Evidence for a subtractive component in motion adaptation

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ABSTRACT

Adaptation to a moving stimulus changes the perception of a stationary grating and also reduces contrast sensitivity to the adaptor. We determined whether the first effect could be predicted from the second. The contrast discrimination (T vs C) function for a drifting 7.5 Hz grating test stimulus was determined when observers were adapted to a low contrast (0.075) grating of the same spatial and temporal frequency, moving in either the same or the opposite direction as the test. The effect of an adaptor moving in the same direction was to move the T vs C function upwards and to the right, in a manner consistent with an increase in divisive inhibition. We also measured the effect of adaptation on the motion-null point for a counterphasing grating containing two components, one moving in the same direction as the adaptor and the other in the opposite direction. Adaptation increased the amount of contrast of the adapted component required to achieve the motion-null point. However, this shift could not be predicted from the effects of adaptation on contrast sensitivity. In particular, the balance point was shifted in gratings of high contrast where there was no effect of adaptation on contrast discrimination. We suggest that adaptation has a subtractive (recalibration) effect in addition to its effects on the contrast transduction function, and that this subtractive effect may explain the movement after-effect seen with stationary tests.

1. Introduction

After adaptation to an upwards-moving grating, a stationary grating will appear to move downwards. Also, a flickering grating will appear to move downwards, even though it is composed of physically equal upwards- and downwards-moving components. According to the contrast-adaptation theory of the motion after-effect (MAE; Mather, Verstraten, & Anstis, 1998; Sekuler & Pantle, 1967; Sutherland, 1961) detectors for downwards motion are inhibited by upwardly-tuned detectors, but after adaptation, the sensitivity of the latter is reduced, and the downward detectors are released from inhibition. The seminal study supporting the contrast adaptation theory was carried out by Sekuler and Ganz (1963) who found a reduction in contrast sensitivity for gratings moving in the adapted direction, but not in the opposite direction. Their psychophysical experiment echoed the finding from physiology that directionally-tuned detectors in rabbit retina lose sensitivity when subjected to prolonged stimulation (Barlow & Hill, 1963).

One version of the disinhibition theory asserts a two-stage model, in which detectors tuned to opposite motion directions inhibit one another at a second stage, as they do in the standard Reichardt model (Hassenstein & Reichardt, 1956; Reichardt, 1961; Solomon et al., 2005). The first stage has been tentatively identified with V1, on the grounds that V1 contains directionally-tuned neurones that also respond to flicker. The second stage has been identified with V5/MT, where directional neurones are inhibited by stimuli moving in their null direction (Kohn & Movshon, 2003; Snowden et al., 1991). Neuroimaging studies have supported the two stage model by showing that the BOLD response in V5/MT to a moving stimulus is reduced by an oppositely-moving stimulus; while there is little evidence for this opponency effect in V1 (Heeger et al., 1999).

The idea that sensitivity loss underlies the MAE thus has strong support, but it is not clear that it is the only explanation. An alternative view is that there is also a subtractive component to the effect, depending on active sensory recalibration of the zero-velocity point (Harris, Morgan, & Still, 1981). To see whether the MAE could be entirely predicted from sensitivity loss, we (Morgan, Chubb, & Solomon, 2006) measured the effects of a moving adapting grating upon, first, the full contrast discrimination (T vs C) function for gratings moving in the same and opposite directions as the adaptor, and second, the effect of the same adaptor on the motion-null

point of a counterphasing compound grating containing components moving in opposite directions. The *T* vs *C* functions were fit using a version of (Legge & Foley, 1980) four-parameter transducer function

$$R = aC^p/(b^{p-q} + C^{p-q}),\qquad(1)$$

where *R* is the response of the detector, *C* is contrast, and *b* is a divisive inhibition factor corresponding to a semi-saturation constant. The parameters *p* and *q* determine the initial acceleration and later saturation of the transducer respectively.

We found that adaptation shifted the *T* vs *C* function upwards and rightwards, as predicted by an increase in divisive inhibition (the *b* parameter in the model), in agreement with previous data for non-moving stimuli (Foley & Chen, 1997); and with changes in the majority of V5/MT neurones described by Kohn and Movshon (2003). We then used the derived transducers for the same-direction and opposite-direction stimuli to predict the null point for a counterphasing grating containing both components. In other words, given an empirical null point containing components of contrast C_1 and C_2 for the two directions, it should be the case that $T_a(C_1) = T_u(C_2)$, where T_a and T_u are the contrast transduction functions for the adapted and unadapted directions respectively. We found that empirically determined null points corresponded quite well to the predicted null points, but that there was a small but significant discrepancy, suggestive of an additional subtractive component to adaptation.

One reason why the estimated subtractive component in this previous study was small might have been that the adaptor was of high contrast (0.9). This would be expected to maximise the loss of contrast sensitivity and lessen the relative impact of a calibration change. In the present experiment we used a low contrast (0.075) adaptor. Our strategy was to adapt to this low contrast and to measure effects with pedestals of higher contrast. To anticipate our results, we found that the effects of a low contrast adaptor on discrimination with a high (0.1) contrast pedestal were negligible. This allowed us then to test whether the effects of the weak adaptor were also negligible when we measured its effect on the perception of motion direction. We found that they were not.

2. General methods

2.1. Apparatus and stimuli

Stimuli were computed with MATLAB and displayed by a Cambridge Research System VSG 2/3 graphics card on a Sony monitor (resolution: 640 pixels width by 479 pixels height; pixel size: 1.03 arcmin; mean luminance: 37.5 cd/m^2). Viewing distance was 2 m. The adapting stimulus consisted of a drifting sinusoidal grating (orientation: 45°; spatial frequency: 2.05 cycles/°; temporal frequency: 7.5 Hz) windowed by a stationary Gaussian envelope ($\sigma = 2.33°$). Its Michelson contrast unless otherwise stated was 0.075. Contrast was controlled by a look-up table with 15 bits resolution. To ensure a linear relation between DAC voltage and luminance, the display was calibrated with the Cambridge Research Systems OPTICAL. The three DAC's were individually calibrated.

2.2. Psychophysics

To determine thresholds for contrast discrimination, we used a two-alternative forced-choice (2AFC) procedure. On each trial there were two temporal intervals, each indicated by the fixation point turning red. In each interval a stimulus was presented for 32 frames (320 ms) with an exponential bell-shaped contrast envelope:

$$C(t) = C_{\max}\exp[-(t-16)^2/(2\sigma^2)]\qquad(2)$$

where $C(t)$ was the contrast in frame *t*, *t* was a number between 1 and 32, $C_{\max}$ was the maximum contrast, and σ was the time constant (in frames), equal to 10. The first stimulus was followed by a mean-luminance screen for 0.5 s and then by the second of the two stimuli. One of the two stimuli had the reference (pedestal) contrast *C* the other was of contrast $C + \Delta C$. The observer used a keyboard to indicate which interval was of higher contrast. The contrast increment (ΔC), which the observer had to detect, was varied by the Psychtoolbox (Brainard, 1997) version of Quest (Watson & Pelli, 1983). To obtain fuller sampling of the psychometric function, a random value between −2 and 1 db was added to Quest's estimate of threshold on each trial. The pedestal contrast was fixed in each block of 80 trials. Data were accumulated over sessions to obtain an overall psychometric function, which was fit by a Weibull function to find the 82% correct point. A bootstrap analysis (Efron, 1982) was used to find 95% confidence intervals. There was no feedback.

The first trial in each block was preceded by 30 s of adaptation; other trials were preceded by 5 s of top-up adaptation. Observers were instructed to keep their eyes on the central fixation point during adaptation. To encourage fixation observers were given a task to perform during each adaptation period. This attentional task was based on a recent paper showing a greater BOLD response to a peripheral stimulus under low vs high load (Schwartz et al., 2005). Coloured 'T' like stimuli were presented at a rate of 2/s, at fixation and within a mean-luminance ellipse of dimensions 1.1 × 0.73°. The low-load task was to spot an infrequent red stimulus, independently of orientation, and to press the 'enter' key on the computer keypad. The high-load task was to spot two conjunctions, e.g. green-upright and blue-inverted. The actual target conjunctions were randomly re-sampled for each block of 50 trials, to prevent the task from becoming automatic. We found no significant effects of low vs high load on the *T* vs *C* functions, so the two conditions have been combined when fitting the *T* vs *C* functions. We shall discuss the absence of an 'attentional load' effect in a companion paper (Morgan, 2011).

In the counterphase flicker test only a single interval was presented, and the procedure was the Method of Single Stimuli rather than 2AFC. The patch contained two components moving in opposite directions. The variable contrast component was varied by a 1-up, 1-down staircase method. The contrast of the other component was manipulated so that the sum of the two component contrasts was constant within a block. On each trial the observer reported whether they saw movement in the upward or downwards direction. Two staircases were randomly interleaved, one starting with a relatively high contrast for the upwards component and the other with a relatively low contrast. These stimuli were readily discriminable but as the contrasts became more equal, the stimulus appeared to flicker rather than to move.

The subjects were one of the authors (MM) and a psychophysically-experienced colleague, (MT) who was not involved in the design or interpretation of the experiment.

3. Results

We wanted to use a relatively low contrast adaptor in order to avoid saturating the effect on contrast detection (Blake et al., 2006), so we first measured the function relating adaptor contrast to test detection threshold, separately for tests moving in the same and opposite directions as the adaptor, and for a stationary grating of the same spatial frequency. These data are well fit by a power function (leaving out the zero contrast adaptor) with slopes between 0.15 and 0.21. In particular, our data contain no evidence of the MAE ever saturating with adapting contrast. In this respect our results differ from duration based measures of the MAE, which

typically do exhibit saturation (Blake et al., 2006; Keck, Palella, & Pantle, 1976; Rezec, Krekelberg, & Dobkins, 2004). Having inspected our data we chose an adapting contrast of 0.075 as a low contrast that produced a reliable same-different effect while being well short of the maximum (see Fig. 1).

We then measured *T* vs *C* contrast discrimination functions following adaptation to a 0.075 contrast moving grating, as well as null points in the flicker test. We discuss the shape of the dipper functions first. The lowest discrimination thresholds ΔC are found at non-zero pedestal values approximately equal to the detection threshold: the classical result. The pedestal value for maximal discrimination facilitation for 'same' tests (that is, moving in the same direction as the adaptor) is shifted upwards and rightwards relative to that for 'opposite' tests, but the functions come together in their masking regions. These data are similar to those of Morgan, Chubb, and Solomon (2006) and are consistent with an effect of adaptation on divisive inhibition, the *b* parameter in the transduction function (1). To see if all the changes could be accounted for in this manner, we fit all the data for the 'same' and 'opposite' tests together, allowing only one parameter of the four parameter transduction model to vary between the two conditions. A likelihood ratio test was used to compare the fits of the two models, one with eight parameters and the other with 5. Let *Lc* and *Lu* be the likelihoods of the best-fitting constrained and unconstrained models. As is well-known (Hoel, Port, & Stone, 1971), under the null hypothesis that the constrained model captures the true state of the world,

$$X = -2\ln(Lc/Lu) \tag{3}$$

is asymptotically distributed as chi-square with three degrees of freedom (for the difference in the number of parameters).

When *b* was the single parameter allowed to vary in the constrained model, the fit was not significantly worse than the fit provided by the unconstrained model. By contrast, when any of *a*, *p* or *q* was the single parameter allowed to vary in the constrained model, the fit was significantly degraded. These results along with the fitted parameter values are summarised in Table 1. We conclude, in agreement with our previous result (Morgan, Chubb, & Solomon, 2006), that the effect of adaptation is well described by a change the divisive inhibition parameter *b* in the transduction function.

We now consider the results of the flicker test. The bottom panels of Fig. 2 show the contrast difference $((C_1 - C_2)/(C_1 + C_2))$ between the two oppositely moving components at which no net motion was seen. If this index is zero the components were equal, indicating no effect of adaptation; if it nears 1, the adapted component has to be a lot stronger than the unadapted component. The horizontal axis shows the summed contrast of the two components, which we refer to as the pedestal to allow comparison with the *T* vs *C* functions in the top row of the figure. The solid curves show the difference between the transduced strengths of the adapted and unadapted direction ([A − U]/[A + U]) at different levels of pedestal contrast. The curves show that the flicker test was carried out at pedestal contrast levels well into the masking region of the *T* vs *C* functions, where the strengths of the adapted and unadapted components were negligibly different. Despite this, adaptation altered the balance point of the counterphase grating considerably.

We also carried out observations in two observers (MJM, JAS) with the highest possible pedestal value of 1.0, and tested a naïve observer with a pedestal of 0.1. These measures confirmed that the component in the adapted motion direction always had to be higher than in the unadapted to achieve motion balance, even in a range where adaptation made negligible differences to the inferred relative strengths of the two components. The imbalance with a pedestal of 1.0 was no smaller than that at 0.1.

4. Discussion

The discrepancy between the effects of adaptation on the *T* vs *C* function and on the counterphasing grating are in the same direction as those previously reported by Morgan, Chubb, and Solomon (2006) but here are considerably greater. Although there are many differences between the two studies in stimulus parameters, we think the most likely explanation is that we used a weak adaptor (0.075) in the present study while in the previous experiment the adaptor contrast was 0.9. The weak adaptor allowed us to use counterphasing gratings of higher contrast, in the masking region of the *T* vs *C* function where there was no effect of adaptation on sensitivity.

We suggest that the reason for the discrepancy is the presence of a subtractive component to the MAE, which is not revealed by the effects of adaptation on contrast sensitivity. This putative subtractive component (Harris et al., 1981) would represent a reduction in the perceived velocity of a stimulus moving in the same direction as the adaptor, and an increase in perceived velocity in the unadapted direction, both of which were informally observed in the present experiment. In fact, we often observed that the test stimulus appeared stationary, even though we knew that it was always moving. Reduction in perceived velocity by a subtractive
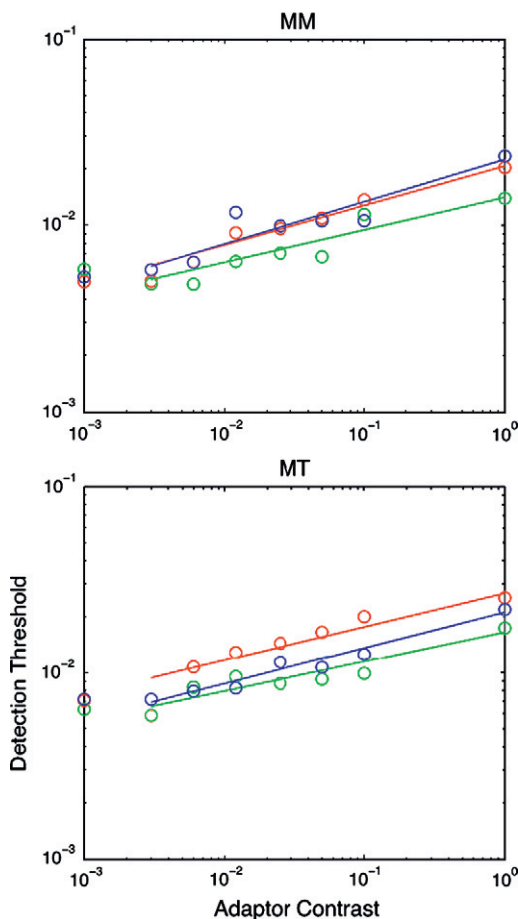

Fig. 1. Effects of adapting contrast (horizontal axis) upon detection threshold for gratings moving in the same direction as the adaptor (triangles: red in Web version), in the opposite direction (circles: green in Web version) and for stationary tests (squares: blue in Web version). Observers were MM (top panel) and MT (bottom panel). The straight lines are best-fitting power functions to the data points. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Observer MM (lines 1–10) fitted parameter values *a*, *p*, *b*, and *q*, from the transduction function (Eq. (1)) for the cases where the *T* vs *C* functions for Same & Opposite (lines 1 and 2) moving test stimuli are separately fitted. Also shown, in lines 3–10 are analyses where the same and different data are fitted together, varying just one of the four parameters. For example, lines 3 and 4 shows an analysis where the *a* parameter was allowed to be different for the same and different conditions but the other three parameters were constrained to be the same. Line 3 shows the value of *a* for the 'same' case and line 4 shows the value of *a* for the 'different' case. Column 7 shows the log likelihoods of the fit. Column 8 shows chi-square values for the significance of the difference between the eight parameter model where the conditions were fit entirely separately and the five parameter model where only one varied. For explanation of the chi-square test see the text. Lines 12–21 show a comparable analysis for the second observer, MST. Three asterisks indicate *P* < .001.

		a	*p*	*b*	*q*			Chi-sq	Sig.
Vary all	Same	39.46	2.59	0.03	0.36	2693.70	L(same)		
Vary all	Opposite	41.74	2.47	0.02	0.41	1256.00	L(opp)		
Vary *a*	Same	35.47	2.06	0.04	0.34	4014.60	L(both)	129.8	***
Vary *a*	Opposite	50.42	2.06	0.04	0.34				
Vary *p*	Same	40.76	2.56	0.04	0.33	3975.80	L(both)	52.2	***
Vary *p*	Opposite	40.76	1.53	0.04	0.33				
Vary *b*	Same	41.37	2.61	0.03	0.40	3950.90	L(both)	2.4	NS
Vary *b*	Opposite	41.37	2.61	0.02	0.40				
Vary *q*	Same	41.56	2.20	0.03	0.46	3997.90	L(both)	96.4	***
Vary *q*	Opposite	41.56	2.20	0.03	0.28				
Vary all	Same	57.18	6.26	0.02	0.59	799.67	L(same)		
Vary all	Opposite	66.54	4.17	0.01	0.64	600.89	L(opp)		
Vary *a*	Same	53.48	3.59	0.01	0.67	1452.20	L(both)	103.28	***
Vary *a*	Opposite	78.97	3.59	0.01	0.67				
Vary *p*	Same	46.70	5.30	0.02	0.45	1425.60	L(both)	50.08	***
Vary *p*	Opposite	46.70	1.79	0.02	0.45				
Vary *b*	Same	62.90	6.06	0.02	0.63	1402.50	L(both)	3.88	NS
Vary *b*	Opposite	62.90	6.06	0.01	0.63				
Vary *q*	Same	61.56	3.66	0.01	0.74	1437.10	L(both)	73.08	***
Vary *q*	Opposite	61.56	3.66	0.01	0.57				
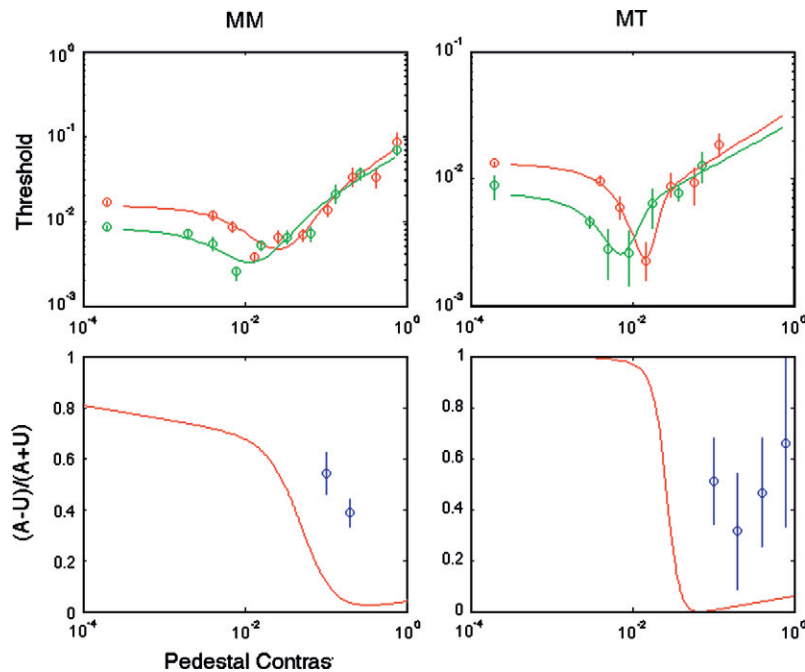
Fig. 2. The top two panels show contrast discrimination thresholds Δ*C* (vertical axis) as a function of pedestal contrast *C* (horizontal axis). Error bars show 95% confidence intervals (not standard errors). Results for observer MM are on the left and for MT on the right. Squares (red in Web version) are for adapted thresholds and circles (green in Web version) are for unadapted version. The solid curves in the bottom panel show (vertical axis) the relative transduced strengths of the two components of the counterphase grating, measured as (Adapted − Unadapted)/(Adapted + Unadapted), as a function of their summed contrasts (horizontal axis). The data points show the actual relative contrasts of the two components at the point where they were balanced. If there were no subtractive recalibration, then these points should fall on the curves, but they do not.

signal would explain why a stationary stimulus appears to move in the opposite direction to the adaptor, the classical MAE. Analogous shifts in other domains include Gibson's 'normalisation' of tilted and curved lines (Gibson, 1933; Gibson & Radner, 1937); perceived blur (Webster, Georgeson, & Webster, 2002); and the shift in the neutral point for face discrimination (Leopold et al., 2001). It is particularly worth noting that the latter occurred without any changes in sensitivity, as revealed by the shape of the psychometric function. Given the pervasive nature of sensory recalibration, it would be remarkable if it were not also present for motion.

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