Centrifugal propagation of motion adaptation effects across visual space

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Perceptual distortions induced by adaptation (aftereffects) arise through selective changes in the response properties of discrete subpopulations of neurons tuned to particular image features at the adapted spatial location. The systematic and well-documented increase of cortical receptive field sizes with eccentricity dictates that visual aftereffects ought to become less tightly tuned for location as stimuli are moved away from fixation. Here, we demonstrate that while this pattern holds for archetypal orientation and spatial frequency aftereffects, the effects of motion adaptation are characterized by precisely the opposite relationship. Surprisingly, adaptation to translational motion close to fixation induces distortions of perceived position and dynamic motion aftereffects that propagate centrifugally across visual space, resulting in a lack of location specificity. In contrast, motion adaptation in more peripheral locations produces aftereffects that are largely limited to the adapted spatial region. These findings suggest that central motion adaptation has the unique capacity to influence the response state of spatially distant neural populations that do not themselves encode the adapting stimulus.

Keywords: vision, motion, position, adaptation, receptive field, visual space

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Introduction

Prolonged inspection of a visual pattern has the potential to profoundly alter subsequent perception—via a process known as visual adaptation. Previous investigations of perceptual distortions induced by adaptation, or after-effects as they are better known, have played a pivotal role in establishing visual selectivity to a broad range of spatial (Blakemore & Campbell, 1969; Gibson & Radner, 1937; Köhler & Wallach, 1944; McCollough, 1965; Pantle & Sekuler, 1968) and temporal (Masland, 1969; Moulden, Renshaw, & Mather, 1984; Pantle, 1974) image properties. Perhaps the most notable among these is that of motion. Sustained exposure to motion in a particular direction results in an inveterate and beguiling phenomenon known as the motion after-effect (MAE), whereby subsequently viewed stationary objects appear to temporarily drift in a direction opposite to that of the adapting stimulus. More recently, it has been shown that this adaptation-induced illusory motion is also accompanied by a perceived shift in the spatial location of the stimulus as a whole (McGraw, Whitaker, Skillen, & Chung, 2002; Nishida & Johnston, 1999; Snowden, 1998). The positional shifts resulting from motion adaptation show several characteristics that distinguish them from the traditional MAE. First, they are immune to changes in spatial frequency, contrast, and chromaticity between adapting and test stimuli—manipulations that dramatically reduce the magnitude of the traditional MAE (McGraw et al., 2002; McKeefry, Laviers, & McGraw, 2006). Second, unlike the traditional MAE, the inter-ocular transfer of these effects is almost complete (McGraw et al., 2002). Finally, the temporal decay properties of each aftereffect differs (Nishida & Johnston, 1999). Taken together, these findings suggest that the traditional MAE and motion-induced positional shifts are likely to be mediated by adaptation mechanisms acting at different levels of visual processing.

Current models of the MAE are based on changes in the population response across neurons tuned to a range of directions of motion. The most rational exemplar of this type of model posits adaptation at least two stages of visual analysis (Mather & Harris, 1998). The initial stage is associated with low binocularity and distinct selectivity for spatial properties, while adaptation at the later stage predicts high degrees of binocularity (or inter-ocular transfer) and broad tuning for stimulus attributes. The perceptual manifestation of adaptation at each stage reflects the physiological properties of the neuronal populations that mediate them. Early adaptation in the model is thought to reveal the adaptive behaviour of neurons in the primary visual cortex (V1), whereas later stage adaptation is though to occur in extra-striate cortical area V5/MT. Indeed, aftereffects consistent with selective adaptation at multiple levels of motion analysis have been demonstrated (Nishida & Ashida, 2000; Nishida & Sato, 1995; Verstraten, van der Smagt, Fredericksen, & van de

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Grind, 1999). The properties of the traditional MAE, measured with static test patterns, are all consistent with early stage cortical adaptation. In contrast, adaptation-induced positional shifts display properties that are consonant with adaptation occurring at a later stage of cortical processing, most likely at the level of V5/MT. The disruption of ongoing cortical activity (using transcranial magnetic stimulation) immediately following motion adaptation dramatically reduces the magnitude of perceived spatial shifts that normally occur, when delivered to V5/MT, but has little or no effect when delivered to V1. This finding strongly suggests that the anatomical locus at which motion and position information interact following adaptation is area V5/MT rather than earlier in the visual pathway (McGraw, Walsh, & Barrett, 2004). More recently, a human neuroimaging investigation reported that spatial representations in V1 maps remain invariant when measured with stimuli containing carrier gratings drifting in different directions (Liu, Ashida, Smith, & Wandell, 2006).

The geometries of receptive fields in V5/MT, like their V1 counterparts, are smallest close to fixation and gradually increase in size with increasing eccentricity. This change in scale is often referred to as "cortical magnification." Although the absolute dimensions of receptive fields in the middle temporal (MT) area are somewhat dependent on the method of measurement (Raiguel, van Hulle, Xiao, Marcar, & Orban, 1995), single cell recordings from macaques indicate that they are about ten times greater than those found in V1 at any given eccentricity and show a linear relationship with eccentricity (Albright & Desimone, 1987).

A consequence of the magnification of receptive field size is that the perceptual consequences of adaptation should be demonstrable over ever increasing spatial regions as the adaptation site is moved further away from the fovea. At fixation, where receptive fields in both V1 and MT are at their smallest, the effects of adaptation at each cortical level should be most specific to the adapted spatial region. This location specificity arises by virtue of the fact that when adapting and test stimuli are presented in the same region, both will be encoded by a common set of receptive fields, thus producing the greatest aftereffect. However, as the degree of spatial misregistration between each site is increased, the magnitude of the aftereffect will decline since the test stimulus will be analyzed by receptive fields progressively distant to those that have undergone adaptation. The spatial tolerance to decoupling the adapting and tests sites should be directly related to the receptive field properties at a given eccentricity. In the periphery, where receptive field sizes are larger, it should be possible to adapt at one region of the receptive field and measure the perceptual consequences of this at another. Effects of this type have previously been reported at the level of MT in macaques (Priebe, Churchland, & Lisberger, 2002).

In the present paper, we examine whether aftereffects become less tightly tuned for spatial location as stimuli are moved away from fixation and are encoded by neurons with progressively larger receptive fields. We show that while this predicted pattern of location tuning is found for orientation and spatial frequency aftereffects, the effects of motion adaptation are characterized by precisely the opposite relationship.

Methods

The basic experimental arrangement used to measure distortions of perceived position resulting from motion adaptation is outlined in Figure 1A and consisted of a cycle of adaptation, followed by a test phase in which observers judged the relative vertical alignment of two horizontally separated elements. Prior to the commencement of the main experiment, two preliminary experiments were conducted. First, performance on the vertical alignment task was measured in the absence of motion adaptation. This allowed us to restrict test patch separations to a range in which alignment thresholds did not vary systematically (Whitaker, Bradley, Barrett, & McGraw, 2002) and provided baseline measures of alignment bias. Second, motion-induced shifts in the perceived position of the adapting patches were measured to enable the creation of individual perceptually aligned adapting stimuli.

In all experiments, stimuli were computed in MATLAB and displayed by a Cambridge Research Systems ViSaGe on a gamma corrected Mitsubishi Diamond Pro 2045U CRT monitor with a refresh rate of 100 Hz and mean luminance of 47 cd/m^2. Seven adults (ages 20–37; two females) participated in the study, the two authors and five individuals who were naïve to the specific experimental purposes. All had normal or corrected-to-normal visual acuity.

Equating positional sensitivity across space

The ability of motion signals to influence the perceived position of a visual object is largely determined by the accuracy with which the object itself can be localized (DeValois & DeValois, 1991). In general, objects with stimulus features that can be localized precisely in space show smaller motion-induced positional shifts. Therefore, in order to ensure that changes in positional sensitivity did not influence the spatial tuning profiles of motion-induced positional offsets, we used a stimulus arrangement where alignment thresholds were constant across the spatial range investigated during the adaptation experiments. A forced choice procedure was implemented, whereby participants were required to indicate which of the two patches (1-dimensional Gaussian blobs; width = 1 deg, Gaussian vertical contrast profile $\sigma = 0.33$ deg; duration = 100 ms)

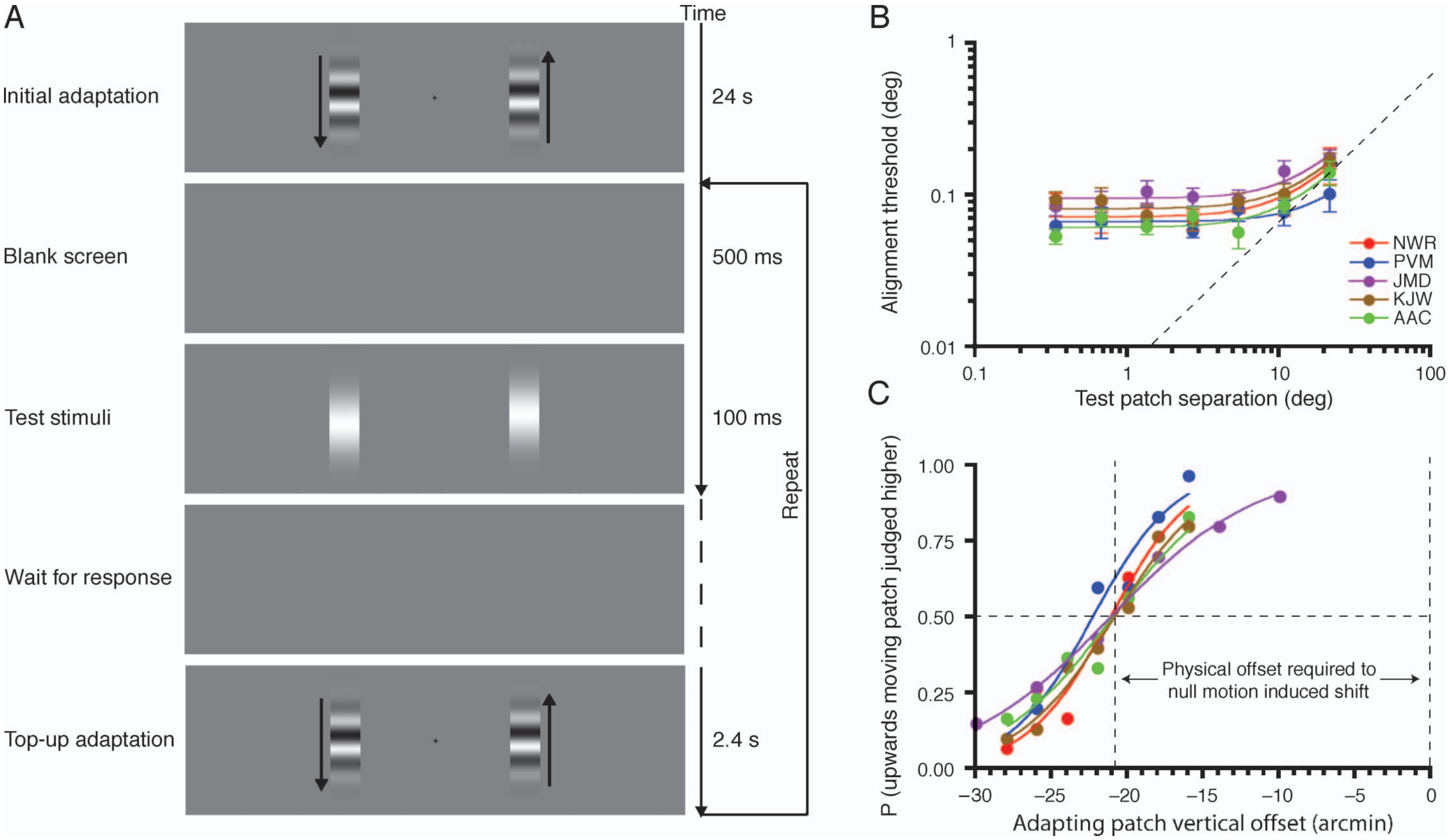

Figure 1. (A) Schematic illustration of the main experiment. Observers adapted to a pair of sinusoidal patches with a Gaussian vertical contrast profile, in which the sinusoidal luminance modulation (grating) in each patch drifted in opposite directions (up/down). Adapting stimuli were presented on either side of a small fixation cross with an edge-to-edge separation of 1, 5, or 10 deg. Following motion adaptation, observers were required to make a vertical alignment judgment on two briefly presented test stimuli. The test stimuli had identical dimensions to the adapting stimuli but contained no sinusoidal luminance modulation. The vertical offset between test stimuli was controlled by physically shifting the position of each patch in opposite directions (up/down). For a range of test stimuli separations (1–10 deg edge-to-edge), motion-induced shifts in perceived position were quantified by calculating the physical offset required for the test stimuli to appear perceptually aligned (point of subjective alignment). (B) Vertical alignment thresholds in the absence of motion adaptation. Manipulations of inter element separation can have a marked influence on observers ability to make alignment judgments. To avoid confounding changes in separation with positional sensitivity, we initially ensured that the vertical spread of the test stimuli was sufficient to minimize changes in observer sensitivity across the range of test separations investigated (see Whitaker et al., 2002). (C) Nulling the perceived misalignment of adapting patches. As predicted by DeValois and DeValois (1991), the perceived position of each stimulus is shifted in the direction of adapting motion. The magnitude of this perceptual misalignment was measured for each subject at each adaptor separation. The adapting stimuli were then physically adjusted in position to ensure that throughout adaptation they were always perceptually aligned. This allowed us to isolate the effects of motion adaptation on the perceived position of the subsequently presented test stimuli. Data are shown for an adapting stimuli separation of 5 deg.

appeared higher. The vertical offset of the test stimuli was controlled in a Method of Constant Stimuli (MOCS, 7 levels ×30 repetitions) by shifting the position of both patches by equal amounts in opposing directions (up or down). For each of a range of interleaved test patch separations, the psychometric function relating participant responses to test patch offset was fit by a logistic function and the alignment threshold was quantified by calculating the just-noticeable-difference (JND; half the offset between the 27% and 73% levels on the psychometric function approximately). Data for all 5 observers are presented in Figure 1B and confirm that alignment thresholds, in the absence of motion adaptation, are constant for test patch separations up to 10 deg.

Creating perceptually aligned adapting stimuli

The adapting stimuli consisted of two strips of sinusoidal grating (spatial frequency of 1 c/deg; width = 1 deg, Gaussian vertical contrast profile σ = 0.33 deg), which drifted in opposite directions (up/down) at 5 deg/s (see

Figure 1B). The two gratings were presented either side of a central fixation cross (10 × 10 arcmin), with an edge-to-edge separation of 1, 5, or 10 deg. To avoid the build up of a lasting retinal-afterimage, the contrast polarity of the fixation cross was alternated at 5 Hz. Drifting the adapting gratings induced a predictable perceived vertical misalignment (DeValois & DeValois, 1991). Participants judged the vertical alignment of pairs of adapting stimuli presented for 2.4 s while the offset of their Gaussian contrast envelopes was manipulated via an MOCs (see Figure 1C). Perceptually aligned adapting stimuli were then created for each observer by offsetting the vertical position of the patches so as to null the motion-induced positional shift. This allowed us to isolate the role of motion adaptation on perceived position and circumvented the influence of any unwanted spatial after-effects that may have otherwise been introduced (Hess & Doshi, 1995).

Distortions of perceived position following motion adaptation

Following these initial measures, subjects repeated the vertical alignment task previously used to measure positional sensitivity (outlined above) with the important exception that they were exposed to a pair of individually adjusted moving adapting stimuli prior to and between test phases (initial period 24 s and 2.4 s top-up between each trial). For each adaptor separation (1, 5, and 10 deg), a range of randomly interleaved test patch separations (1–10 deg) were presented and motion-induced shifts were quantified by calculating the shift in the point of subjective alignment (the physical offset required for the test patches to be perceptually aligned) of the resulting psychometric functions. In each condition, separate estimates of positional shifts were obtained for each combination of adapting motion direction (left patch moving up/right patch moving down and vice versa) and averaged for each participant.

To quantify the location tuning of motion-induced positional shifts, group averaged results were fitted with Gaussian functions of the form:

$$Y = Ae^{\frac{-(X_{\text{test}}-X_{\text{adapt}})^2}{s}}, \qquad (1)$$

where the amplitude parameter A sets the maximum effect, x_{test} denotes the test patch separation, x_{adapt} denotes the adapting patch separation (fixed), and s is a space constant that controls the width of the fitted function. For an adaptor separation of 5 deg (Figure 2B), separate Gaussians were fitted to data for test patch separations less than 5 deg and greater than 5 deg, so that each provided an independent estimate of the space constant.

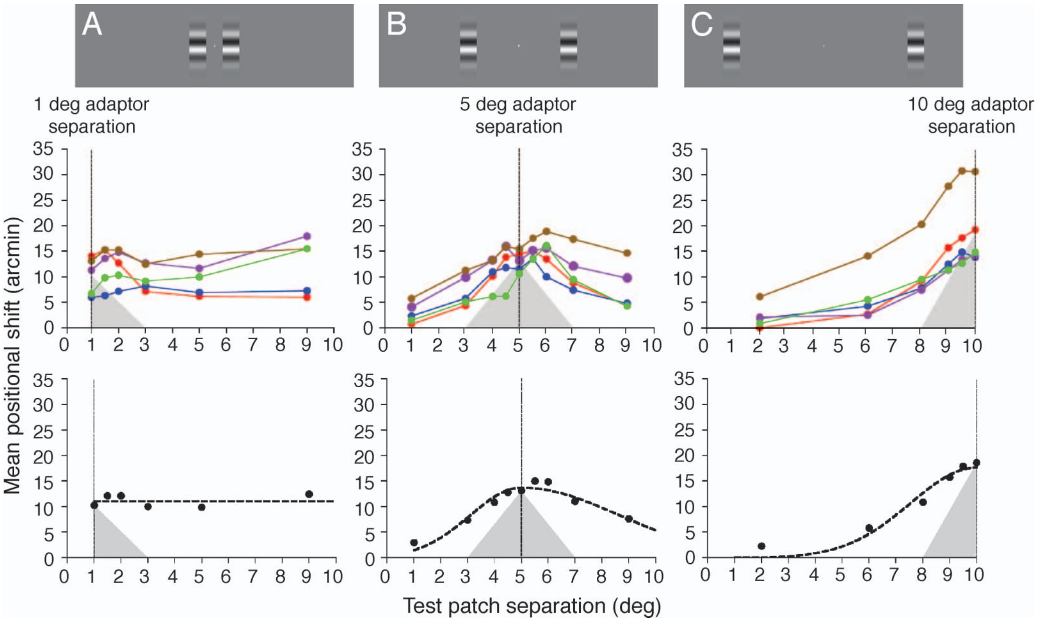

Figure 2. Summary plots showing mean positional shifts (half the difference between the points of subjective alignments (PSAs) in the two adaptation direction conditions) following motion adaptation. In each plot, the separation of the pair of adapting stimuli is indicated by the position of the vertical dotted line (A) 1 deg; (B) 5 deg; (C) 10 deg. The gray triangle on each plot provides an indication of the degree of spatial overlap between adapting and test stimuli. Where the vertical peak coincides with the dashed line, the adapting and test stimuli were in exact spatial register. Test patch separations away from this point represent increasing spatial decoupling of adapting and test sites. The lower panels show the mean data for each test separation, at each of the adaptor separations, fitted with Gaussian tuning functions as described in the text.

Orientation, spatial frequency, and dynamic motion aftereffects

Unless otherwise stated, the size, configuration, and duration of adapting and test stimuli and methods of data analysis in subsequent experiments were equivalent to those described above. Orientation (tilt) aftereffects were induced by pairs of 1 c/deg adapting stimuli, with carrier gratings oriented 15 deg clockwise and anti-clockwise from vertical, which counter-phase flickered at 2.5 Hz. Test stimuli were pairs of 1 c/deg gratings with equal and opposing orientations away from vertical. Participants were required to indicate whether the carrier gratings of the test patches “leaned” towards or away from one another (i.e., / \ or \ /). Post-adaptation shifts in perceived orientation were repulsive in nature, requiring that test patch carriers be tilted slightly in the same direction as the adapting stimuli for them to appear vertical. Reported effects denote the shift in this perceived vertical point for each patch (rather than the relative orientation of the pair).

To produce shifts in perceived spatial frequency, observers adapted to pairs of 1 c/deg and 4 c/deg horizontal gratings that counter-phase flickered at 2.5 Hz. Test stimuli were pairs of horizontal gratings with spatial frequencies that were equivalent log steps above and below 2 c/deg. Participants were required to indicate which of the two test patches appeared to have the higher spatial frequency carrier. The obtained effects were again repulsive in nature, requiring that the spatial frequency of test patches be shifted towards that of the adapting stimuli for them to appear equivalent.

In order to measure the magnitude of the dynamic MAE, identical adapting stimuli to those described in Figure 1 were employed. Test stimuli consisted of compound gratings, where two grating components were made to drift in opposite directions at 5 deg/s. The spatial frequency of each component was 1 c/deg. Observers were required to indicate which of the two test patches moved upwards. Using an MOCs procedure, the relative contrast of each component was manipulated. Note that overall patch contrast was kept constant, and the relative component contrast ratio for the patch on the right was always the reciprocal of that on the left. Dynamic MAE strength was quantified by establishing the degree of contrast imbalance between test component contrasts required to null the illusory motion.

Results and discussion

The distortions of perceived position resulting from motion adaptation, for each of the three adaptor separations, are shown in Figure 2. Regardless of adaptor site, when adapting and test elements are presented in the same spatial location (peak of gray triangle and vertical dashed lines), marked positional shifts are produced. More interestingly, a completely different pattern of after-effect emerges as the adapting and test site are spatially decoupled in different directions. For adapting stimuli separated by 10 deg (Figure 2C), marked spatial tuning of the positional after-effect is evident; the magnitude of the distortion of perceived position is maximal when the test stimuli are also widely spaced and declines continuously for smaller test patch separations. The space constant of the tuning function fitted to the mean data is 12.05 deg. Comparable spatial tuning is also found for adapting stimuli separated by 5 deg (Figure 2B), although for most observers the drop-off of in the effect size is more dramatic when test separation was less than 5 deg (space constant = 7.21 deg) than when it was greater than 5 deg (space constant = 26.64 deg). Most strikingly, when motion adaptation occurs close to fixation (Figure 2A—adaptor separation of 1 deg), little evidence of spatial tuning is found. Rather, similar distortions of perceived position are manifested across the full range of test separations. This unexpected pattern of results suggests that the influence of motion adaptation close to fixation is qualitatively different to situations where it occurs more peripherally. The tuning profiles produced by adaptation close to fixation cannot be explained by a simple uniform spreading of effects across visual space from each adaptor site. Because we used pairs of adapting stimuli moving in opposite directions, this ought to result in a cancellation of effects across the midline. Instead, the results are more consistent with a propagation of the effects away from fixation (i.e. centrifugally).

Next, we sought to establish whether this counter-intuitive result was unique to the combination of motion adaptation and subsequent judgements of spatial position. In order to do this we examined the spatial tuning properties of two other well-documented after-effects: the tilt after-effect (TAE) and the spatial frequency after-effect (SFAE). Using almost identical stimulus configurations, we asked observers to make judgements of perceived orientation and perceived spatial frequency following matched periods of adaptation. As before, maximal after-effects in both orientation and spatial frequency domains were obtained when the adapting and test stimuli occupied the same region of visual space (see Figures 3A and 3B). In contrast to motion adaptation, however, both tasks showed tight spatial tuning when the adapting stimuli were closely spaced (1 deg). For widely separated adapting stimuli (10 deg), spatial tuning was also evident but was broader in both cases—in keeping with the increasing scale of underlying receptive fields. On the whole, spatial tuning was broader for spatial frequency as compared with orientation adaptation at each adaptor location. Both tasks showed tuning effects consistent with previous studies (Gibson & Radner, 1937; Ware & Mitchell, 1974), yet strikingly neither displayed the very broad tuning observed for motion adaptation close to fixation (see Figure 2A).

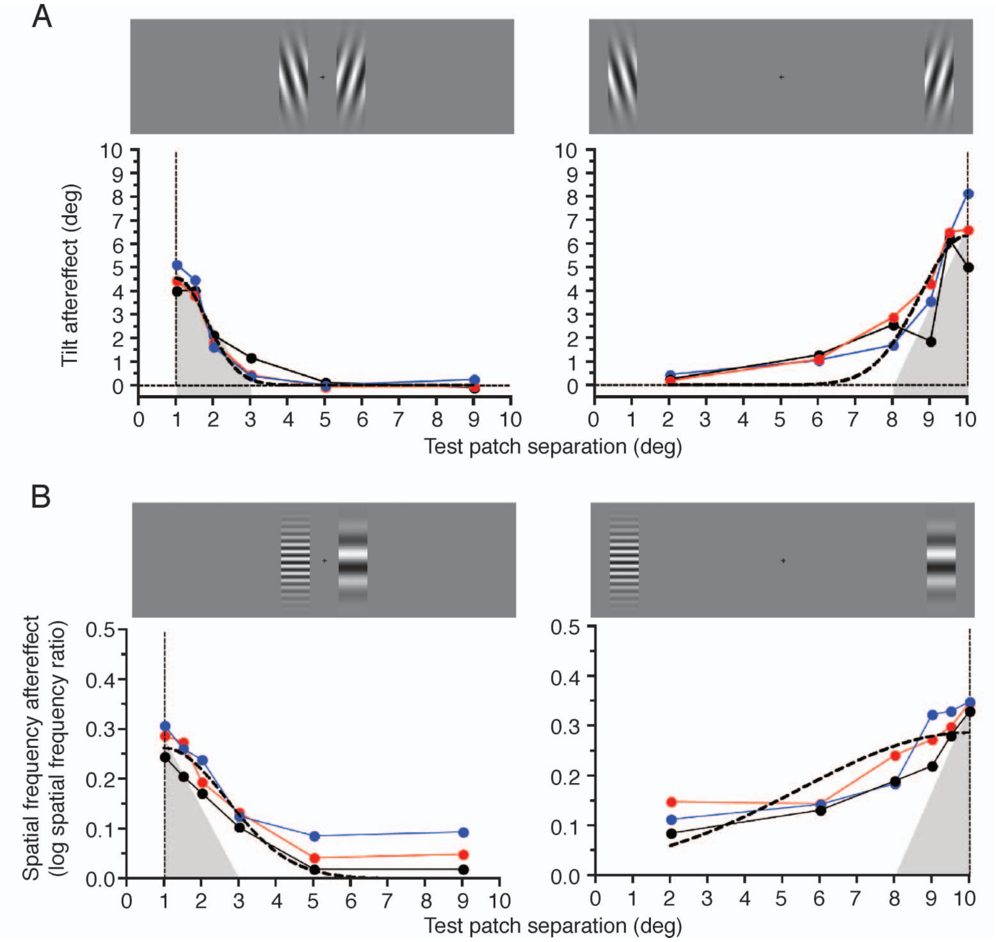

Figure 3. Comparison of spatial tuning profiles for aftereffects of (A) orientation and (B) spatial frequency. The experimental configuration was identical to that outlined in Figure 1 except that observers adapted to orientation or spatial frequency differences and subsequently made relative judgements of the orientation and spatial frequency content of test stimuli. The mean data have again been fitted with Gaussian tuning functions (black dashed line). For both orientation adaptation and spatial frequency adaptation, best fitting space constants (width) were broader at an adaptor separation of 10 deg (orientation = 3.1 deg; spatial frequency = 40.44 deg) than an adaptor separation of 1 deg (orientation = 1.4 deg; spatial frequency = 5.71 deg).

One possible explanation for this unexpected pattern of results is that the adapting stimuli, despite containing only linear motion either side of fixation, might stimulate receptive fields sensitive to more complex forms of motion components such as rotation or radial contraction and expansion. Physiological studies in primates have previously identified neurons with large receptive fields selective to such motion properties (Duffy & Wurtz, 1991; Tanaka & Saito, 1989). As stated at the outset, a corollary of adapting neurons with relatively large receptive fields is that it should be possible to adapt one region of the receptive field and measure the perceptual consequences of this process in another region of the same receptive field (Priebe et al., 2002). This is indeed borne out in human psychophysical studies where it has been shown that adapting centrally to rotational motion results in both motion after-effects (Snowden & Milne, 1997) and positional after-effects (Whitney & Cavanagh, 2003, see also Whitney & Cavanagh, 2000) that extend to areas beyond the adapted region of visual space. If our closely spaced adapting stimuli were to preferentially adapt larger rotational receptive fields, a proposal that would not be unreasonable, we would predict broad spatial tuning for this condition, but not for widely separated adapting stimuli where the sense of rotation might be much weaker. In order to test this explanation, we conducted two control experiments. In the first, we maintained the spatial separation of our adapting stimuli but changed their orientation such that they were located above and below fixation and now drifted left and right rather than up and down. This configuration should be equally effective in adapting large receptive fields sensitive to rotational motion (compare Figures 4A and 4B). The location of the test stimuli remained, as before, to the left and right of fixation and the task was again a vertical alignment judgment. The resulting data for three subjects are presented in Figure 4 and reveal a very different pattern of results from those obtained with the original adaptor

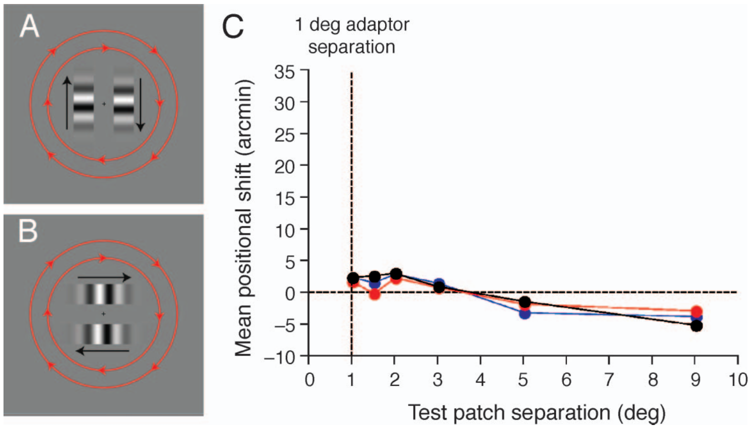

Figure 4. (A–B) To investigate the potential role of rotational motion signals in producing the broad spatial tuning of positional aftereffects, the original adaptor configuration of upwards and downwards moving patches separated by 1 deg was rotated through 90 degrees. Changing the adaptor configuration in this way should be equally effective at stimulating receptive fields that respond to rotational motion. (C) This new configuration, however, produced little or no systematic shift in the predicted direction. In actual fact, all three subjects showed a slightly negative shift in perceived position for the widest test patch separations.

configuration (see Figure 2A). The data show that this manipulation of the adapting stimulus failed to produce any appreciable positional offsets, in the predicted direction, at any of the original horizontal test separations. Next, we adapted with a single adapting stimulus located 0.5 deg from the fixation cross (see Figure 5). This ensures that only linear motion is present and that this motion is restricted to a single hemi-field. Entirely in keeping with our earlier results, we found motion-induced positional offsets, of approximately half the magnitude, that displayed little or no evidence of spatial tuning. Taken together, these results indicate that the lack of spatial tuning, or indeed the differential tuning profiles found at each adaptor eccentricity, is unlikely to be related to adaptation of large-scale mechanisms sensitive to rotational motion.

A second possibility is that the size of the adapting patches in the widely separated adaptor condition may not be optimum for underlying receptive fields in more peripheral locations. In macaque area MT, receptive field sizes are on average about ten times larger than their V1 counterparts and increase linearly with eccentricity (Albright & Desimone, 1987). If scaled appropriately to match the underlying changes in neural architecture, the differences in spatial tuning for motion adaptors at each eccentricity might be reduced or even disappear. This of course would not explain the differences in tuning between motion, orientation, and spatial frequency adaptation but merely provide an explanation for the changes in tuning profiles for motion adaptation in different regions of space. It is well established that the perceived velocity of a drifting sinusoidal grating decreases with

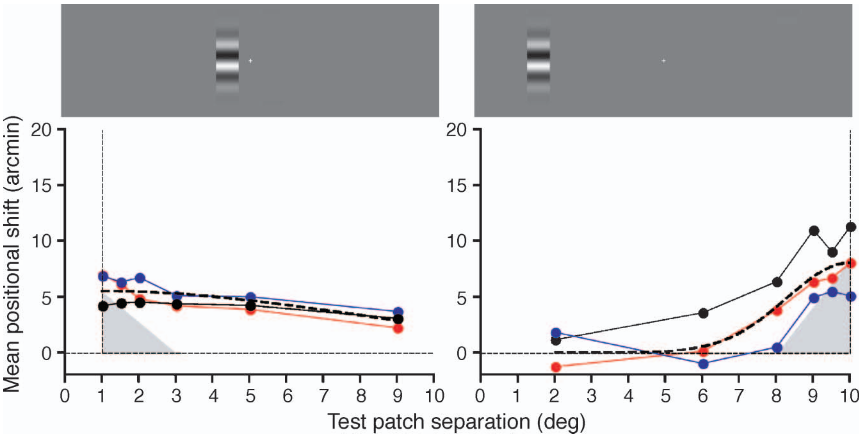

Figure 5. Motion-induced positional shifts produced by a single adapting patch. Comparison with results plotted in Figure 2 confirms that although removing one of the adapting patches reduces the absolute magnitude of positional shifts by ~50%, the overall pattern of the data remains unchanged. The spatial specificity of the positional aftereffects becomes more tightly tuned as the adapting patch is moved away from fixation (space constants of best fitting Gaussian functions for the left and right plots are 98.25 deg and 5.86 deg, respectively).

increasing eccentricity (Johnston & Wright, 1986; Tynan & Sekuler, 1982). This fact can be exploited to obtain a psychophysical estimate of the scaling factor required to compensate for eccentricity dependent changes in the cortical magnification factor (Johnston & Wright, 1986; Rovamo, Virsu, & Nasanen, 1978). To this end, we measured the increase in patch size for widely separated (10 deg) adapting patches required to equate the perceived velocity to that of the closely separated (1 deg) adaptor configuration (see Figure 6A). Scaling factors consistent with previous studies (between 1.6 and 1.7; see Figure 6B) were obtained for each subject (Johnston & Wright, 1986). Using magnified adapting stimuli, we then re-measured the tuning profile for the widely separated adaptor condition (10 deg) and the data are presented in Figure 6C. Despite scaling the stimuli such that the adaptors at each eccentricity have the same geometric relationship to underlying cortical receptive fields, the shape of the tuning profiles remained unchanged.

Previous studies have investigated the relationship between motion and positional after-effects (Nishida & Johnston, 1999; Whitney & Cavanagh, 2003). MAEs are often divided into two categories based on the temporal nature of the test stimuli used to measure the degree of adaptation-induced illusory motion. When illusory motion is perceived using a stationary test patch the term static MAE is applied, whereas test stimuli that flicker, or change their spatial structure over time, are used to expose dynamic MAEs. As stated previously, the traditional (static) MAE and positional MAE display very different properties and are almost certainly mediated by distinct mechanisms. In contrast, the dynamic MAE and positional MAE show several commonalities. Despite this, some important differences persist. For example, positional MAEs show storage of the effect (Whitney & Cavanagh, 2003); that is, illusory positional shifts are found even when intervals of several seconds are introduced between the adapting and test stimuli. After-effect storage is a hallmark of the static MAE and is not a characteristic associated with the dynamic MAE (Verstraten, Fredericksen, Van Wezel, Lankheet, & Van de Grind, 1996). The lack of consistent evidence has led to the extant notion that positional MAEs represent a new type of after-effect—one that is phenomenally distinct from other classes of motion after-effects (Whitney & Cavanagh, 2003). If this is the case, then the changes in spatial tuning profiles we report here for different eccentricities may be specific to positional judgements rather than represent a more general feature of motion adaptation *per se*. To address this issue, we conducted a further experiment in which we directly compared the spatial tuning of the dynamic MAE with those obtained for the positional MAE. Once again, we adopted a virtually identical experimental configuration. However, in this instance subjects were required to null any illusory motion resulting from adaptation using a standard contrast-based technique (Ledgeway, 1994). The data are presented in Figure 6 and show a reasonably good correspondence to the results obtained for positional judgements (see Figure 2). Predictably, the aftereffect was largest, regardless of adaptor location, when the adapting and test stimuli completely overlap in visual space. However, consistent with our previous positional judgements, marked spatial tuning is found for the widely spaced adapting stimuli, while much broader tuning was found for the closely separated adapting stimuli. This strongly suggests that the underlying mechanism mediating the pattern of tuning across space is common to both tasks and may be reflective of a more universal feature of motion processing. Having said this, it remains to be seen whether similar eccentricity-dependent changes in spatial tuning are

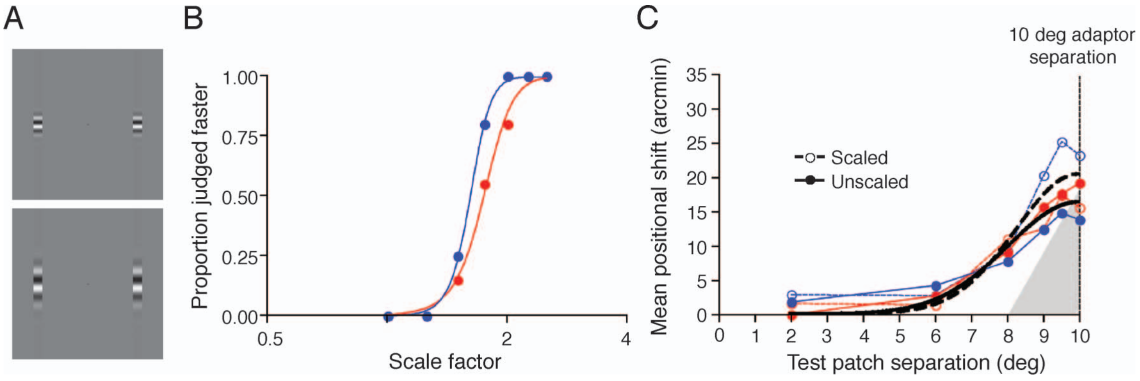

Figure 6. (A) Schematic representation of widely separated adapting stimuli before and after psychophysical size scaling. We measured the change in patch size required to equate the perceived velocity of the widely separated (10 deg) adapting patches to that of the closely separated (1 deg) adaptor configuration. The individual scaling functions are presented in panel B and are consistent with a previous study. (C) Using these individually magnified adapting stimuli, we then re-measured the tuning profile for the widely separated adaptor condition (10 deg) for two of the subjects whose data was presented in Figure 2. The fitted data showed a small increase in the amplitude of the effect (unscaled = 16.29 arcmin; scaled = 20.38 arcmin) with the scaled stimuli but very little change in the width of the tuning functions for each condition (unscaled = 7.70 deg; scaled = 5.97 arcmin).

characteristic of other motion adaptation phenomena such as the static MAE and elevations in contrast sensitivity. In contrast to the effects examined here, both of these consequences of motion adaptation typically exhibit marked retinotopic specificity. However, it is unclear whether this tight coupling of the effects to the adapted site changes with eccentricity. Other types of MAE, such as those generated via attentive tracking display little retinotopic specificity (Culham, Verstraten, Ashida, & Cavanagh, 2000). This high level MAE is revealed with dynamic (but not static) test stimuli and can compete or even counteract low level MAEs (Culham et al., 2000). The precise role attention-based MAEs play in the effects we report is presently unknown. Given that attentive tracking can produce a dynamic MAE, this adaptive process could, in principle, contribute to motion-induced shifts in perceived position. That said, it is not readily apparent how a high-level effect of this type could produce systematic changes in retinotopic specificity as a function of eccentricity.

A key assumption of visual adaptation is that the perceptual after-effects arise from the engagement of common sets of neurons by both the adapting and test stimuli. If, for example, adapting and test stimuli differ significantly in terms of their spatial frequency, orientation, or chromatic content, adaptation is unlikely to induce any perceptual distortions by virtue of the fact that each stimulus will be analyzed by ostensibly independent neural populations. The same principle applies when the adapting and test stimuli are presented in different regions of visual space. If each stimulus is encoded by neurons with non-overlapping receptive fields, there exists no obvious substrate for interaction. This axiom is supported by our results from orientation and spatial frequency adaptation (see Figures 3A and 3B) and by a number of previous studies (Gibson & Radner, 1937; Masland, 1969; Ware & Mitchell, 1974). Is it possible that the underlying change in scale of receptive fields in V5/MT can explain the results? The receptive fields of MT neurons are approximately circular, have a Gaussian shaped spatial response profile, and range from about 1 to 4 degrees in the foveal region, depending on the method of measurement (Raiguel et al., 1995). Receptive field sizes increase linearly with eccentricity, and at any point in space, the eccentricity of the receptive field center approximates to the spatial extent (diameter) of the field. Application of this rule to the stimuli used in the present experiment predicts that when the adapting stimuli are close to fixation (0.5 deg) and the test stimuli are presented more peripherally (5 deg from fixation), it is unfeasible that both stimuli will fall within a single receptive field. Moreover, the increase in spatial scale that occurs with changing eccentricity predicts exactly the opposite arrangement of the adaptation effects we observe with motion (see Figure 7). Larger receptive fields should be associated with broader tuning as the possibility of both adapting and test stimuli falling within a single receptive field increases. This is precisely the relationship we find for both orientation and spatial frequency adaptation. Motion adaptation, in contrast, produces exactly the opposite pattern of spatial specificity.

The spatial constraints of motion adaptation have recently been investigated in MT neurons of the macaque monkey (Kohn & Movshon, 2003). This group set out to establish whether contrast gain control governs adaptive changes in MT responses and the level in the visual hierarchy where this modulation originates. Previous work had suggested that short-term motion adaptation in MT emerges from an intra-cortical circuit within MT (Priebe et al., 2002). Contrast gain control is a widely acknowledged property of V1 neurons, many of which provide a direct input to MT (Maunsell & van Essen, 1983). Indeed, maps of directional interactions within MT receptive fields reveal an underlying substructure entirely consistent

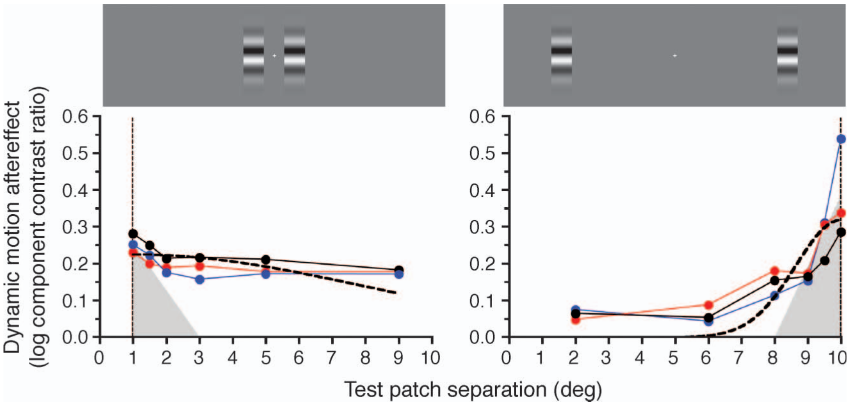

Figure 7. Spatial tuning profiles for the dynamic MAE. The magnitude of the dynamic MAE was measured using a technique that quantified the degree of imbalance between test component contrasts required to null the resulting illusory motion. A similar pattern of location tuning was obtained for measures of the dynamic MAE and the motion-induced positional offsets. The mean data have been fitted with the tuning function described in the text and reveal very broad tuning (space constant = 273.14 deg) when the adaptors are closely spaced (1 deg) and much narrower tuning (space constant = 3.79 deg) when they are widely separated (10 deg).

in scale with V1 input (Livingstone, Pack, & Born, 2001). Kohn and Movshon (2003) reasoned that the spatial specificity of adaptive effects should be limited by the receptive field properties of the neurons mediating them. Therefore, effects that occur directly at the level of MT, in contrast to those inherited from earlier stages of visual processing, should occur over very different spatial extents. They provided a clear demonstration that activity in MT neurons is regulated primarily by changes in contrast gain and that this effect is spatially distinct within the receptive field. Adapting one localized region within the MT receptive field did not affect the sensitivity to test stimuli presented in other regions of the same receptive field. This result adds considerable credence to the notion that adaptive properties of higher-level neurons (in this case MT) can be directly inherited from their visual inputs (in this case V1). This "down stream" inheritance is in some ways less surprising than the effect that we report in the present study, where substantial adaptation effects are transferred across visual space.

Conclusions

We show that the consequences of motion adaptation can be transferred across substantial regions of visual space. However, the emergence of this mechanism is highly dependent on where in the visual field motion adaptation takes place. When motion adaptation occurs close to fixation, the resulting aftereffects propagate centrifugally across visual space. These results present a challenge to any explanation based on known receptive field properties of neurons in striate and extra-striate cortex implicated in motion analysis and point to some form of inheritance of the adapted state between distinct neural populations. The precise physiological mechanisms underpinning this inheritance are yet to be uncovered. At present it is unclear whether this involves intra-cortical circuits at a particular level of motion analysis or is mediated by feed-forward/feed-back connections between successive stages in the cortical hierarchy.

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