

The segregation and integration of colour in motion processing revealed by motion after-effects

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Analysis of the colour and motion of objects is widely believed to take place within segregated processing pathways in the primate visual system. However, it is apparent that this segregation cannot remain absolute and that there must be some capacity for integration across these sub-modalities. In this study, we have assessed the extent to which colour constitutes a separable entity in human motion processing by measuring the chromatic selectivity of two kinds of after-effect resulting from motion adaptation. First, the traditional motion after-effect, where prolonged inspection of a unidirectional moving stimulus results in illusory motion in the opposite direction, was found to exhibit a high degree of chromatic selectivity. The second type of after-effect, in which motion adaptation induces misperceptions in the spatial position of stationary objects, was completely insensitive to chromatic composition. This dissociation between the chromatic selectivities of these after-effects shows that chromatic inputs remain segregated at early stages of motion analysis, while at higher levels of cortical processing there is integration across chromatic, as well as achromatic inputs, to produce a unified perceptual output.

Keywords: colour; luminance; motion after-effects

1. INTRODUCTION

The extent to which the chromatic properties of a moving stimulus can be used by the visual system in the analysis of its motion has been a contentious issue in visual neuroscience for some considerable time. Early physiological and psychophysical studies emphasized the segregation and parallel processing of colour and motion information in the visual system, with each sub-modality having distinct anatomical pathways and separate areas of the cerebral cortex dedicated to their analysis (Ramachandran & Gregory 1978; Zeki 1978; Livingstone & Hubel 1987). A corollary of these findings was that motion perception was considered to be based primarily on spatio-temporal changes in luminance or achromatic signals in a visual scene, with changes in colour making little or no useful contribution. More recent studies have tended to challenge this strict segregationist view and have shown that while the perception of chromatic motion may be more difficult in comparison to its luminance-defined counterpart (Cavanagh *et al.* 1984), colour can nevertheless provide unambiguous cues to the motion of visual stimuli (Dobkins & Albright 1994; Gegenfurtner *et al.* 1994; Cropper & Derrington 1996; Dougherty *et al.* 1999; Seidemann *et al.* 1999). Whether this colour information is analysed by dedicated chromatic motion detectors that are separate from luminance motion detectors remains unclear. Certain studies, echoing earlier ideas of parallelism and segregation, advocated a clear distinction between colour and luminance motion mechanisms (Krauskopf & Farrell 1990; Willis & Anderson 1998), while others have demonstrated strong interactions and overlap between them (Cavanagh & Favreau 1985; Dobkins & Albright

1994). A further complication to this issue has been the realization that colour vision is served by not one, but two, anatomically distinct processing pathways. Colour signals originating from long- and middle-wavelength (*L*- and *M*-) cones are linearly combined to form what is known as the *L/M* or 'red–green' opponent system. Signals which are mediated by short-wavelength sensitive (*S*-) cones show a very different combinatorial architecture with *L*- and *M*-cones, and form the basis for the *S/(L+M)* or 'blue–yellow' opponent system (Martin *et al.* 1997; Chatterjee & Calloway 2003).

In this study, we investigated the chromatic specificity of two different kinds of motion after-effect (MAE), both resulting from unidirectional motion adaptation, in order to examine the extent to which chromatically defined motion (in both opponent pathways) remains either segregated from, or is integrated with, luminance-defined motion. Adaptation to a moving stimulus can profoundly alter the perception of motion in subsequently viewed static stimuli, leading to the generation of well-known MAEs (Wohlgemuth 1911; Mather & Harris 1998). In its most traditional form, prolonged adaptation to motion in one direction leads to the perception of illusory motion in the opposite direction, when a stationary stimulus is viewed afterwards. Prolonged inspection of unidirectional moving stimuli can also induce changes in the perceived spatial position of subsequently viewed stationary visual stimuli (Snowden 1998; Nishida & Johnston 2000). These two kinds of after-effect, while both the direct result of motion adaptation, display very different characteristics. The traditional MAE exhibits a high degree of dependence upon the basic spatio-temporal attributes of the adapting and test stimuli (Thompson 1981; Cameron *et al.* 1992). Such tuning implies that this form of MAE is generated by the selective adaptation of neural populations with a

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physiological preference for certain spatial and temporal properties. Evidence for colour selectivity in the traditional MAE presents two very different pictures. While equiluminant chromatic motion (i.e. motion that is signalled purely by changes in colour) can both induce and null MAEs in a similar fashion to luminance motion (Cavanagh & Favreau 1985; Derrington & Badcock 1985; Mullen & Baker 1985), there does appear to be some degree of cross-adaptation between colour and luminance defined motion stimuli (Cavanagh *et al.* 1984; Derrington & Badcock 1985). This non-selectivity is suggestive of a common motion mechanism that pools both colour and luminance input (Derrington & Badcock 1985). On the other hand, the existence of colour-contingent MAEs (Hepler 1968; Favreau *et al.* 1972; Lovegrove *et al.* 1972; Mayhew & Anstis 1972; Murch 1974), where the after-effect displays some direct dependency on the chromatic properties of the stimuli, argues against pooling and instead supports the existence of separate motion detectors that have some degree of colour specificity.

While tuning is a ubiquitous feature of the traditional MAE, in contradistinction, changes in the perceived position of objects induced by motion adaptation display perceptual immunity to the manipulation of basic stimulus properties such as spatial frequency, orientation and contrast (McGraw *et al.* 2002). This implies that the neuronal population involved in the generation of this kind of after-effect is much less selective to the spatial properties of the adapting and test stimuli—one possible reason being that it pools the inputs across different visual sub-modalities. Here, we present the first examination of the colour dependency of such positional MAEs.

2. MATERIAL AND METHODS

(a) Stimuli

The visual stimuli were generated by a VSG2/3 graphics card (v. 5, Cambridge Research Systems) and presented on a Sony 21 inch FD Trinitron cathode ray tube (CRT) monitor with a refresh rate of 120 Hz. Adapting and test stimuli had a mean luminance of 12.5 cd m^{-2} and were presented on a grey background of the same mean luminance (see figure 1*a,b*). The chromaticities of the adapting and test stimuli could be independently controlled so as to produce chromatic modulations along a series of axes in MBDKL colour space as shown in figure 1*c* (MacLeod & Boynton 1979; Derrington *et al.* 1984). *L*-, *M*- and *S*-cone modulation can be varied in this space by variation of azimuth (ϕ) in the equiluminant plane (see figure 1*d*). Two axes within this space are of particular importance. First, $0\text{--}180^\circ$ or *L/M* axis modulates only *L*- and *M*-cones and minimally activates *S*-cones (1931 CIE chromaticity co-ordinates: $x_0=0.3819$, $y_0=0.2826$, $x_{180}=0.238$, $y_{180}=0.3494$). Second, $90\text{--}270^\circ$ or *S/(L+M)* axis, modulates only the *S*-cones, keeping *L*- and *M*-cone activation constant ($x_{90}=0.2724$, $y_{90}=0.228$, $x_{270}=0.348$, $y_{270}=0.404$). In addition to these two principal axes, a series of intermediate chromatic axes were also used along which the relative activations of the *L*-, *M*- and *S*-cones varied. Calibration of stimuli in all experiments was performed using a PR650 Spectrascan SpectraColorimeter. The achromatic or luminance contrast of the stimuli could also be systematically varied by changing the elevation (θ) in colour space. Nominally, the equiluminant plane constitutes $\theta=0^\circ$; however, isoluminance for all chromatic stimuli was determined

subjectively by each observer using a minimum motion method (Anstis & Cavanagh 1983) at the specific retinal location of the stimulus. Stimuli of $\theta=\pm 90^\circ$ represent purely achromatic contrast stimuli that are light (+) or dark (-); in between these extremes are stimuli that contain combinations of both achromatic and chromatic contrast. The contrasts of all stimuli (both colour and luminance) were scaled in terms of multiples above their own particular motion detection thresholds, which were measured in preliminary experiments.

(b) Traditional MAE

A motion-nulling paradigm was used to measure the traditional MAE. Initially, observers underwent a period of pre-adaptation for 2 min to a centrally placed circular 3° stimulus which contained leftwards motion (2 deg s^{-1}) of a 1 c deg^{-1} sinusoidal grating of a particular chromatic (ϕ) and/or achromatic contrast (θ) content (see figure 1*a*). Following a 6.66 s top-up period of adaptation, spatially coincident test stimuli were presented for 1.66 s. The test stimuli were of variable velocity and moved either to the left or right, and the subject's task was to indicate the perceived direction of motion by pressing an appropriate button. A two-alternative-forced-choice (2AFC) paradigm utilizing a method of constant stimuli was used to measure the magnitude of the MAE. Seven velocities were tested in 0.05 deg s^{-1} steps (i.e. from $+0.15$ to -0.15 deg s^{-1}); presentation was randomized with 20 repetitions for each condition and psychometric curves were then obtained from the data utilizing Bootstrap Software (Foster & Bischof 1991). The strength of the MAE was taken as the point at which the subject was equally likely to indicate the perception of leftward or rightward motion of the test stimulus. In control experiments, a smaller diameter (1.5°) adapting stimulus was placed 1.9° above fixation in order to replicate the spatial configuration of the positional experiments (see figure 1*b*), but this was found not to affect the selectivity of the traditional MAE.

(c) Positional MAE

To study the effects of motion adaptation on the perceived position of objects we employed a two-element Vernier alignment task to measure the magnitude of spatial offsets generated between Gabor stimuli following prior exposure to motion. The Gabor patterns comprised a 1 c deg^{-1} sinusoidal carrier grating windowed by a Gaussian envelop, the s.d. of which was 0.32° , and the elements were vertically displaced above and below a central fixation point by 1.9° (see figure 1*c*). During the adaptation period, the carrier grating drifted either to the left or right with a velocity of 1.75 deg s^{-1} , while the envelope remained stationary. In all experiments, the carrier drifted to the right in the stimulus placed above the fixation point and to the left in the one below. During the test phase, both the carrier and envelope were stationary. Following adaptation, the subsequent presentation of a physically aligned test stimulus produced the illusion of misalignment between the test elements which was opposite to the direction of motion of the carrier in the adapting stimulus, so that the upper stimulus was displaced to the left and the lower stimulus to the right. The size of this positional shift was measured by a 2AFC paradigm in conjunction with a method of constant stimuli. The presented test stimuli contained a range of real physical offsets between the upper and lower patches that spanned a range either side of the point of subjective alignment. The actual point of subjective

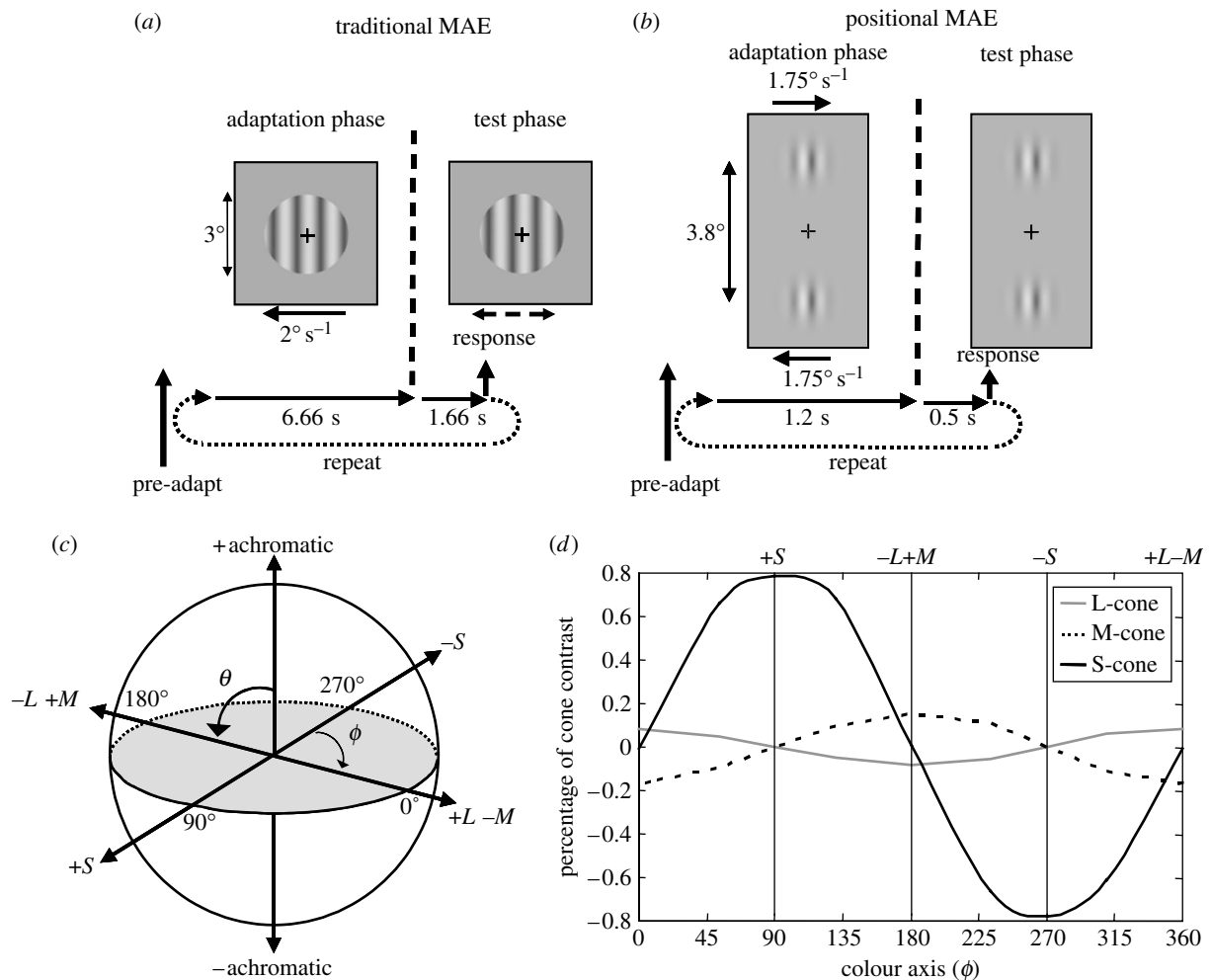


Figure 1. (a) The traditional MAE was measured using a motion nulling paradigm in which test stimuli of different chromatic and luminance contrast content (only achromatic stimuli are shown) were presented at variable speeds in order to null the perception of motion induced by the adapting stimulus. See §2 for full details. (b) The positional MAE was measured using a two-element Vernier alignment task in which the movement, in opposite directions, of two Gabor adapting stimuli generated a perceived misalignment in subsequently viewed stationary test stimuli (see §2). (c) The chromatic and/or achromatic contrast content of all test and adapting stimuli could be modified by variation in azimuth (ϕ) and elevation (θ), respectively, in MBDKL colour space. (d) Plot of the variation of the L -, M - and S -cone modulations generated by the chromatic stimuli as a function of azimuth (ϕ) in the ideal equiluminant plane of this colour space.

alignment was taken as that where the observer responded that the upper pattern was displaced to the right or left 50% of the time and was determined using the same psychometric curve fitting techniques employed in the static MAE experiment. The physical misalignment between centres of the upper and lower Gabors (in minutes of arc) in the test stimulus at the point of subjective alignment is a measure of the magnitude positional MAE.

3. RESULTS

In initial experiments, we examined how the magnitude of the traditional MAE was influenced by differences in the chromatic and achromatic contrast content between adapting and test stimuli. To this end, we measured MAEs induced by L/M and $S/(L+M)$ equiluminant, as well as luminance-defined adapting stimuli, on a variety of test stimuli. All test and adapting stimuli were equated in terms of their visibility and set at contrast levels which were equal multiples above their respective motion detection thresholds. The basic experimental paradigm is illustrated in figure 1a. The results in figure 2a show that adaptation to moving L/M , $S/(L+M)$ chromatic or

luminance-defined gratings induces the strongest MAEs in test stimuli of a similar orientation in colour space. Moreover, the magnitude of the after-effect declines to a minimum for test stimuli which are orthogonal in colour space. While figure 2a shows how the traditional MAE is selective for the cardinal axes of colour space, figure 2b shows how this tuning is maintained when intermediate stimuli of varying luminance contrast content (i.e. varying elevation, θ) are employed. The data show evidence of selectivity in that adaptation to moving L/M or $S/(L+M)$ equiluminant gratings induces the strongest MAEs in similar equiluminant test stimuli. However, the magnitude of the after-effects declines as test stimuli shift away from the equiluminant plane and contain increasingly larger amounts of luminance contrast. Adaptation to luminance-defined motion ($\theta = \pm 90^\circ$) produces the opposite effect. The strongest MAEs in such cases are induced in test stimuli with maximum luminance contrast content, but as the test moves closer to the equiluminant plane, the MAE decreases.

Figure 3a shows how the MAE varies when adapting and test stimuli are restricted to the equiluminant plane.

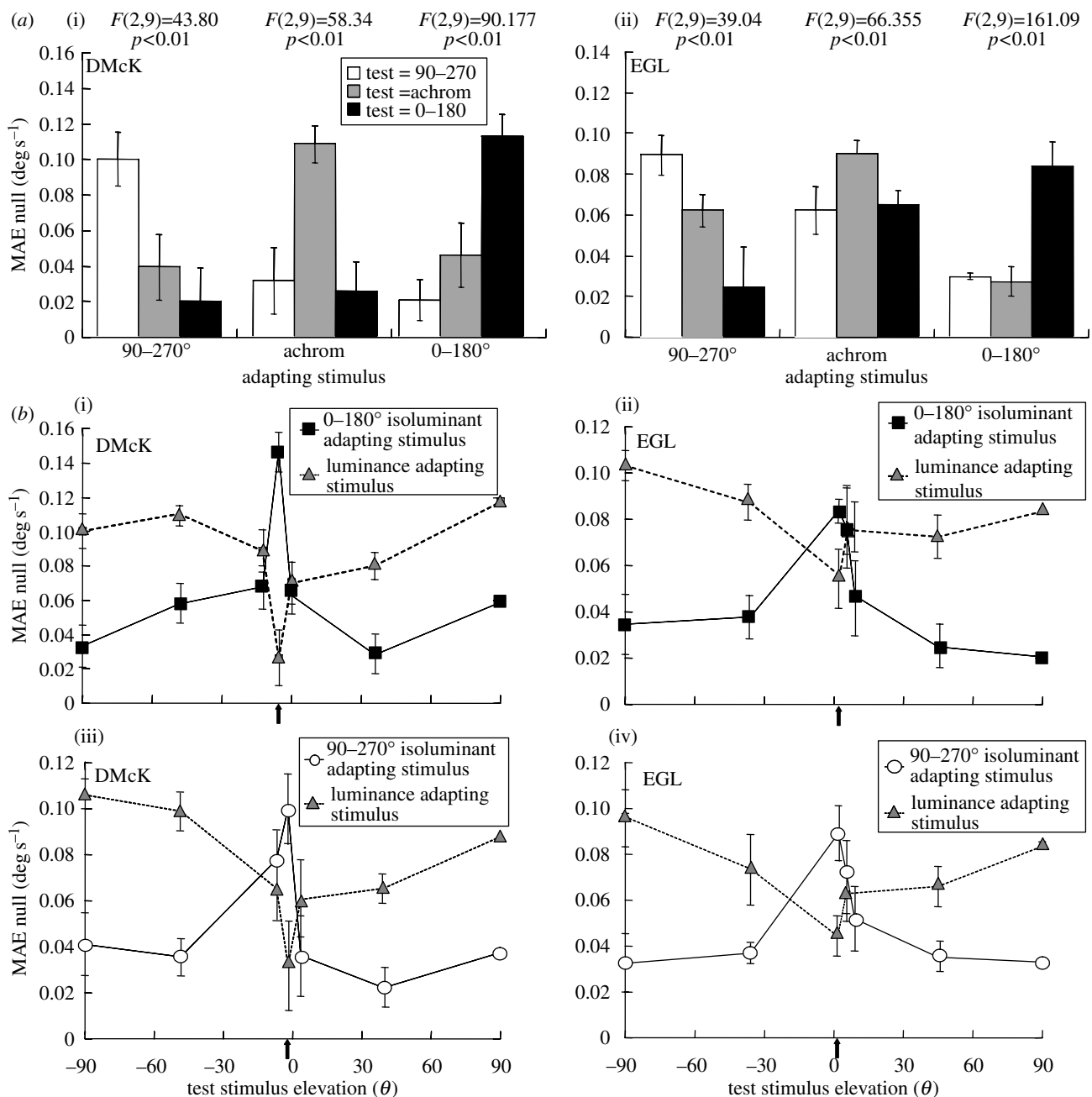


Figure 2. (a) Magnitude of the traditional MAE induced by adaptation to moving L/M , $S/(L+M)$ chromatic and luminance stimuli, in test stimuli that are modulated along the same three cardinal axes. Error bars in this and subsequent figures represent ± 1 s.d. from the mean. (b) Variation in the strength of the traditional MAE generated by adaptation to L/M ($\phi=0-180^\circ$), $S/(L+M)$ ($\phi=90-270^\circ$) and achromatic grating stimuli as a function of test stimulus elevation, θ . $\theta=0$ represent stimuli which lie on the ideal equiluminant plane while $\theta=\pm 90^\circ$ represent achromatic stimuli. Note that elevation is expressed in degrees from the ideal equiluminant plane ($\theta=0^\circ$) with which the observers' subjective isoluminant point (dark arrow) may not exactly coincide. Data are shown for two observers, DMcK and EGL with all stimuli at $12\times$ motion detection threshold (contrast (%)) at threshold: $\phi=0-180^\circ$ DMcK: L -cone=0.14, M -cone=0.26; EGL: L -cone=0.15, M -cone=0.29; $\phi=90-270^\circ$ DMcK: S -cone=3.5; EGL, S -cone=1.8; achromatic contrast thresholds: DMcK=0.343; EGL=0.364).

Once again the induced MAEs show a clear selectivity, this time for the chromatic composition of the stimuli. Adaptation to both L/M ($\phi=0-180^\circ$) and $S/(L+M)$ ($\phi=90-270^\circ$) equiluminant stimuli generates the strongest MAEs in test stimuli of the same chromaticity, while the weakest MAEs are induced in gratings that are orthogonal in colour space. Intermediate axes generate MAEs somewhere in between these extremes. Thus, in the traditional MAE, not only is adaptation selective as to whether stimuli are defined by chromatic or luminance information, it is highly specific to the particular

chromaticity of equiluminant stimuli. However, the possibility remains that this specificity is highly dependent upon the intensities of the adapting and test stimuli used in the experiment. Figure 3a shows that the colour tuning evident in the equiluminant plane is observed only at high stimulus contrasts (greater than or equal to $10\times$ threshold) and is less evident at lower levels (less than $5\times$ threshold). This can be observed more clearly in figure 3b where the effect of increasing the adapting and stimulus contrast is shown for test stimuli which are either identical to the adapting stimulus

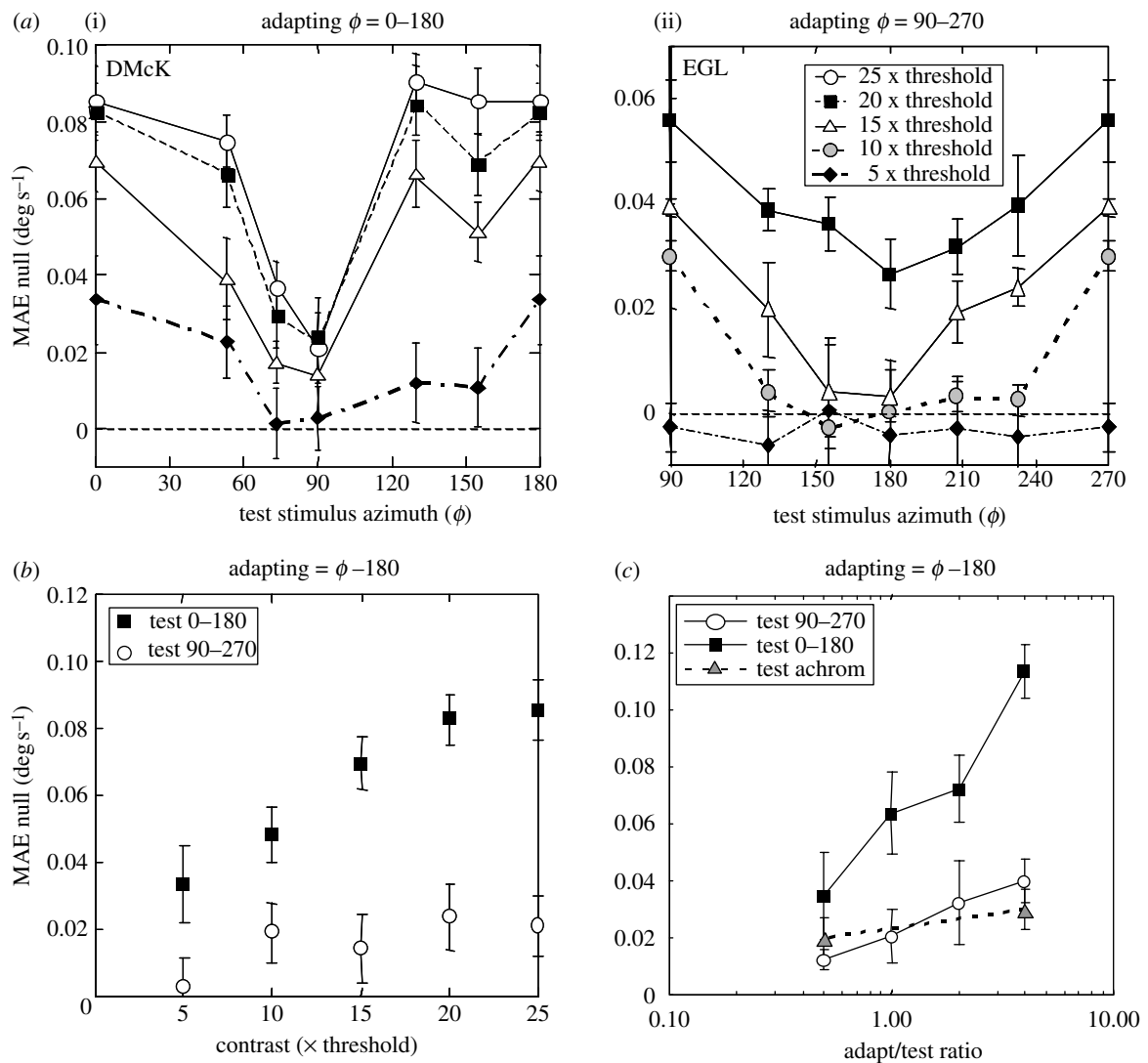


Figure 3. (a) Variation in traditional MAE in the equiluminant plane. The graphs plot the variation in MAE strength as a function of test stimulus azimuth (ϕ) for adapting stimuli that modulated the L/M ($\phi=0-180^\circ$) and $S/(L+M)$ ($\phi=90-270^\circ$) chromatic axes at a series of different contrast levels. (b) The effect of increasing adapting and test stimulus contrast on the traditional MAE. The data shown represent the differential growth in the strength of the MAE generated by adaptation to a moving L/M ($\phi=0-180^\circ$) grating in chromatic test stimuli of the same and orthogonal ($\phi=90-270^\circ$) orientations in colour space. (c) The variation in traditional MAE magnitude as a function of adapt/test ratio. Adapting conditions are similar to those in (b) except that here the relative magnitude of the adapting and test contrast was manipulated. For ratios greater than unity the adapting stimulus is of higher contrast than the test, for ratios less than unity the converse applies. When the adapt/test ratio = 1 both stimuli are at equal multiples of their respective detection thresholds.

($\phi=0-180^\circ$) or lie orthogonal to it in colour space ($\phi=90-270^\circ$). To explore this issue of colour selectivity further we also measured MAE strength as a function of adapt/test contrast ratio and the results are shown in figure 3c. What is observed is that as adapt/test ratio increases (i.e. as the contrast of the adapting stimulus is increased relative to the test) there is an increase in the induced MAE for all test stimuli (L/M , $S/(L+M)$ and achromatic). However, the increase is greatest for the test stimulus identical to the adapting stimulus, in this case the L/M ($\phi=0-180^\circ$) stimulus. Only at the lowest adapt/test ratios employed (0.5), where the contrast of the adapting stimulus is half that of the test, is selectivity lost.

Having shown how chromatic and luminance contrast can influence the perception of motion following periods of adaptation, we examined how these same parameters might influence the generation of perceived shifts in position following adaptation to motion. The experimental

paradigm is outlined schematically in figure 1b and, as previously, all adapting and test stimuli were presented at equal multiples of their respective detection thresholds. Figure 4a illustrates the magnitudes of positional MAEs induced by cardinal chromatic and luminance adapting stimuli. In marked contrast with the traditional MAE, the size of the induced positional offsets are not significantly affected by the chromatic or achromatic contrast composition of either the test or adapting stimuli, even when the stimuli constitute mutually orthogonal axes in colour space. Figure 4b shows the maintenance of this non-selectivity in the equiluminant plane. In marked contrast to the traditional MAE, the positional MAE appears to be immune to differences in chromatic composition between the adapting and test stimuli.

Another departure of the positional MAE from the behaviour of the traditional MAE lies in its variation with contrast. Figure 4c demonstrates how little the measured

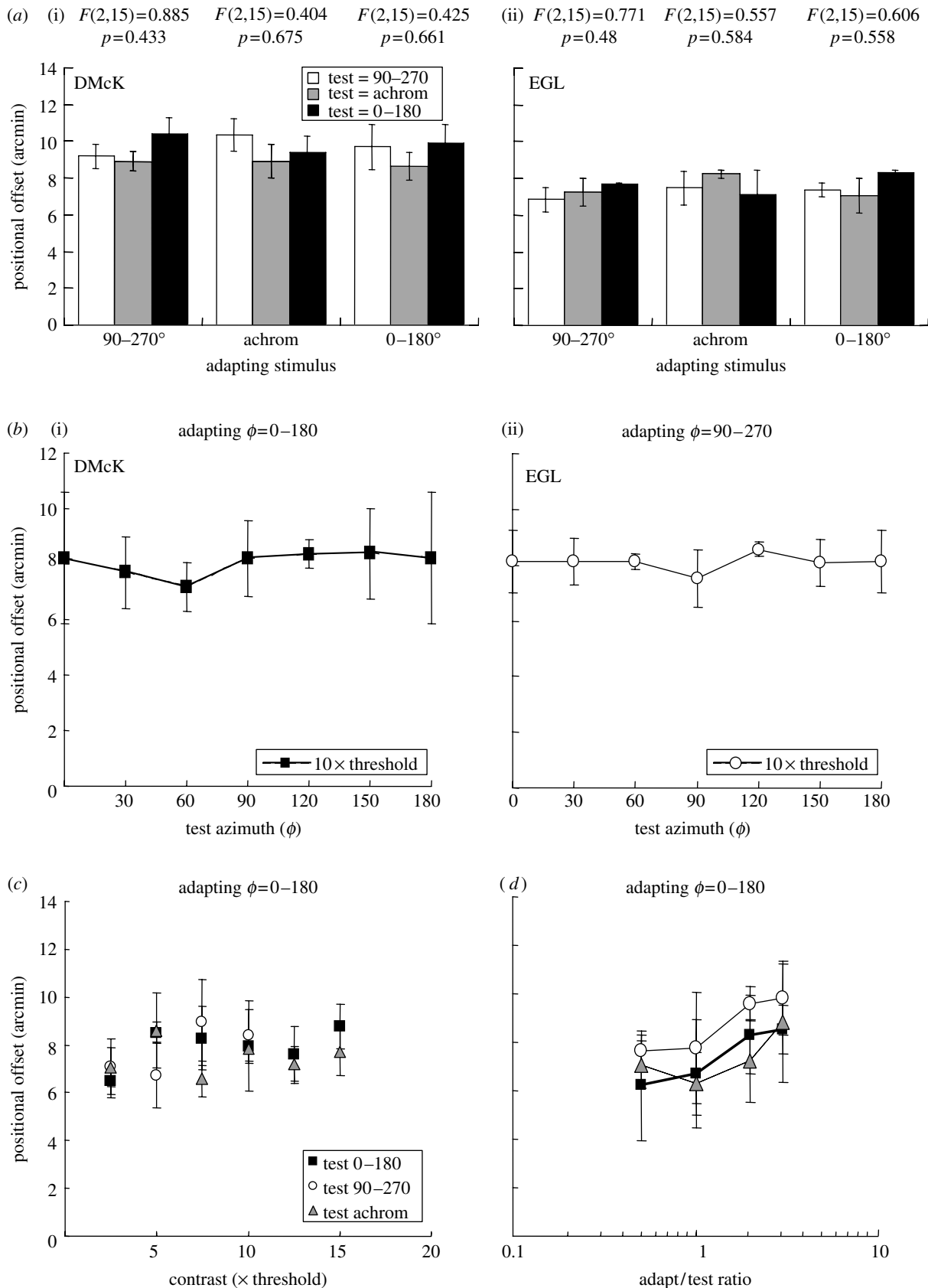


Figure 4. (a) Magnitude of the positional MAE induced by adaptation to moving L/M , $S/(L+M)$ chromatic and luminance stimuli, in test stimuli that are modulated along the same three cardinal axes. All stimuli were set at $10\times$ threshold (contrast (%)) at threshold: $\phi=0-180^\circ$ DMcK: L -cone = 0.65, M -cone = 1.28; EGL: L -cone = 0.63, M -cone = 1.21; $\phi=90-270^\circ$ DMcK: S -cone = 7.0; EGL: S -cone = 10.0; achromatic contrast thresholds: DMcK = 1.9; EGL = 2.0). (b) Magnitude of the positional MAE induced in equiluminant chromatic test stimuli of variable azimuth (ϕ), by L/M ($\phi=0-180^\circ$) and $S/(L+M)$ ($\phi=90-270^\circ$) equiluminant adapting stimuli. (c) The effect of increasing adapting and test stimulus contrast on positional MAEs generated by adaptation to a moving L/M ($\phi=0-180^\circ$) grating in L/M , $S/(L+M)$ chromatic and achromatic test stimuli. (d) Variation in positional MAE magnitude as a function of adapt/test ratio. The adapting stimulus is an L/M grating and three test stimuli were used, an L/M , $S/(L+M)$ and an achromatic grating.

size of the positional offset varies as a function of stimulus contrast compared to the traditional MAE which exhibits an approximately threefold increase over a similar contrast range. Moreover, even at the highest contrast levels the extent of the positional offsets generated are not significantly greater for test stimuli of the same orientation in colour space as the adapting stimulus, compared to those test stimuli which are orthogonal to the adapting stimulus. The data in figure 4c confirm that the lack of colour specificity exhibited by the positional MAE is not simply due to an inappropriate choice of adapt and test stimulus contrast levels. The graph plots the size of the positional offset induced by L/M ($\phi=0-180^\circ$) adapting stimuli on $S/(L+M)$ ($\phi=90-270^\circ$) and achromatic test stimuli as a function of adapt/test ratio. Unlike the pattern of change observed in the analogous traditional MAE experiment, the positional MAE exhibits a non-selective increase for all test stimuli and not just for the test stimuli of the same orientation in colour space as the adapting stimulus.

4. DISCUSSION

The results from these experiments indicate that motion adaptation reveals two very different patterns of selectivity, each of which is determined by the post-adaptation behavioural goal of the observer. On the one hand, the traditional form of the MAE where the observer is required to null illusory motion, is colour-selective, exhibiting a clear sensitivity to any difference between the chromatic composition of the adapting and test stimuli. On the other hand, motion-induced shifts in the perceived location of stimuli occur regardless of any differences in chromatic composition between adapting and test patterns. This dual level of effects is consonant with current models of the MAE which propose at least two stages of adaptation; an early stage that displays a high degree of spatial specificity, and a later stage of adaptation where selectivity for the spatial properties is low (Mather & Harris 1998). We show that not only is there a segregation between colour and luminance input to low-level motion detectors, but that there is also a further chromatic division between red-green (L/M) and blue-yellow ($S/(L+M)$) colour opponent inputs. The selective adaptation effects for L/M and $S/(L+M)$ in the traditional MAE is consistent with the idea that chromatic motion (at least at high contrast) is analysed by cone-opponent channels, often equated with the psychophysically derived 'cardinal mechanisms' (Krauskopf & Farrell 1990), and mirrors the parvo-, konio- and magno-cellular parcellation of anatomical inputs to the primary visual cortex (Chatterjee & Calloway 2003). The results show that when chromatic and luminance stimuli are equated in terms of their salience it is possible to psychophysically dissect different levels within the motion processing pathway where information from different sub-modalities is either processed separately and has the potential, under appropriate conditions, to be independently adaptable, or undergoes integration and is not independently adaptable. In the latter case, an important caveat is that the extent of the segregation revealed is very much dependent upon the relative strengths of the adapting and test stimuli. In previous studies where chromatic and luminance stimuli were not directly equated, strong cross-adaptation

effects were reported for colour and luminance stimuli (Cavanagh *et al.* 1984; Derrington & Badcock 1985). Our results, with equated stimuli, indicate that adaptation does exhibit colour selectivity but that cross-adaptation effects, while being minimized, never actually fall to zero (see figure 2a) indicating that the segregation between colour and luminance is not absolute. However, the exact means by which the visual system deals with chromatic motion remains a contentious issue and numerous different processing mechanisms have been proposed for its analysis. These range from chromatically sensitive low-level or motion-energy analysers, of the kind mentioned above, to 'higher-order' processes that involve more cognitively complex analysis, such as feature tracking for example (Seiffert & Cavanagh 1998). A picture is emerging that appears to suggest that the involvement of either low-level or higher-order cognitive processing is dependent upon the parameters of the stimulus; high contrast chromatic stimuli, for example, are more likely to be analysed by low-level motion detectors while low contrast chromatic stimuli are more likely to be analysed by position tracking (Cropper & Derrington 1994, 1996; Seiffert & Cavanagh 1998). Our data provide some support for this view, the reduced colour tuning exhibited by the static MAE at low chromatic contrasts (less than $5\times$ detection threshold) compared to that found at high contrasts may be a reflection of such a transition from chromatically selective low-level motion detectors, to chromatically insensitive feature trackers.

The ability of motion to generate changes in the perceived position of visual stimuli provides a vivid and compelling demonstration of the fact that interactions must occur at some level between the respective processing pathways within the visual cortex. Two potential models have been proposed for these interactions (Whitney & Cavanagh 2003): the first postulates that a single motion adapted site is responsible for the traditional MAE and positional after-effects; the second that motion can generate different kinds of adaptation in motion and positional processing pathways. In the latter model the different colour specificities of the traditional and positional MAEs may be explained in terms of how motion processing and position encoding utilize chromatic and luminance input. In the case of motion processing, numerous studies have demonstrated very different dependencies upon chromatic and luminance input (Krauskopf & Li 1999), while for position encoding, at least in the case of Vernier judgements, chromatic and luminance signals appear to have similar efficacy (Krauskopf & Farrell 1991; Krauskopf & Forte 2002). Thus, adaptation to luminance and chromatic motion could have different consequences in the different processing pathways. Against this view, however, are recent results from our laboratory that clearly demonstrate that positional judgements are, in fact, based on independently adaptable outputs from colour-opponent mechanisms (McKeefry *et al.* 2004; McGraw *et al.* 2004a,b). In these experiments, adaptation to static luminance and chromatic contrast patterns induce large positional shifts only if the test stimuli are of a similar orientation in colour space. This colour selectivity in position encoding following adaptation to static patterns is juxtaposed with a complete lack of colour selectivity that is exhibited by the positional MAE following adaptation to

motion. It implies that at the level where motion and positional mechanisms interact, the nature of the cue used to generate the motion signal, whether it be chromatic or luminance contrast, is irrelevant.

This kind of integration which takes place across different visual sub-modalities is very much in keeping with models of processing in the visual brain that emphasize the multi-dimensional nature of neural analysis (Lennie 1998), whereby information from different sub-modalities can be processed within the same neurons. A clear example of this kind of interaction has been shown to exist in a motion sensitive region of the macaque monkey cortex, the superior temporal sulcus, where neurons have been found to respond to form cues which imply motion despite the absence of real motion signals (Krekelberg *et al.* 2003). In the light of this data it is tempting to speculate that human V5/hMT+ is the cortical locus of the kind of integration observed between colour and motion in the positional MAE. This speculation is based on three lines of evidence. First, while neurons in macaque V5/MT seem to be able to respond indiscriminately to a variety of moving chromatic stimuli, they do not appear to play a significant role in the identification of such colours (Gegenfurtner *et al.* 1994). Second, area V5/MT also possesses neurons that are cue-invariant, i.e. maintain their response to motion regardless of the feature that is signalling the motion (Albright 1992). Third, targeted cortical disruption (using transcranial magnetic stimulation) of area V5 in human subjects reduces the perceived spatial misalignments generated in the positional MAE (McGraw *et al.* 2004a,b). In marked contrast, disruption of V1 has little or no influence on motion-induced positional shifts.

While multi-dimensional processing allows for the integration of visual information at the level of the single neuron, in its strictest sense it precludes the selective processing by neurons of different visual sub-modalities. The data presented here clearly demonstrate colour selectivity in the traditional MAE which necessitates some form of functional segregation of colour and luminance motion processing, at least in the early stages of motion processing. At higher levels of motion processing, positional MAEs are generated irrespective of the particular chromaticity of adapting and test stimuli, or whether they are defined by an entirely different cue altogether. These important findings support models of visual processing which depict outputs, from initially segregated colour-opponent and luminance mechanisms, being made available and combined at later stages of processing in order to achieve particular behavioural objectives (Chichilinsky *et al.* 1993; Dougherty *et al.* 1999).

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.