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Predicting the motion after-effect from sensitivity loss

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Abstract

The widely accepted disinhibition theory of the motion after-effect (MAE) proposes that the balance point of an opponent mechanism is changed by directional adaptation. To see if the post-adaptation balance point could be predicted from contrast adaptation, we measured threshold-vs-contrast (i.e., *T*-vs-*C* or dipper) functions, before and after adaptation to moving gratings. For test stimuli moving in the same direction, adaptation shifted the point of maximum facilitation (i.e., the dip) upwards and rightwards. For tests moving in the opposite direction, adaptation produced a similar, but smaller, shift. These shifts are consistent with a change in divisive gain control. They are also consistent with subtractive inhibition followed by half-wave rectification. We attempted to use transducer functions derived from these data to predict the strength of the MAE. When combined, gratings moving in the adapted and opposite directions appeared perfectly balanced (i.e., counterphasing) when the latter was given approximately 2% more contrast than was predicted on the basis of the derived transducers. This small under-prediction may be indicative of sensory recalibration. Finally, we found that adaptation did not alter the fact that low-contrast stimuli could be detected and their direction identified with similar accuracy. We conclude that both static and dynamic forms of MAE are primarily caused by a decreased sensitivity in directionally tuned mechanisms, as proposed by the disinhibition theory.

Keywords: Psychophysics; Motion; Adaptation; Contrast discrimination; Calibration

1. Introduction

The motion after-effect (MAE) is a phenomenal movement of physically motion-balanced stimuli in the opposite direction to an adapting stimulus. For example, after adaptation to an upwards-moving grating, a flickering grating will appear to move downwards, even though it is composed of physically equal upwards- and downwards-moving components. According to the disinhibition theory of the MAE (Mather, Verstraten, & Anstis, 1998; Sekuler & Pantle, 1967; Sutherland, 1961) detectors for downwards motion is 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 disinhibition 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, 1961; Solomon, Chubb, & Morgan, 2005; Solomon, Chubb, John, & Morgan, 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, Treue, Erickson, & Andersen, 1991). Neuroim-

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aging 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, Boynton, Demb, Seidemann, & Newsome, 1999).

Compelling support for the two-stage model has come from a recent study (Kohn & Movshon, 2003) of anaesthetised monkeys, showing that adaptation in the preferred direction of neurones in V5/MT reduces their sensitivity to the preferred direction in a manner consistent, in many cases, with an increase in divisive inhibition. The response to directionally balanced flicker was increased by adapting to motion in the null direction for the cell. However, null adaptation had no effect on the spontaneous discharge rate. Adaptation in one half of the receptive field did not affect sensitivity in the other half of the receptive field, indicating that the adaptation is inherited from V1, in line with many studies showing strong effects of adaptation in V1 (Maffei, Fiorentini, & Bisti, 1973; Movshon & Lennie, 1979).

Despite the evident success of the disinhibition theory, some facts are difficult to fit in. First, there is evidence that the dynamic motion after-effect (exemplified by a counterphasing grating) differs from the static effect, exemplified by the ‘waterfall phenomenon’ (Addams, 1834; Thompson, 1993), in which *stationary* contours appear to move in the opposite direction to an adapting stimulus. There is even evidence for an MAE when testing with a homogeneous flickering test field (Green, Chilcoat, & Stromeyer, 1983). The existence of a static MAE does not, in itself, challenge the disinhibition theory (Clifford, 2002), since many direction-selective neurones in MT/V5 show such broad tuning for speed, that they respond to stationary stimuli (Lagae, Raiguel, & Orban, 1993). However, different mechanisms for the static and dynamic MAE are suggested by the relatively greater magnitude of the latter to non-luminance defined motion (Nishida & Sato, 1995) and high adaptation speeds (Nishida, Ashida, & Sato, 1994; Verstraten, van der Smagt, & van der Grind, 1998). It also enjoys complete inter-ocular transfer (Nishida et al., 1994), unlike the static MAE (Moulden, 1980).

Other facts to consider include the absence of the MAE from full-field movement (Wohlgemuth, 1911; though this could be explained by vection) the asymmetry between the expanding and contracting MAE’s (Wohlgemuth, 1911) and one report that the MAE is reduced if the adapting motion is correlated with motion of the observer (Harris, Morgan, & Still, 1981). These facts made us wonder if there might be a component of the MAE due not to loss of sensitivity, but to recalibration of the balance point. An analogy may be made to normalisation where, for example, adaptation to slightly curved lines makes straight lines appear curved in the opposite direction (Gibson, 1933). One possibility is that recalibration is the main explanation of the static MAE, while the dynamic MAE depends both upon recalibration and disinhibition. Recalibration might be prevented if the observer were aware that the retinal movement is caused by self-motion, as argued by Harris et al. (1981). Within this framework, a reduction in the stationary MAE from unattended adaptors (Rees, Frith, & Lavie, 1997) would suggest that recalibration depends on attentional awareness. (Although the same fact could alternatively be explained by inattention’s reducing the response of V1 to movement as observed by Ghandi, Heeger, & Boynton (1999).)

The purpose of this paper is to see whether the MAE is exclusively due to a loss of sensitivity, or whether there is, in addition, a recalibration component to the effect. Recalibration could occur by re-labelling the lines coming from a population of velocity-tuned detectors. For example, the output of neurones tuned to slow movements in the adapted direction could be re-labelled as indicating movement in the unadapted direction. Gilbert and Wiesel (1990) discuss recalibration in the context of the tilt illusion.

Measurement of a single sensitivity point on a transducer function cannot be used to predict the balance point for counterphase gratings. In particular, the absolute threshold (detection) is useless in predicting suprathreshold balance points. Our strategy is to measure sensitivity loss across a wide range of baseline contrasts, by measuring contrast discrimination functions. In the unadapted state, these functions (sometimes called threshold vs contrast or *T*-vs-*C* functions) show a characteristic ‘dipper’ shape, in which T first decreases with pedestal contrast (facilitation) and then enters a masking regime where it increases. (Examples are shown in our Fig. 1.) A generally accepted account of the ‘dipper’ is that it reflects a signal transduction function with an initial threshold non-linearity, accounting for facilitation, and a subsequent saturation, accounting for masking. There is also general agreement that the effect of adaptation to a grating of the same spatial frequency and orientation is to move the point of maximum facilitation of the *T*-vs-*C* function upwards and rightwards, with a convergence at higher (masking) contrasts (Foley & Chen, 1997; Ross, Speed, & Morgan, 1993). An upwards and rightwards shift can be produced by changing a single parameter in the transduction function, that specifying the amount of signal-independent divisive inhibition.

If sensitivity loss were the only reason for the MAE, then we should be able to predict the contrasts of oppositely moving gratings for which their combination does not appear to drift. Note that there will be a family of these balance points, producing apparently counterphasing gratings of various intensities. Having derived the full transducer functions from the *T*-vs-*C* measurements, we should be able to predict the contrast of a component moving in the adapted direction that balances any oppositely moving component and vice versa.

Our strategy was therefore as follows: first we measured the *T*-vs-*C* function for a high temporal frequency moving grating. Then we re-determined the same function after adaptation to the same and opposite directions of movement. From these functions we derived transducers, which we used to predict the relative strengths of the components

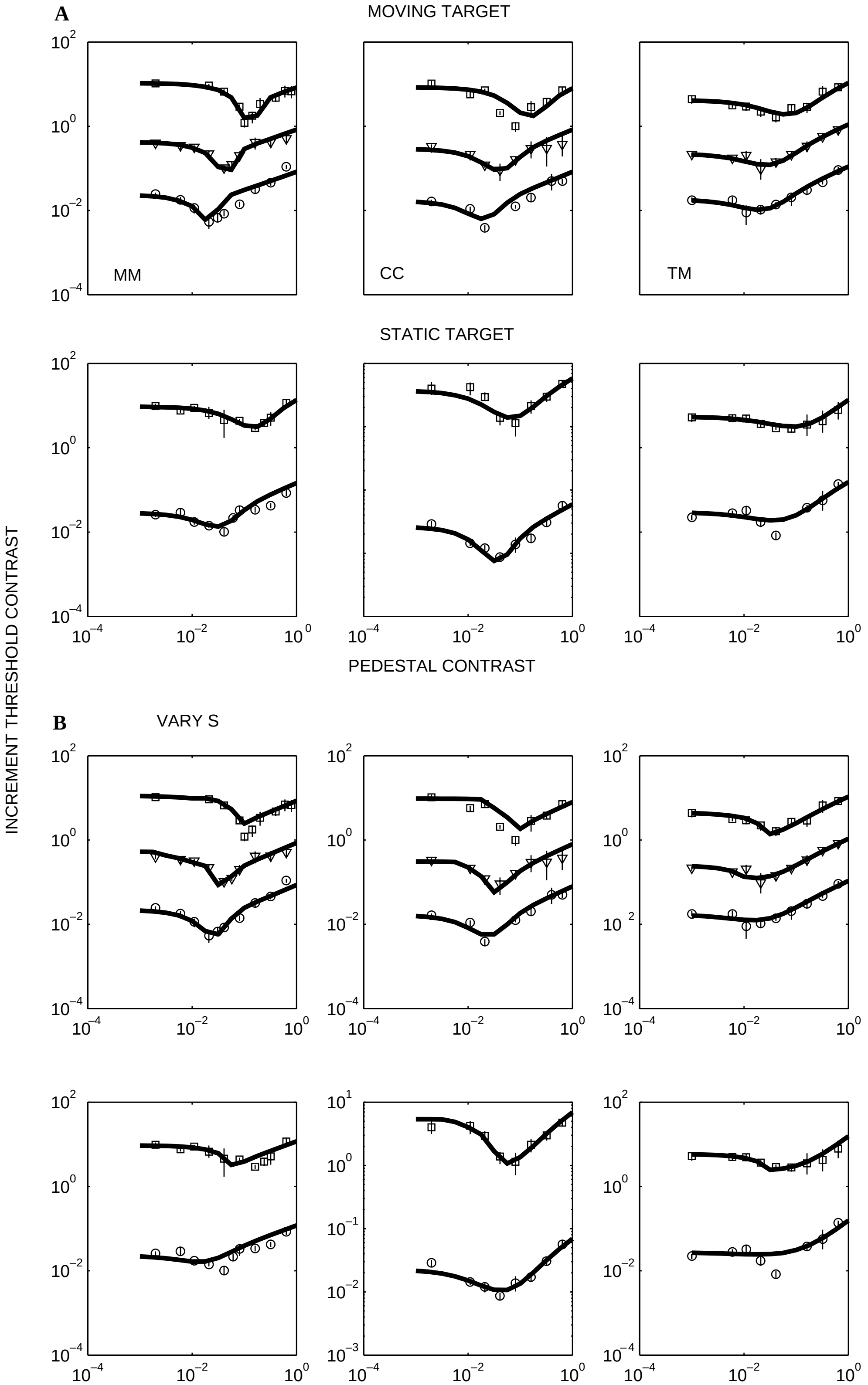

Fig. 1. Threshold vs. contrast functions from Experiment 1. The horizontal axis shows pedestal contrast, and the vertical axis the corresponding contrast increment threshold. Error bars show 95% confidence intervals. Results for different observers (MM, CC, TM) are in different columns. The top row shows results obtained when the test stimulus was moving. Circles, results before adaptation; triangles, results after adaptation to motion in opposite direction to target; squares, results after adaptation to same direction. Triangles have been moved vertically by one log unit and squares by two log units for legibility; in reality the results for all three conditions converge at high pedestal contrasts. Row 2 shows results obtained when the test was static. Circles, results before adaptation; squares, results after adaptation. The continuous curves in (A) show fits obtained by allowing the divisive inhibition parameter of the Foley (1994) model to vary as a function of adaptation condition. The bottom two rows (B) show exactly the same data as the top two, but the continuous curves were obtained by allowing a subtractive inhibition parameter to vary as a function of adaptation condition.

of a flickering grating, and thus the component contrasts at which the grating would appear balanced.

Our logic assumes that, for a given spatial and temporal frequency, the most sensitive mechanism for detection is also directionally specific. To reassure ourselves further on this point we measured direction discrimination at contrast threshold in a 2 × 2FC design (Nachmias & Weber, 1975; Watson & Robson, 1981). If the most sensitive mechanism for detection were also direction specific, we would expect the same thresholds for detection and identification.

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 Mitsubishi DiamondPro monitor (pixel resolution 0.46 arcsec, mean luminance 37.5 cd/m^2). Viewing distance was 2 m. Two Gabor patches were positioned symmetrically to the left and right of the central fixation point at an eccentricity of 1.67°. Each patch consisted of a horizontal, vertically drifting 2 cyc/° carrier windowed by a stationary Gaussian envelope W, where

$$W(x,y) = \exp\left[-\frac{(x \pm 1.67^\circ)^2 + y^2}{2(0.25^\circ)^2}\right]. \qquad (1)$$

The grating was moved in 90° phase steps every 20 ms, giving a drift frequency of 12.5 Hz. Contrast was controlled by a look-up table with 15-bit resolution. The look-up table was split into two halves of 128 entries each, controlling the left-hand and right-hand patch contrast, respectively. One of the patches had the reference contrast (the pedestal) which was constant within a block of trials; the other (the test) had the pedestal contrast plus the cue (ΔC). 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.

2.1.1. Psychophysics

To determine thresholds for contrast discrimination, the procedure was 2 AFC (spatial). The contrast increment ΔC, which the observer had to detect, was varied by the QUEST procedure (Watson & Pelli, 1979) using the version in the Psychtoolbox (Brainard, 1997), modified to jitter the chosen contrast from trial to trial in the range ±1 dB, in order to obtain fuller sampling of the psychometric function. The pedestal contrast was fixed in each block of 100 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, 1979) was used to find 95% confidence intervals. Feedback was provided in the form of a brief tone after a correct response. There was no feedback for direction discrimination.

2.2. Procedure

(a) *Contrast discrimination.* The stimuli on either side of the fixation point were identical except for their contrast. The observer's task was to decide which patch had the higher contrast. The side with the higher contrast varied randomly over trials. The trial began when the observer pressed a button to indicate the decision from the previous trial. Stimulus exposure was 0.16 s, preceded by a brief tone.

(b) *Adaptation.* Contrast discrimination trials were run as before, but each was preceded by an adaptation period to two high contrast vertically drifting patches in the same position as the subsequent reference and test patches. Apart from contrast and direction of drift, the adapting patches were identical to the test patch. The initial trial, and every 10th trial thereafter, was preceded by 30 s of adaptation; other trials were preceded by 3 s adaptation. Observers were instructed to keep their eyes fixed on the central fixation point during adaptation.

(c) *Direction discrimination at threshold.* This was exactly the same as (a) except that a 2 × 2FC task was used. The observer first indicated the side of fixation (1 or 2) on which the target appeared, and then used the same two buttons to indicate whether the target moved upwards (1) or downwards (2). The pedestal had zero contrast.

(d) *Direction discrimination for counterphasing gratings.* Only a single patch was presented, randomly to the left or right of fixation and the procedure was the Method of Single Stimuli rather than 2 AFC. The patch contained two components moving in opposite directions. One component had a fixed contrast F. The contrast V, of the other component was varied by a staircase method. When $F = V$, the stimulus was physically identical to a counterphase flickering grating.

3. Results

3.1. Experiment 1: T-vs-C functions

Contrast discrimination functions were obtained for moving stimuli and for stationary stimuli both before and after adaptation (see Section 2). The results are shown in Fig. 1 and fits are in Table 1. Data were fit using the Foley's (1994) four-parameter version of Stromeyer and Klein's (1974) transducer function

$$R_1 = \frac{aC^p}{b^{p-q} + C^{p-q}}, \qquad (2)$$

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

We also considered an elaborated transducer, with subtractive inhibition and half-wave rectification

$$R_2 = \max\left[\frac{aC^p}{b^{p-q} + C^{p-q}} - s, 0\right]. \qquad (3)$$

The difference ΔR, between transduced signals elicited by the pedestal and target + pedestal was assumed to have a standard normal distribution. Thus the predicted accuracy for discriminating between any pair of contrasts i, is given by

$$p_i = \Phi(\Delta R). \qquad (4)$$

Best-fitting parameter values were those that maximised

$$L = \sum_i P_i \ln p_i + Q_i \ln(1 - p_i), \qquad (5)$$

where P_i and Q_i denote the number of correct and incorrect responses, respectively. Maximisation was obtained using the MATLAB function FMINSEARCH. Note that our procedure differs from the commonly used method of fitting thresholds (e.g., Yu, Klein, & Levi, 2003), in that we fit all the information available, and thus the slope of the

Table 1
Model fits (L) to pre- and post-adaptation contrast-discrimination data

	Target	Adapt	Vary	a	p	b	q	s	L
MM	Moving	No	b	27.98	6.68	0.02	0.55	0.00	2185.60
			s	32.19	4.06	0.03	0.46	0.00	2176.10
		Same	b	—	—	0.14		—	
			s	—	—	—	—	9.99	
		Different	b	—	—	0.05	—	—	
			s	—	—	—	—	3.94	
CC	Moving	No	b	31.98	3.16	0.02	0.48	0.00	1285.80
			s	37.79	2.84	0.03	0.42	0.00	1278.50
		Same	b	—	—	0.17		—	
			s	—	—	—	—	11.24	
		Different	b	—	—	0.05	—	—	
			s	—	—	—	—	3.94	
TM	Moving	No	b	26.34	2.14	0.03	0.44	0.00	1602.70
			s	26.78	1.70	0.04	0.44	0.00	1607.50
		Same	b	—	—	0.10		—	
			s	—	—	—	—	2.33	
		Different	b	—	—	0.04	—	—	
			s	—	—	—	—	0.66	
MM	Static	No	b	20.00	2.71	0.04	0.45	0.00	958.80
			s	20.04	2.23	0.02	0.54	0.00	975.40
		Yes	b	—	—	0.18	—	—	
			s	—	—	—	—	3.71	
CC	Static	No	b	39.60	3.35	0.04	0.54	0.00	706.04
			s	41.49	1.94	0.07	0.43	0.00	707.92
		Yes	b	—	—	0.08	—	—	
			s	—	—	—	—	2.80	
TM	Static	No	b	22.54	1.73	0.08	0.35	0.00	857.95
			s	24.86	1.24	0.19	0.25	0.00	862.10
		Yes	b	—	—	—	—	0.18	
			s	—	—	—	—	1.40	

psychometric function. Predicted thresholds are those for which $p_i = 0.82$.

When fitting the data, we allowed the parameters a, b, p, and q to vary one at a time between adaptation conditions, with the others constrained to be the same between adaptation conditions. The fits obtained by varying b were better than those obtained by varying any other of the parameters.[1] We conclude from this, and from the visual quality of the fits in Fig. 1, that changes in b account for most of the effects of adaptation. The fits (L) where b was varied are summarised in Table 1 in the rows labelled 'b.' The table also shows (in rows labelled 's') the best fits obtained when the subtractive inhibition parameter s was allowed to vary between adaptation conditions, but a, b, p and q were not (s was constrained to be zero in the unadapted condition). These fits appear (Fig. 1) to be very similar to those obtained by varying b. Table 1 shows that, for moving test stimuli the s-fits were better than the b-fits for observers MM and CC, while for TM this was reversed. For static test stimuli, the b-fits were better than the s-fits for all observers. Overall, we conclude there is little to choose between the two models.

We conclude that the effects of adaptation are well accounted for by an increase in divisive inhibition (b), 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 cannot reject the alternative model of subtractive inhibition with half-wave rectification.

Qualitatively, the results show that adaptation was greater when adaptor moved in the same rather than in opposite directions. The surprising result is the large effect of adapting to a moving stimulus on a stationary grating. This means either that the most sensitive channel for detecting a stationary grating is directly responsive to a 12.5 Hz adaptor; or that detectors of the latter contribute to a widely tuned adaptation pool.

3.2. Experiment 2: Direction discrimination at threshold

The directional tuning of adaptation suggests that the most sensitive channel for detecting contrast increments is directionally tuned. This being the case, identification of direction should be as accurate as identification of position at threshold. We tested this with a 2 × 2 AFC design in

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[1] When p was allowed to vary, the best fit was at least 22,000 times more likely (i.e., L was larger by at least 10) than when a, b or q was allowed to vary.

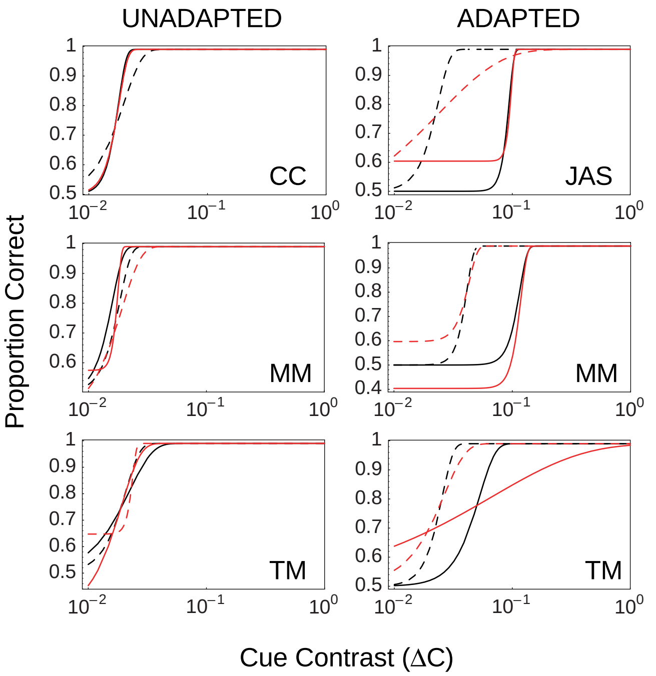

Fig. 2. Weibull functions, maximum-likelihood fit to detection (black) and identification (red) results with targets moving in the adapted (solid) and null (dashed) directions. (NB: ceilings pegged at 0.99; detection floors pegged at 0.5; for identification, adapted and null floors constrained to sum to 1.) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

which the observer had to make one response to indicate the position (left vs right) of the stimulus and a second response to indicate its direction (up vs down). ‘Up’ trials and ‘Down’ trials were randomly interleaved with separate QUEST staircases for each, but contrast values were controlled by the accuracy of the location (detection) response only. A post hoc analysis was then carried out of the psychometric function for direction identification and this was compared to the psychometric function for detection. Note that this design allows us to measure the accuracy of direction identification after adaptation. Although sensitivity will be much less in the adapted direction, the QUEST procedure will automatically raise contrast in this condition to produce the 82% level of detection. We can therefore see whether direction identification accuracy is the same at comparable levels of detection.

Thresholds are shown numerically for eight conditions (Adaptation State × Task × Direction) in Table 2 and psychometric functions for all conditions are shown graphically in Fig. 2.

To test whether identification was possible at detection threshold, proportions correct were (maximum likelihood) fit with four Weibull functions of contrast

$$P_j(\Delta C) = \gamma_j + (0.99 - \gamma_j)\left(1 - \exp\left[-(\Delta C/\alpha_j)^{\beta_j}\right]\right) \qquad (6)$$

one for each condition j ($j = 1$, detect target moving up; $j = 2$, detect target moving down; $j = 3$, identify target moving up; $j = 4$, identify target moving down). A χ^2 (Mood, Graybill, & Boes, 1974) test was performed on the null hypothesis

$$H_0 : \alpha_1 = \alpha_3,\ \beta_1 = \beta_3,\ \alpha_2 = \alpha_4,\ \beta_2 = \beta_4,\ \gamma_3 = 1 - \gamma_4,$$
$$\gamma_1 = \gamma_2 = 1/2,$$

against the alternative

$$H_1 : \alpha_1 \neq \alpha_3,\ \beta_1 \neq \beta_3,\ \alpha_2 \neq \alpha_4,\ \beta_2 \neq \beta_4,\ \gamma_3 = 1 - \gamma_4,$$
$$\gamma_1 = \gamma_2 = 1/2.$$

P values are given in Table 2. As the psychometric plots (Fig. 2) suggest, the best evidence for a difference between detection and identification comes from TM’s adapted data. However, the P value for MM’s adapted data is so high, that we might reasonably accept the null hypothesis that, once corrected for bias, the psychometric functions for identification are the same as those for detection, with the implication that detection was accomplished by a directionally tuned channel.

3.3. Experiment 3: Direction discrimination with counterphasing gratings

We determined the subjective balance point for a mixture of two component gratings—one moving up, the other moving down—both before and after adaptation to one of the components. When the two components were equal in contrast the stimulus was physically identical to a counterphase flickering grating, but after adaptation it appeared to move in the opposite direction to the adaptor. We nulled this effect by changing the contrast V, of the variable component with a staircase procedure (see Section 2). Both directions of adaptation (up, down) and direction of the fixed component (up, down) were used, giving four conditions, each of which was repeated at each level of the fixed component contrast at least three times. Five levels of fixed

Table 2
Thresholds for identification (ID) and detection (DT) when targets moved up (U) and down (D) and P values for rejecting the null hypothesis that detection and identification psychometric functions are the same

	NA DT U	NA DT D	NA ID U	NA ID D	Prob	A DT U	A DT D	A ID U	A ID D	Prob
MM	0.0161	0.0185	0.0178	0.0193	0.20	0.1161	0.0414	0.1184	0.0433	0.65
TM	0.0223	0.0208	0.0192	0.0238	0.17	0.0259	0.0256	0.0666	0.0264	0.07
JAS						0.0941	0.0236	0.0981	0.0242	0.25
CC	0.0178	0.0198	0.018	0.018	0.40					

component contrast were used, but it was not always possible to obtain data for all of them (for example, when the contrast was beneath threshold following adaptation).

3.4. Results

Interpretation of the data was complicated by a consistent bias in favour of the fixed component. In control (i.e., no adaptation) conditions, the amount of bias, was found to vary as a power function of the contrast of the fixed component, such that a balance was perceived when

$$V - F = aF^p, \tag{7}$$

where V and F are the contrasts of the fixed and variable components, and a and p were free parameters. In other words, the staircases tended to converge on a point where the variable component was greater than the fixed. We interpret this bias as arising from an asymmetry in the effect of the two components. When the V was subthreshold, unique movement was seen in the direction of the fixed component. However, when V was large, the fixed component was still present, so there was motion energy in both directions. In general, when $F > V$ the observer would be more likely to report the dominant component than they would when $V > F$.

Biases aF^p, fit to pre-adaptation results, were subtracted from the pre- and post-adaptation contrasts V, which produced subjective balances with various values of F. These variable-component contrasts appear as red symbols in Fig. 3. Finally, we estimated the post-adaptation contrasts V, using Eq. (2) and the fits in Table 1. These estimates appear with the measured pre-adaptation contrasts V, both corrected for bias, as blue symbols in Fig. 3.

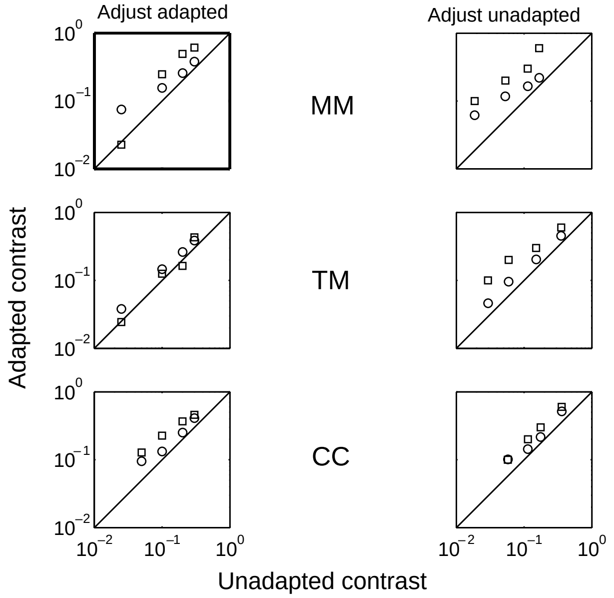

Fig. 3. Each point represents the contrast of the adapted component (vertical axis) at a given value of the unadapted component (horizontal axis) at the point where the two components cancel. Square symbols are contrast values transformed to get rid of directional bias. Circles are further transformed for sensitivity following adaptation, using Eq. (1) and the parameter values in Table 1. Data are averaged over direction of adaptation (up and down). For further explanation see the text.

If the transduced contrasts of both components were equal whenever balanced motion was perceived, then all the blue points should have fallen along the principal diagonals in Fig. 3. The fit is close, but not exact. Instead, there is a trend for the adapted component to be slightly stronger than predicted by the loss of sensitivity in order to balance the unadapted component. The mean discrepancy in contrast was .023 (2.3%) over observers and conditions. The discrepancies for MM, TM and CC were .035, .018 and .016, respectively.

It might be argued that the discrepancy results from inaccuracies in the fits of the T-vs-C functions in Fig. 1, which were obtained with only the b parameter varying across adaptation conditions. To obtain more accurate fits, we allowed all four parameters of the transducer to vary between conditions, and repeated the prediction of the motion-balance data. The discrepancy remained, with a very similar pattern across observers and conditions.

4. Discussion

Our findings are relevant to a number of issues, which we discuss in turn.

4.1. Adaptation and the *T*-vs-*C* function

Our findings are consistent with previous investigations of the effects of adaptation on static stimuli (Foley & Chen, 1997), and with single-cell recordings of MT/V5 (Kohn & Movshon, 2003). Adaptation causes an increase in divisive inhibition or subtractive inhibition (or both), which moves the T-vs-C function upwards and rightwards. As others have noted (Ross et al., 1993) this settles the question whether adaptation can improve sensitivity by moving the operating range of the detector. There is a range of pedestal contrasts where this occurs (see Fig. 1), but equally there is a range where adaptation reduces sensitivity to contrast change. In the masking part of the T-vs-C function there is little effect of adaptation.

A new finding in our experiments is that cross-adaptation (adapt to one direction, test in the opposite direction) also results in a change of divisive inhibition. This differs from results in the orientation domain, where cross-adaptation has more complicated effects, involving several parameters of the transduction function (Foley & Chen, 1997). It also differs from Kohn and Movshon's (2003) report that null adaptation has no effect on the sensitivity of MT/V5 neurones. It may be that directional tuning to the high temporal frequency (12.5 Hz) used in our experiments is comparatively weak, resulting in direct adaptation to both directions of movement. Broad tuning would also explain the effects of directional adaptation on static gratings.

4.2. Do changes in sensitivity cause the dynamic motion after-effect?

The logic behind our prediction of the balance point for a counterphase grating depends on the following four assumptions:

I The combination of two oppositely moving components will appear to move in the direction of the component producing the stronger neural signal.
II If the two components produce signals having equal strength, then the observer will select the two directions with equal probability.
III The component producing the stronger signal when presented alone will also produce the stronger signal when combined with the other component.
IV If the two components produce signals having equal strength when presented alone, then they will also produce signals having equal strength when they are combined.

This last assumption does not imply that the signals are just as strong when the components are combined as they are when the components are presented separately. Mutual masking may well occur. We merely assume that equally strong signals mask each other with equal strength.

T-vs-C measurements allowed us to predict 98% of the adapted component contrast producing a subjective balance. Although relatively meagre, the remaining 2% could be taken as evidence for recalibration. An alternative possibility is that one of the assumptions listed above is not exactly correct. It would be desirable to repeat our experiment over a wider range of temporal frequencies and adapting contrasts before concluding that there really is recalibration. For now, we can at least conclude that if recalibration exists, it is small.

4.3. What explains the static motion after-effect?

The motion after-effect is seen with retinally stabilised images (Sekuler & Ganz, 1963), which argues that image motion is not required. However, this does not rule out the possibility that directionally tuned mechanisms are stimulated by additive sensory noise, even when the stimulus is stationary. We found that the detection thresholds for stationary stimuli were raised by adaptation to a moving stimulus, consistent with detection of the stationary stimulus by directionally tuned mechanisms. Further, we saw a clear motion after-effect in these stationary stimuli after adaptation, consistent with activation of motion-labelled lines. We therefore suggest that there are no labelled lines for static stimuli, and that stimuli are seen as stationary by a population code over directionally tuned detectors, many of which are tuned to low speeds. Adaptation to a high temporal frequency moving stimulus reduces the sensitivity of detectors tuned to that direction of motion, by the mechanism of divisive inhibition, and shifts the peak (or the centroid) of the population response towards the opposite direction. We therefore agree with those (Nishida & Sato, 1995; Verstraten et al., 1998) who have suggested different mechanisms for the static and dynamic MAE's. The dynamic effect is a direct consequence of disinhibition in the mechanism tuned to the velocity of the adaptor. The static effect, on the other hand, is mediated by mechanisms tuned to much lower speeds than the adaptor, and depends on a shift in the population response. Our interpretation is consistent with the observation that the static MAE is considerably slower than the dynamic (Verstraten et al., 1998).

5. Uncited references

Craik (1939), Morgan and Chubb (1999), Reichardt (1961), Simoncelli and Heeger (1998), Stromeyer, Kronauer, Madsen, and Klein (1984).

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