The dynamics of velocity adaptation in human vision

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Since Barlow and Hill's classic study of the adaptation of the rabbit ganglion cell to movement [1], there have been several reports that motion adaptation is accompanied by an exponential reduction in spike rate, and similar estimates of the time course of velocity adaptation have been found across species [2–4]. Psychophysical studies in humans have shown that perceived velocity may reduce exponentially with adaptation [5,6]. It has been suggested that the reduction in firing of single cells may constitute the neural substrate of the reduction in perceived speed in humans [1,5–7]. Although a model of velocity coding in which the firing rate directly encodes speed may have the advantage of simplicity, it is not supported by psychophysical research. Furthermore, psychophysical estimates of the time course of perceived speed adaptation are not entirely consistent with physiological estimates. This discrepancy between psychophysical and physiological estimates may be due to the unrealistic assumption that speed is coded in the gross spike rate of neurons in the primary visual cortex. The psychophysical data on motion processing are, however, generally consistent with a model in which perceived velocity is derived from the ratio of two temporal channels [8–14]. We have examined the time course of speed adaptation and recovery to determine whether the observed rates can be better related to the established physiology if a ratio model of velocity processing is assumed. Our results indicate that such a model describes the data well and can accommodate the observed difference in the time courses of physiological and psychophysical processes.

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Results

We have re-examined the time course of speed adaptation and recovery in order to determine whether the observed rates of adaptation can be better related to the established physiology if a ratio model of speed processing is assumed. We have also tackled one problem facing all psychophysical studies of speed adaptation; perceived contrast reduces with adaptation [15–17] and perceived speed is itself modulated by contrast [13,18]. Previous studies [5,6] have attempted to isolate the contribution of contrast adaptation to perceived speed by measuring its effect and subsequently controlling for contrast. Although this procedure effectively equalised the perceived contrast of the stimuli at any one point in time, the stimulus contrast (both physical and perceptual) was continuously changing during the course of the experiment. Thus, previous investigations have not completely evaded the possibility that their estimates were confounded by concomitant contrast adaptation. We have measured the time course of motion adaptation and subsequent recovery using a protocol that eliminates any measurable effect of contrast adaptation, namely, by adapting to low-contrast patterns and measuring perceived speed at high contrast (as low-contrast adaptors elicit no reduction in perceived contrast of high-contrast test patterns) [15,19,20]. Our results indicate that, under such controlled conditions, the dynamics of motion adaptation are contingent upon the speed employed, and estimates of the time constant of the effect are highly sensitive to experimental parameters.

Figure 1 shows the reduction in perceived speed as a function of adaptation duration, measured immediately after the adaptation period and the subsequent recovery following the longest adaptation period of 64 seconds. The results have been normalised to facilitate comparison across speeds. For both subjects, the effect of adaptation was to reduce perceived speed and this reduction increased approximately exponentially as adaptation duration increased. The asymptotic magnitude of the effect was similar for both speeds but the time course appeared faster for fast speeds. Indeed, for the mean of both subjects, the best-fitting exponential of the form $R = Rmax\,(e^{-t/T}) + C$ gave values of T of 15.9 seconds at 2 degrees per second, and 1.9 seconds at 12 degrees per second.

In the recovery from adaptation, the slow speed appeared to recover more rapidly than the fast speed; the best-fitting exponential for recovery after 64 seconds adaptation yielded time constants of 11.9 seconds and 30 seconds for slow and fast speeds, respectively. Given that the magnitudes of adaptation were similar (after 64 seconds) for both speeds but recovery dynamics differed, our results suggest that recovery is not simply determined by adaptation magnitude. In other words, both speed and adapted state appear to play a role in the dynamics of the recovery phase.

Figure 1
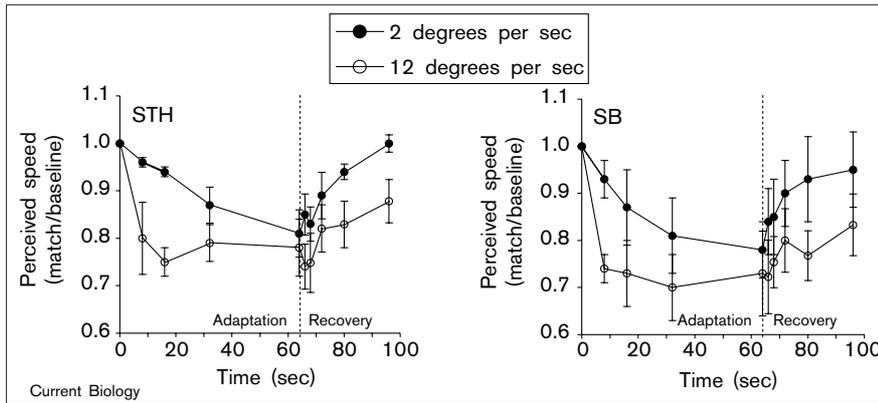
Perceived speed as a function of adaptation duration and recovery duration for two subjects, STH and SB. The ordinates represent the ratios of perceived speed before and after adaptation (match/baseline values below 1 indicate a reduction in perceived speed). Error bars represent ± SEM.

Discussion

Our results indicate that perceived speed decreases approximately exponentially as a function of adaptation duration. The asymptotic magnitude of the effect was very similar for both high and low adaptation speeds. For fast speeds, however, the rate of adaptation was faster and recovery slower. At 2 degrees per second, the time constants for adaptation and recovery were 15.9 seconds and 11.9 seconds, respectively, whereas at 12 degrees per second the respective time constants were 1.9 seconds and 30 seconds.

Clearly, these time constants do not agree well with either the physiological or the psychophysical estimates of previous studies [2,5,6]. Such discrepancies lend further support to our view that the responses of single cells *per se* cannot mediate our conscious perception of speed.

The ratio model of speed coding could throw light on the discrepancies between single-cell time constants and those reported here. We assume that the response of the

underlying mechanisms, both the putative 'fast' and 'slow' channels, would be attenuated exponentially by adaptation and that perceived speed would be determined by the ratio of their responses at any point in time. Thus, the responses of the underlying fast (R_f) and slow (R_s) mechanisms are given by:

$$R_f = R_{fmax}\,(e^{-t/Tf}) + C_f \quad 0 < R_f = < 1$$

$$R_s = R_{smax}\,(e^{-t/Ts}) + C_s \quad 0 < R_s = < 1$$

where the time constants of the fast and slow channels, T_f and T_s, and R_{fmax}, R_{smax}, C_f and C_s are free parameters and t is time. Normalised perceived speed is thus defined as the ratio, $R = R_f/R_s$.

To estimate the time courses required to model our psychophysical data, we found the best-fitting values for R_f and R_s using the error minimisation routine in Microsoft Excel 4.0. Values of R_f and R_s were found simultaneously by solving for the least squares for R. As we had no *a priori*

Figure 2
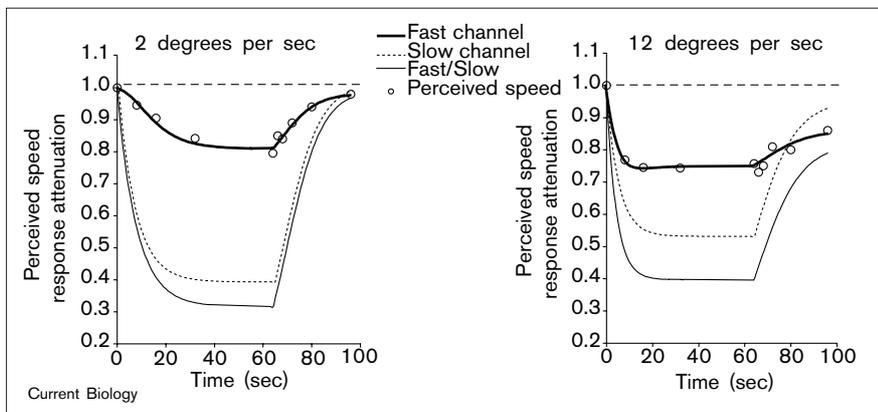
Speed adaptation and subsequent recovery from adaptation after 64 sec. The data points represent the data averaged across two observers (perceived speed has been normalised with respect to baseline to facilitate comparison). The thick solid line represents the ratio of the two putative underlying functions (see text for details).

reason to assume that adaptation and recovery time constants would be the same, we solved independently for adaptation and recovery (after 64 seconds adaptation). The results are plotted in Figure 2. The line in bold represents the ratio R_f/R_s, and the underlying mechanisms are shown on the same graph for comparison. At 2 degrees per second, the best-fitting values of T_f and T_s were 8.00 and 7.25 seconds for adaptation, and 7.29 and 7.48 seconds for the recovery phases. At 12 degrees per second, adaptation constants were somewhat shorter ($T_f = 4.21$ seconds, $T_s = 5.31$ seconds) and recovery time constants were 9.71 seconds and 9.39 seconds for T_f and T_s, respectively. Thus, the best-fitting values of a simple ratio scheme yield very similar estimates of time course (between 4 and 9 seconds) to those obtained for single cells, and simultaneously capture the much wider ranging time constants obtained psychophysically.

In summary, previous investigators have suggested that exponential decay characteristics in both single cells and psychophysical studies may have a common basis and may thus be directly related. Such straightforward neural correlation models of perception have gained much favour in recent philosophical studies [21] and are either implicit or explicit in many studies of adaptation aftereffects. For instance, Vautin and Berkley [22] comment that "If human visual cortex neurons respond in a similar way to those observed in the cat, then visual contour adaptation and its aftereffects could be simply and adequately described by the temporal response properties of neurons in striate cortex". The present results indicate that such a scheme is unlikely to hold in the case of speed adaptation. A simple ratio model of speed perception can, however, account for the present results and accommodate both psychophysical and single-cell estimates of response dynamics.

Materials and methods

Apparatus and stimuli
All stimuli were horizontally oriented sinusoidal gratings generated on a VSG 2/3W (Cambridge Research Systems) waveform generator and displayed on an EIZO 6600-M monochrome monitor. The monitor was gamma corrected using the CRS OPTICAL photometric system. Mean luminance was 32 cd m^{-2} and the frame rate was 120 Hz. The active display subtended $30° \times 24°$ and the gratings were presented in circular windows (diameter = 6°) situated 1° to the left (adapting patterns) and 1° to the right (test patterns) of a small dark fixation spot. The spatial frequency was always 1 cycle per degree and the adapting pattern drifted upwards at 2 or 12° per second. The stimuli were windowed with sharp edges in both space and time. The adapting contrast was 10% and the test contrast was 50%. The viewing distance was 57 cm.

Procedure
An adapting pattern was presented to the left of the central fixation point for one of four durations (8, 16, 32 or 64 sec). Following adaptation, the adapting stimulus was replaced with a blank field of mean luminance for 10 msec. Subsequently, two stimuli were presented simultaneously for 500 msec. A standard, of the same speed as the adapting pattern, was located in the original position of the adapting pattern, and a test, whose speed was controlled by a modified PEST procedure [23], was located to the right of the fixation point. The subjects' task

was to indicate which of the two patterns (left or right) appeared faster by pressing a button. To estimate recovery from adaptation, further standard and test pairs were presented at 2, 4, 8, 16 and 32 sec after adaptation using multiple, interleaved staircases [17,24,25]. A homogeneous blank screen of the same mean luminance was presented between each stimulus presentation. The speed of the test patterns was altered by independent PEST procedures that were set to converge on the 50% point. After each such run, subjects rested for at least 2 min in order to minimise build up of adaptation. Thirty such runs were taken and the 50% point of the resultant psychometric function was estimated by Probit [26]. The mean of four such estimates was taken as the PSE.

The experiments were conducted binocularly in a semi-darkened room with no head restraint. The subjects were two of the authors.

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