temporal frequency, we first measured the effect of varying temporal frequency on perceived duration and the effect of flicker adaptation on perceived temporal frequency. We then measured the consequence of temporal adaptation on perceived duration again, this time with test patterns matched in terms of perceived temporal frequency. We found that the perceived duration of a 500 ms interval of flicker was greater for high temporal frequencies relative to a 10 Hz test and was reduced for lower temporal frequencies (Figure 2a). Adaptation at 20Hz reduced the perceived temporal frequency of the 10Hz test and adaptation at 5Hz increased it by around 3 Hz in each case (Figure 2b). Therefore a reduction in perceived temporal frequency may have contributed to the reduction in perceived duration of the 10 Hz test after 20 Hz adaptation. However, when the standard and

comparison stimuli were matched in perceived temporal frequency the reduction in perceived duration after 20Hz adaptation remained (Figure 2c).

Many cortical structures are duplicated, one for each hemispheres. 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 2d). There was no evidence that adaptation influenced temporal judgements across one whole adapted hemifield.

Flicker adaptation should result in a reduction of contrast sensitivity, which in turn might reduce the apparent duration of the flicker test by making low contrast periods less visible. This is unlikely to be an important influence, since we randomised the temporal phase of the test flicker relative to the stimulus onset. In addition, the adaptation effect remained when we used oscillating drifting gratings that had a constant contrast (Figure 3) over time. However a reduction in stimulus contrast has been found to lengthen the temporal impulse response function [22] and contrast adaptation could potentially have a similar effect, with as yet unknown consequences for duration perception. We introduced comparison gratings that either had the same orientation as the adapting stimulus (parallel) or were rotated by 90 degrees (orthogonal). The effects of adaptation were independent of the orientation of the comparison grating (Figure 3) indicating that any reduction in perceived contrast, which is known to be orientation specific [23,24], did not contribute to the duration aftereffect. The lack of orientation specificity and the specificity of the duration effect to high temporal frequencies implicates selective adaptation of the magnocellular pathway which occurs as early as the retinal ganglion cell level[25]. The temporal frequency shift was also indifferent to the orientation of the test (Figure 3), confirming the temporal frequency specificity of the neural mechanism underlying the adaptation effects we observed.

The grating stimulus configuration also meant that subjects would find it virtually impossible to count the number of brightness reversals at a point, which was a strategy that they might have adopted with flicker stimuli. To further ensure that subjects were encoding temporal interval rather than responding to some other attribute of the stimulus, such as apparent temporal frequency, we asked them to press a button for a period of time that matched the apparent duration of the 500 ms interval. The data for this behavioural, temporal interval reproduction task showed equivalent effects of adaptation, reinforcing the conclusion that adaptation can affect apparent duration in the adapted region (Figure 3).

Intriguingly, the changes in temporal duration perception are the result of temporal frequency adaptation not the result of adaptation of duration channels *per se*, precluding matched template or channel[1,26] based explanations of temporal duration perception. Changes in duration only occurred after high frequency adaptation. This specificity can be related to recent findings that saccadic eye movements, which have been associated with reduced magnocellular pathway activity, can cause a compression of apparent stimulus duration [27,28]. As temporal frequency can be calculated as the ratio of bandpass to lowpass response filters, selective post-

adaptation suppression of high-frequency sensitive mechanisms can readily account for changes in apparent temporal frequency. The relationship between this type of selective adaptation and perceived duration is less clear. We speculate that the spatially localised distortions of perceived duration observed here are the result of adaptation induced changes in the rate at which the perceptual system samples the physical stimulus, thereby distorting the mapping between physical and perceptual time.

The local affect of temporal flicker on perceived duration indicates that, although a network of brain areas are implicated in decisions about temporal duration, the temporal scale of visual processing can be modified in spatially localised and therefore peripheral parts of the visual system. Temporal frequency adaptation provides a way of experimentally manipulating apparent temporal duration that could be exploited in neurophysiological studies of time perception.

Methods

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 1) subjects compared the duration of a flickering Gaussian comparison pattern (s.d. = 1.15° of visual angle) against a standard (Figure 1a). An adapting temporally modulated Gaussian was displayed on one side of fixation (9.2° degree of visual angle to the left or right of a central fixation point) for 15 seconds with 5 second top-up between trials. 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 centre of the Gaussian patch alternated between light and dark relative to the grey 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[29]. Stimulus onset and offset was 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 adapted 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 comparison required to null the effects of adaptation. This null point was taken as a measure of the perceived duration of the standard for ease of reporting. 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 using the Weibull function. Discrimination thresholds (Figure 1c) 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 a comparison pattern (10 Hz; ranges 100-400; 200-800; 300-1200) for three standard (10 Hz) durations (250, 500, 750 milliseconds) after adaptation to 5Hz or 20 Hz flicker.

We investigated perceived duration as a function of stimulus temporal frequency using a method similar to the previous experiment (Figure 2a). However, in this experiment subjects (unadapted) simply compared the duration of a 10 Hz standard against a range of comparison temporal frequencies (5-20 Hz) for a 500 ms standard and comparison. The comparison interval was varied systematically to generate the psychometric function. The intervals in this and subsequent experiments were equal on a log scale to reflect the approximately constant Weber fraction for duration discrimination.

We measured perceived temporal frequency of a flickering Gaussian after adaptation to flicker in a way that was procedurally the same as the first experiment (Figure 2b) except that subjects compared the temporal frequency of a flickering comparison stimulus after adaptation to 5 Hz and 20 Hz flicker against a 10Hz, 500 ms standard. The comparison was always presented on the adapted side and the temporal frequency of the comparison 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 standard was set at 13 Hz after 20Hz adaptation and 7 Hz after 5 Hz adaptation (Figure 2c). 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 2d). Which hemifield was stimulated varied randomly from trial to trial.

In the remaining experiments (Figure 3) the flickering Gaussian was replaced with a moving sinusoidal grating (1 c/deg). In the adapt phase the grating was vertical and drifted at a velocity of 5 or 20 deg/sec. The adapting gratings oscillated to avoid direction specific motion adaptation. Drift direction reversed with a temporal frequency of 2 Hz. Following the adapt phase, there was a 500ms blank interval before the test phase. During the test phase, 10 deg/sec oscillating gratings appeared sequentially on the adapted and unadapted sides. Order of presentation was randomised on a trial-by-trial basis. The duration of one of the two gratings (the standard, shown on the adapted side) was fixed (600ms). The duration of the other grating (the comparison, shown on the unadapted side) was varied between +/- 1 octave of the standard duration (300 – 1200ms). Both stimuli were presented in a Gaussian temporal window (amplitude 1.0; standard: s.d. = 100 ms; comparison: s.d. = comparison duration/6). In any run of trials, the orientations of the comparison and standard gratings were randomly set to vertical or horizontal.

The interval reproduction experiment was similar to the previous experiment, however on any one trial, either the standard or the comparison gratings were shown in isolation (for equal periods of time - 600ms). Observers attempted to replicate the perceived duration of the stimulus presentation by pressing a lever for an equivalent period.

Figure Legends

Figure 1 a) Time course of the experiments showing an adaptation period followed by two test intervals. The subject's task was to report which test interval appeared to last longer, or in some cases which had the higher temporal frequency. b) Perceived duration of an interval of 10Hz flicker after adaptation to 5Hz and 20Hz flicker. c) Duration discrimination threshold, plotted as a Weber fraction, as a function of stimulus duration. Each point is the average of four determinations, each based on 360 trials. Error bars show ± 1 s.e.
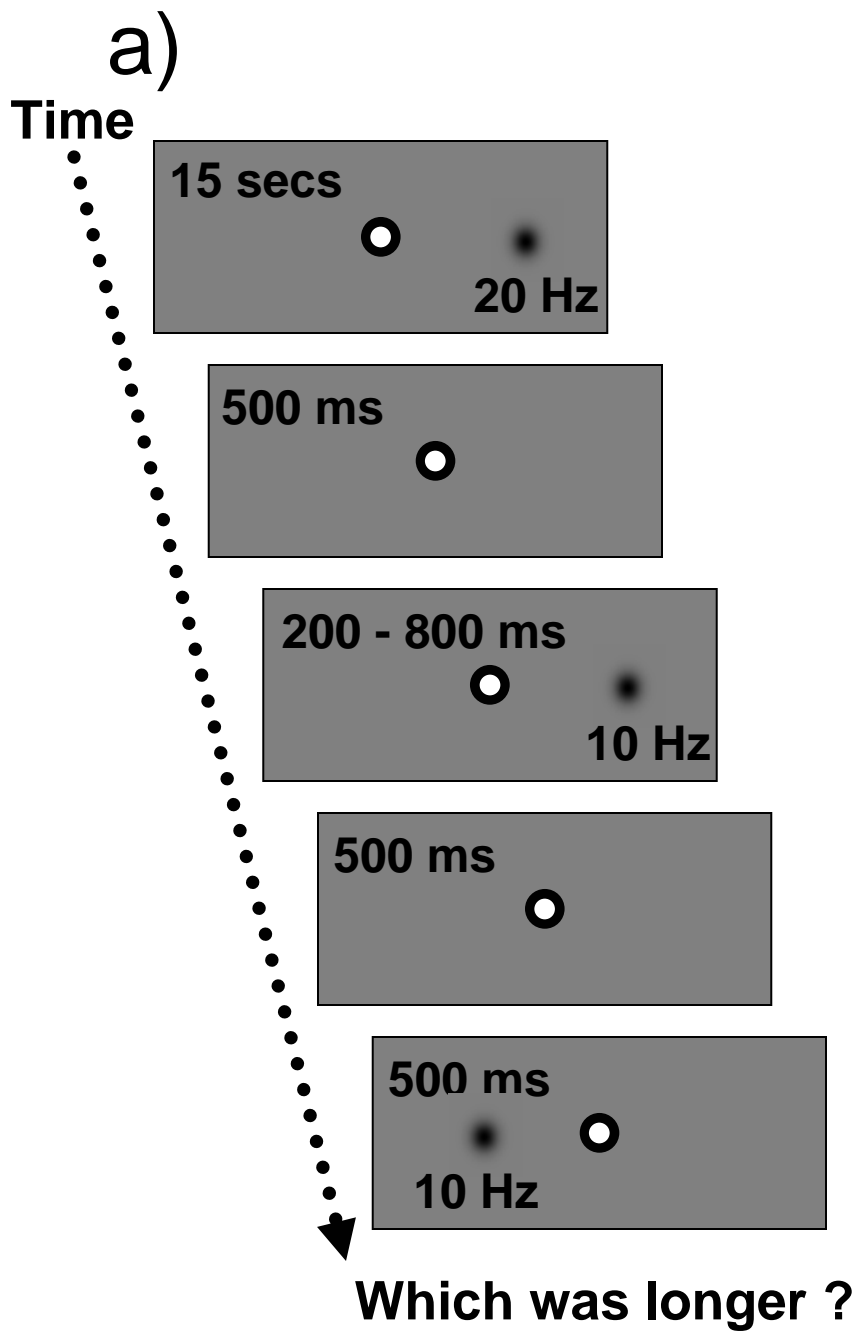

Figure 2 a) Perceived duration of a 500 ms flickering Gaussian luminance patch as a function of flicker temporal frequency. b) The perceived temporal frequency of a 10Hz flickering Gaussian patch for two adapting temporal frequencies. c) Perceived duration of a 500 ms interval of flicker as a function of the temporal frequency of prior adaptation with the test temporal frequency in the adapted region adjusted (13Hz or 7Hz) to have the same apparent frequency as the 10Hz standard. d) as in (c) but with the standard and test in the same visual hemifield. Each point is the average of four determinations, each based on 360 trials. Error bars show ± 1 s.e.

Figure 3 Perceived duration of a 500 ms sine grating drifting at a temporal frequency of 10 Hz after adaptation to 5 or 20 Hz temporal drift frequency for comparison gratings that are either parallel or orthogonal to the adapting grating. Perceived duration was also measured using a behavioural matching technique (central bars). The effect of adaptation on temporal frequency rate is shown on the right of the figure. Each point is the average measurement over four subjects, each based on 360 trials . Error bars show ± 1 s.e.
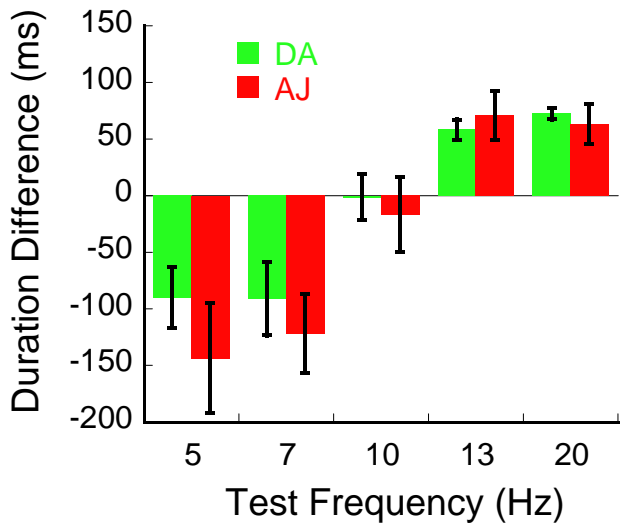
References

1.	Buonomano, D. V. & Karmarkar, U. R. How do we tell time? *Neuroscientist* **8**, 42-51 (2002).
2.	Nobre, A. C. & O'Reilly, J. Time is of the essence. *Trends in Cognitive Sciences* (2004).
3.	Lewis, P. A. & Miall, R. C. Distinct systems for automatic and cognitively controlled time measurement: evidence from neuroimaging. *Curr Opin Neurobiol* **13**, 250-5 (2003).
4.	Coull, J. T., Vidal, F., Nazarian, B. & Macar, F. Functional anatomy of the attentional modulation of time estimation. *Science* **303**, 1506-8 (2004).
5.	Handy, T. C., Gazzaniga, M. S. & Ivry, R. B. Cortical and subcortical contributions to the representation of temporal information. *Neuropsychologia* **41**, 1461-73 (2003).
6.	Treisman, M. Temporal rhythms and cerebral rhythms. *Ann N Y Acad Sci* **423**, 542-65 (1984).
7.	Treisman, M., Faulkner, A., Naish, P. L. & Brogan, D. The internal clock: evidence for a temporal oscillator underlying time perception with some estimates of its characteristic frequency. *Perception* **19**, 705-43 (1990).
8.	Wearden, J. H. "Beyond the fields we know...": exploring and developing scalar timing theory. *Behavioural Processes* **45**, 3-21 (1999).
9.	Droit-Volet, S. & Wearden, J. Speeding up an internal clock in children? Effects of visual flicker on subjective duration. *Q J Exp Psychol B* **55**, 193-211 (2002).
10.	Snowden, R. J. & Hess, R. F. Temporal frequency filters in the human peripheral visual field. *Vision Res* **32**, 61-72 (1992).
11.	Johnston, A. & Clifford, C. W. A unified account of three apparent motion illusions. *Vision Res* **35**, 1109-23 (1995).
12.	Tolhurst, D. J., Sharpe, C. R. & Hart, G. The analysis of the drift rate of moving sinusoidal gratings. *Vision Res* **13**, 2545-55 (1973).
13.	Foster, K. H., Gaska, J. P., Nagler, M. & Pollen, D. A. Spatial and temporal frequency selectivity of neurones in visual cortical areas V1 and V2 of the macaque monkey. *J Physiol* **365**, 331-63 (1985).
14.	Ikeda, H. & Wright, M. J. Receptive field organization of 'sustained' and 'transient' retinal ganglion cells which subserve different function roles. *J Physiol* **227**, 769-800 (1972).
15.	Kulikowski, J. J. & Tolhurst, D. J. Psychophysical evidence for sustained and transient detectors in human vision. *J Physiol* **232**, 149-62 (1973).
16.	Robson, J. G. Spatial and temporal contrast sensitivity of the visual system. *Journal of the Optical Society of America* **56**, 1141-1142 (1966).
17.	Kelly, D. H. Motion and vision. II. Stabilized spatio-temporal threshold surface. *J Opt Soc Am* **69**, 1340-9 (1979).
18.	Blakemore, C. & Sutton, P. Size adaptation: a new aftereffect. *Science* **166**, 245-7 (1969).
19.	Smith, A. T. & Edgar, G. K. Antagonistic comparison of temporal frequency filter outputs as a basis for speed perception. *Vision Res* **34**, 253-65 (1994).
20.	Johnston, A. & Wright, M. J. Matching velocity in central and peripheral vision. *Vision Res* **26**, 1099-109 (1986).
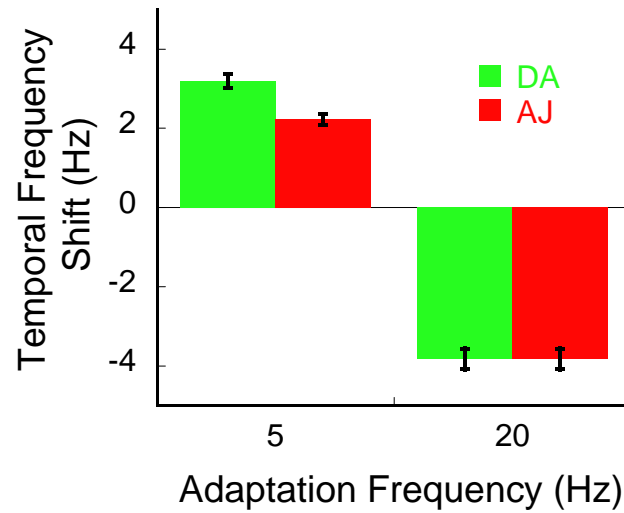
21.   DeValois, R. L. & DeValois, K. K. *Spatial Vision* (Oxford University Press, Oxford, 1990).

22.   Stromeyer, C. F., 3rd & Martini, P. Human temporal impulse response speeds up with increased stimulus contrast. *Vision Res* **43**, 285-98 (2003).

23.   Blakemore, C. & Campbell, F. W. On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *J Physiol* **203**, 237-60 (1969).

24.   Blakemore, C., Muncey, J. P. & Ridley, R. M. Stimulus specificity in the human visual system. *Vision Res* **13**, 1915-31 (1973).

25.   Solomon, S. G., Peirce, J. W., Dhruv, N. T. & Lennie, P. Profound contrast adaptation early in the visual pathway. *Neuron* **42**, 155-62 (2004).

26.   Miall, R. C. The storage of time intervals using oscillating neurones. *Neural Computing* **1** (1989).

27.   Ross, J. & Diamond, M. R. Effect of saccades on perceived time. *Perception* **26**, 69 (1997).

28.   Morrone, M. C. Perceiving objects and locating them in space. *Perception* **33, Sup.**, 2 (2004).

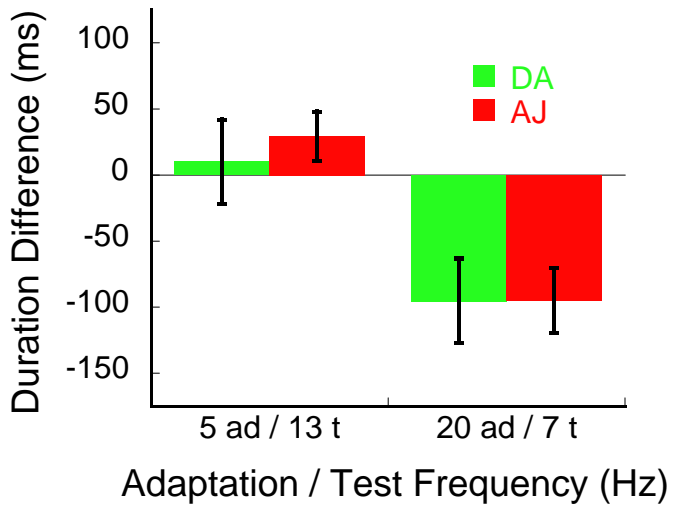29.   Georgeson, M. A. The effect of spatial adaptation on perceived contrast. *Spat Vis* **1**, 103-12 (1985).
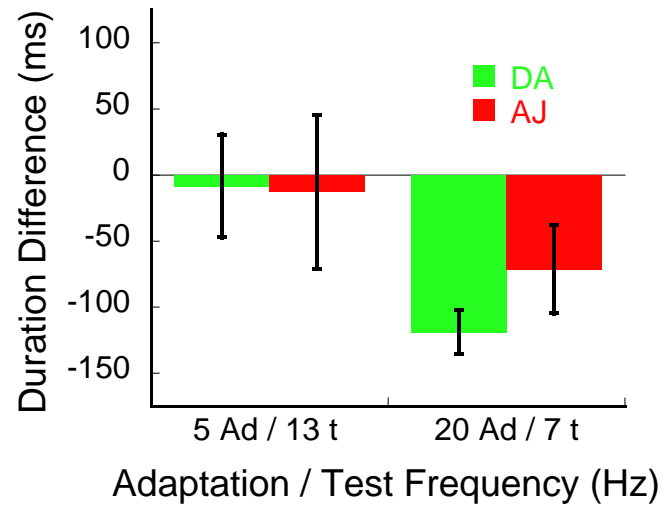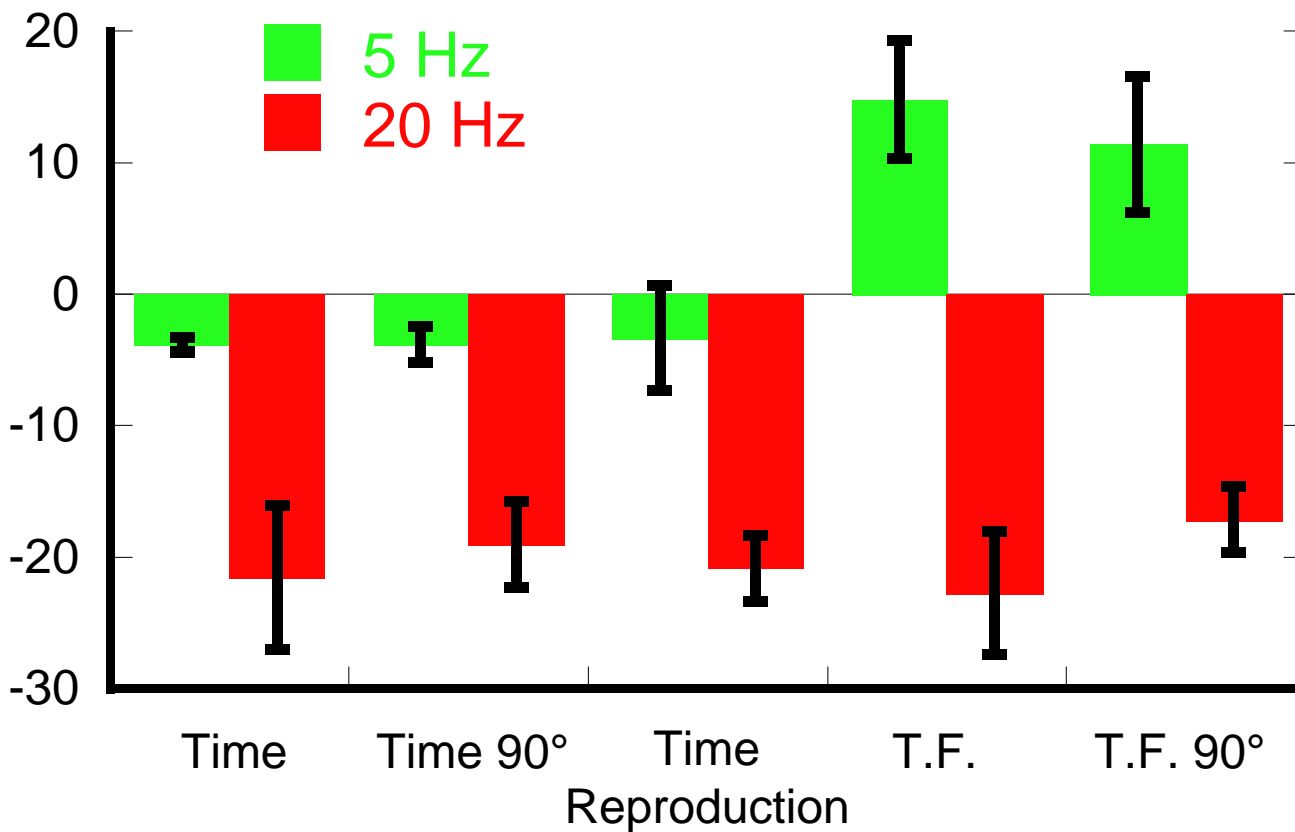
a)

Time

15 secs

20 Hz

500 ms

200 - 800 ms

10 Hz

500 ms

500 ms

10 Hz

Which was longer ?

b)

○ DA - 5 Hz
● DA - 20 Hz
◇ AJ - 5 Hz
◆ AJ - 20 Hz
▽ SK - 5 Hz
▼ SK - 20 Hz
■ Avg - 5 Hz
■ Avg - 20 Hz

Duration Difference (ms)
(Adapted – Unadapted)

Standard Duration (ms)

c)

Discrimination Threshold
(Wener Fraction)

Standard Duration (ms)