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The Influence of Adaptation on Perceived Visual Location

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We demonstrate a marked effect of prior adaptation upon the perceived position of subsequently presented stimuli using both first-order (luminance-defined) and second-order (texture-defined) stimuli. The effect of varying the contrast of the adapting and test stimuli depends only upon the ratio of adapting/test contrast. Adaptation effects for the two types of stimuli differ in terms of interocular transfer and rate of decay. Whilst adapting and testing with the same type of stimulus (first- or second-order) produces large shifts in perceived position, little or no crossover effect was found. The data are accounted for by a model in which the centroid of the linear combination of after-image and test stimulus is extracted. © 1997 Elsevier Science Ltd.

Adaptation After-image Localization Centroid Human

INTRODUCTION

Many aspects of visual function have been elucidated through adaptation experiments. Included amongst these aspects are the domains of contrast and spatial frequency (Pantle & Sekuler, 1968; Blakemore & Campbell, 1969), colour (McCollough, 1965), motion (Pantle, 1974), shape (Gibson, 1933) and orientation (Gibson & Radner, 1937; Georgeson, 1973). The judgement of spatial position has also been examined in the form of figural aftereffects, whereby successively presented contours appear to repel one another (Köhler & Wallach, 1944). In recent years, however, the capacity of the visual system to perform spatial localisation tasks has received little attention in the form of adaptation studies. Even the limited studies which appear to have examined the process of relative localisation may not have actually done so. Wolfe (1987) showed that adaptation to a stimulus consisting of two abutting gratings with a small vernier offset produced an apparent vernier shift in a subsequently viewed vertical test grating. Wolfe concludes, however, that this phenomenon is probably simply a version of the tilt aftereffect, rather than being a manifestation of positional adaptation. Yeh *et al.* (1991) and Hess & Doshi (1995) adapted to a three-element stimulus whose central element was offset to the left or right of the midline. Subsequent viewing of an aligned three-element stimulus results in a perceived offset of the central element in a direction opposite that of the adapting stimulus. Once again, although this phenomenon might appear to result from positional adaptation, Hess & Doshi (1995) state that the aftereffect is probably based upon orientational grouping rather than on spatial position.

One possible reason why the effect of adaptation upon spatial location has received limited attention may be the widely held view that position is an elementary, irreducible property of objects, one which is not amenable to further manipulation (Westheimer, 1979; De Valois *et al.*, 1990). There is, however, strong evidence that spatial phase is malleable by prior adaptation. Georgeson & Turner (1984) discovered that adaptation to a grating had substantial effects upon the perceived nature of a complex test grating containing first and third harmonic components, and that these effects depended critically upon the phase of the adapting grating relative to the test. The results could be directly predicted by the formation of negative after-images produced by the adapting grating. In another example of adaptation-induced phase manipulation, Tulunay-Keesey *et al.* (1987) have observed that, following the disappearance of a stabilised retinal image, the addition of a uniform luminance increment results in a perceived phase reversal of the original image. In the present study, we demonstrate marked effects of adaptation upon the perceived location of subsequently viewed stimuli. These effects are quite distinct from those involving orientation, since they are invoked by adapting stimuli which themselves contain no oriented components.

Georgeson (1991) makes the important distinction between luminance and contrast adaptation. Luminance adaptation typically results in negative after-images and is probably of retinal origin, whilst contrast adaptation is

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orientation and spatial-frequency selective, and of cortical origin. In this study we use two classes of visual stimuli, which have previously been termed first- and second-order (Chubb & Sperling, 1988; Cavanagh & Mather, 1989). First-order stimuli involve luminance modulations which are suited to detection by the centre surround nature of early neural mechanisms. Second-order stimuli, on the other hand, require some form of non-linearity (such as rectification) before becoming amenable to analysis by conventional Fourier mechanisms. Use of these latter types of stimuli has therefore proved useful in providing information about processing later in the visual pathway. In an attempt to investigate the mechanisms involved in localising first- and second-order stimuli we now describe a series of experiments which investigate the effects of prior adaptation upon perceived spatial location of subsequently presented stimuli.

METHODS

Stimuli

A three-element vernier alignment test stimulus was used in which the horizontal location of a central element had to be judged with respect to two vertically separated reference elements [Fig. 1(b)]. The vertical separation between each of the elements was 2 deg. The elements consisted of symmetric Gaussian blobs whose mathematical description is given by

$$L_{\text{mean}} + (L_{\text{mean}} * \text{contrast} * \exp(-(x^2 + y^2)/2\sigma^2)) \quad (1)$$

where L_{mean} is the mean luminance of the background, σ is the standard deviation of the Gaussian envelope (which was maintained at 0.4 deg) and x and y are the respective horizontal and vertical distances from the peak of the Gaussian. Except where stated otherwise, contrast was 0.84, or 84%. Prior to the presentation of this test stimulus, subjects adapted to a stimulus which represents the first derivative of a gaussian in the x-direction, which will be subsequently referred to as an antisymmetric gaussian [Fig. 1(a)]. The mathematical description of these stimuli is given by:

$$L_{\text{mean}} + (L_{\text{mean}} * \text{contrast} * \exp(-(x^2 + y^2)/2\sigma^2) * (-x/\sigma) * (\exp(0.5))) \quad (2)$$

The reader should be able to verify the phenomenon under investigation in the present study by fixating midway between the stimulus elements in Fig. 1(a) for approximately 5 sec and then quickly fixating the centre of the stimulus in Fig. 1(b). Despite the physical alignment of the elements in Fig. 1(b), a perceived offset of the central element to the right should be noticed. Note that the positions of the outer elements are shifted by adaptation, and we use the (unadapted) central patch as a high fidelity probe for perceived shifts of the outer patches.

In addition to luminance-defined stimuli, the adaptation-test paradigm was also performed using texture patches (random static noise of r.m.s. contrast 0.29, windowed by a gaussian or an antisymmetric gaussian). The texture patches consisted of 2×2 square pixel luminance increments or decrements taken randomly from a uniform distribution, and then windowed by either the gaussian or the antisymmetric gaussian. Thus, the mathematical description of the test stimuli [Fig. 1(d)] is given by:

$$L_{\text{mean}} + ((\text{rand} - 0.5) * (\text{Eq.1})) \quad (3)$$

where rand is a uniformly distributed random variable between 0 and 1. Similarly, the description of texture-defined adaptation stimuli is

$$L_{\text{mean}} + ((\text{rand} - 0.5) * (\text{Eq.2})) \quad (4)$$

Again, adaptation to Fig. 1(c) followed by fixation at the centre of Fig. 1(d) should be perceived as a rightwards misalignment of the central element.

For all stimuli, the standard deviation (σ) was set at 15 pixels which, at the viewing distance of 70 cm, represents

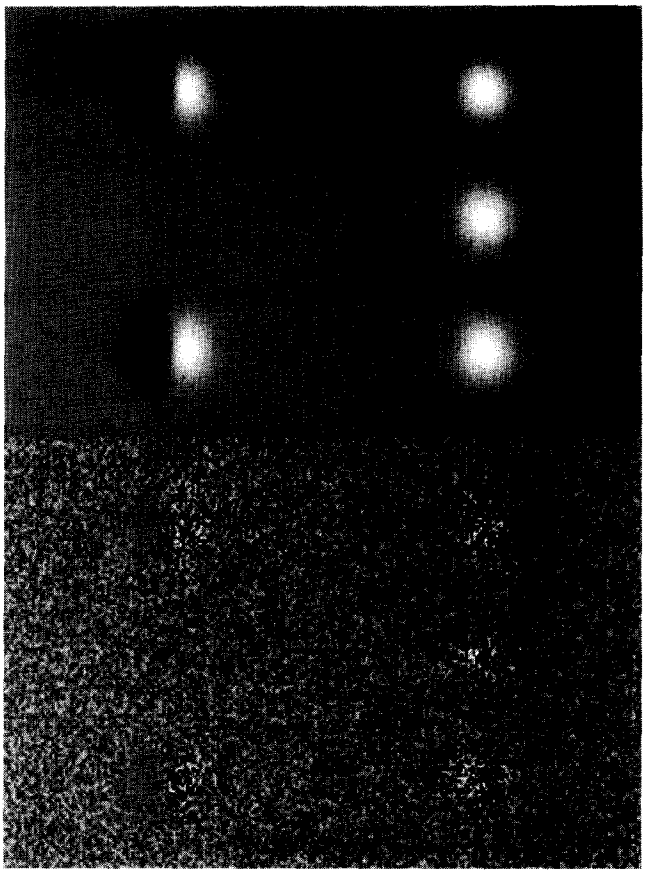

FIGURE 1. Examples of the stimuli used in the present experiments. The top-left figure (a) represents the first-order adaptation stimulus in which observers were requested to fixate the small dot at the centre of the two antisymmetric blobs for the duration of the adaptation phase. The top-right figure (b) represents the subsequent test stimulus, a three-element gaussian blob alignment task. The lower figures represent equivalent stimuli for second-order adaptation (left (c), with a central fixation cross) and test (right (d)). Rather than consisting of variations in luminance, these are composed of variations in contrast. The experimental stimuli, and indeed the original figures, were corrected so as to avoid luminance artefacts in the second-order stimuli. However, due to reproduction non-linearities, some variation may still be present in this figure.

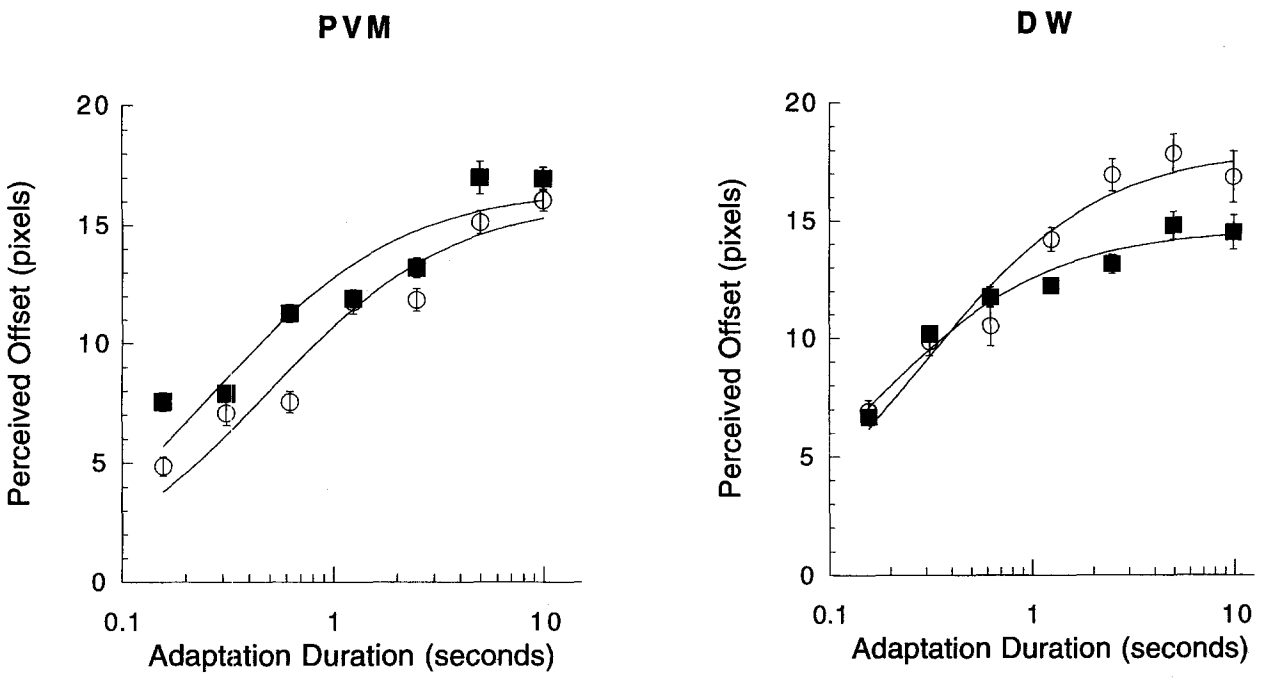

FIGURE 2. Shows perceived offset of the central blob of the three-blob alignment task as a function of the duration of the adaptation phase. Offsets are defined in pixels, where each pixel represents an angular subtense of 1.6 min of arc. Data are shown for both the first-order (filled squares) and second-order (open circles) stimuli. Standard deviations of the data are shown. The two figures represent data from the two observers. The data are fitted with a saturating function whose form is described in the text.

0.4 deg of visual angle. Each pixel therefore subtended 1.6 min arc (an inter-pixel separation of approximately 0.326 mm). All stimuli were generated using the macro capabilities of the public domain software NIH Image™ 1.59 (developed at the U.S. National Institutes of Health and available from the Internet by anonymous FTP from zippy.nimh.nih.gov or on floppy disk from the National Technical Information Service, Springfield, Virginia, part number PB95-500195GEI). Stimuli were presented on a Mitsubishi Diamond Pro 20″ monitor at a mean luminance of 30.1 cd m^{-2} and a frame rate of 75.1 Hz. The non-linear luminance response of the display was linearised by using the inverse function of the luminance response as measured with a Minolta CS-100 photometer. Contrast resolution of up to 12-bit accuracy was obtained by combining the red, green and blue outputs of the video board using a video summation device constructed according to Pelli & Zhang (1991). The host computer was a Power Macintosh 7100/80.

For one experiment, we used a dichoptic arrangement in which two NEC MultiSync XV 15″ monitors were controlled by a Power Macintosh 7200/66 and viewed via adjustable front-surface mirrors. The linearised luminance response of both monitors was matched, with a resulting mean luminance of 48.7 cd m^{-2}. Frame rate of the monitors was 74.4 Hz.

Methods

Observers fixated the centre of the adapting stimulus [Fig. 1(a) or Fig. 1(c)] for 5 sec, immediately followed by a 180 msec exposure of the test stimulus [Fig. 1(b) or Fig. 1(d)]. No change in fixation occurred so that the outer elements of the test stimuli appeared at the same retinal location as those of the adapting stimulus. Following this the observer was required to respond via the mouse as to whether the central element of the test stimulus was offset to the right or left of the midline defined by the outer reference elements. The observer's response immediately initiated the next 5 sec adapting phase. One of seven values of central element offset could be randomly presented on any trial, the mid-point of these approximating to subjective alignment as estimated by pilot experiments. A step size of 2 pixels between each of the seven offsets usually resulted in a satisfactory spread of responses, ranging from almost 100% rightward to 100% leftward. Occasionally the step size was increased to 3 or 4 pixels to obtain a satisfactory range of responses. The results of the first ten trials were discarded to allow time for the observer to familiarise himself with the stimulus sequence and for the adaptation effect to reach a plateau. Following this, between 10 and 20 trials were presented at each of the seven offsets, and the proportion of "rightward" responses was calculated for each offset. The resulting data were analysed by bootstrap analysis of the psychometric function (Foster & Bischof, 1991) to reveal the offset corresponding to perceived alignment (50% response level) and also the threshold, defined as the difference in offset between the 50% and 84% response levels.

In some experiments, stimuli were set to multiples of their detection threshold contrast. Contrast detection thresholds were established using a 2-interval forced

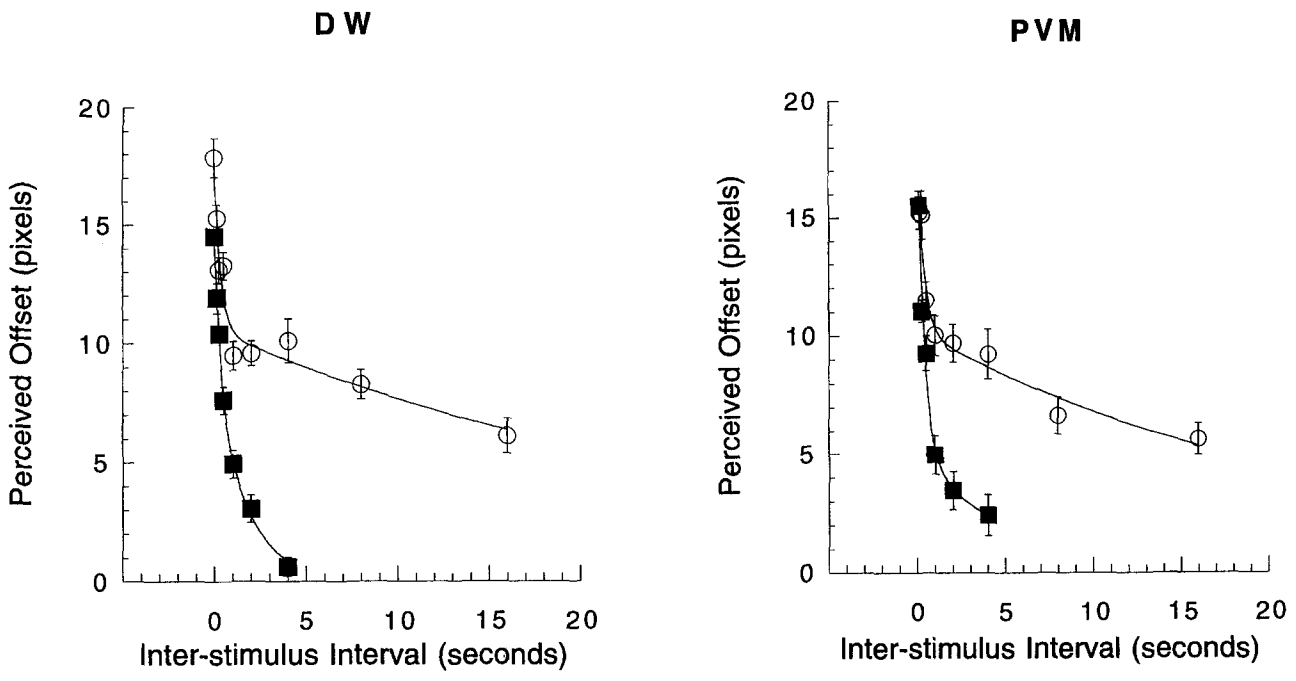

FIGURE 3. Shows the decay of the adaptation effect as a function of the time interval between adapting stimulus offset and the test stimulus onset. Adaptation duration was 5 sec. Data are shown for both the first-order (filled squares) and second-order (open circles) stimuli. Standard deviations of the data are shown. The two figures represent data from the two observers. The data are fitted with a weighted sum of two exponential decay functions whose form is described in the text.

choice method of constant stimuli. Seven levels of contrast were used, each separated by 0.1 log units. The subject had to decide which one of two 180 msec presentations contained the stimulus element. Ten presentations were run randomly at each of the seven contrast levels, and again bootstrap analysis was run on the data in order to find the contrast resulting in 75% correct response level on the 2-interval forced choice psychometric function.

Observers

Two of the authors (DW and PVM) acted as observers in the experiment. Each observer used their dominant eye for observation (right eye in the case of DW and left for PVM) and undertook several pilot sessions before data collection began. Observations were carried out in a dimly lit room in order to avoid reflections from the monitor. Both observers were pre-presbyopic and wore their distance refractive correction, where necessary.

RESULTS

Time course of adaptation and recovery

Figure 2 shows the effect of adaptation upon perceived offset of the central blob as a function of the duration of the adaptation phase. The 180 msec duration test stimulus appeared immediately after the offset of the adaptation phase. Data are shown for both first-order (filled squares) and second-order (open circles) stimuli. At the shortest adaptation time, 125 msec, there is a small yet measurable effect upon perceived location. This effect increases with adaptation duration until it reaches a plateau above about 5 sec duration. The data are fitted with a saturating equation of the form:

$$\text{offset} = O_{\max}/(1 + (AD_{50}/\text{duration})) \quad (5)$$

where $O_{\max}$ and AD_{50} are constants indicating the perceived offset at the plateau and the adaptation duration corresponding to half this plateau value, respectively. For subject DW, values of $O_{\max}$ are 14.6 and 18.0 pixels for first- and second-order stimuli, respectively. Subject PVM shows almost identical maximum offset values (16.5 and 16.0 pixels) for the two types of stimuli.

Figure 3 demonstrates the decay of the adaptation effect following 5-sec adaptation periods. Data are plotted as a function of the temporal interval between the offset of the adaptation stimulus and the onset of the test stimulus. Again the first-order stimuli are shown as filled squares, the second-order stimuli as open circles. As expected, in the absence of an inter-stimulus interval, offsets are similar to those found in Fig. 2 for a corresponding 5-sec adaptation duration. Perceived offset for the first-order stimuli rapidly falls towards zero. Values for the second-order stimuli also begin to fall rapidly, but then start to plateau, indicating that the adaptation phenomenon lasts significantly longer than for the first-order stimuli. The data are fitted with a weighted sum of two exponential decay functions. This takes the form:

$$O_{\text{zero}} * [(\exp(-\text{ISI}/Tc_1) + \exp(-\text{ISI}/Tc_2))/2] \quad (6)$$

where O_{zero}, Tc_1 and Tc_2 are constants. O_{zero} represents the perceived offset when ISI = 0, Tc_1 and Tc_2 are the

TABLE 1. Constants derived from the curve fits to the data shown in Fig. 3

	O_{zero} (pixels)	Tc_1 (sec)	Tc_2 (sec)	R
DW first-order	14.5 ± 0.3	0.39 ± 0.04	2.0 ± 0.2	0.999
DW second-order	18.2 ± 1.0	0.43 ± 0.14	59 ± 33	0.965
PVM first-order	17.4 ± 1.0	0.33 ± 0.11	2.3 ± 0.5	0.988
PVM second-order	16.0 ± 0.9	0.96 ± 0.35	58 ± 35	0.963

time constants of the first and second exponential decay functions. Values for these constants for the two observers and two types of stimuli are shown in Table 1.

All the decay functions can therefore be described by an initial, relatively rapid phase with a time constant of under 1 sec, followed by a slower phase whose time constant depends upon whether the stimulus is first- or second-order in nature. For first-order stimuli the duration is approximately 2 sec, whereas the second-order adaptation effect results in a very long recovery phase with a time constant of around 60 sec.

Contrast dependence

The data presented so far have been for first- and second-order stimuli at a single, high contrast (84%). We now examine the role of stimulus contrast by manipulating the contrast of both the adapting stimuli [Fig. 1(a) and Fig. 1(c)] and test stimuli [Fig. 1(b) and Fig. 1(d)]. Contrasts of 84, 42, 21 and 10.5% were used. For any single test contrast, the magnitude of the perceived offset increased as a function of adapting contrast. For any given adapting contrast, perceived offset was greatest for lower contrast test stimuli. The combined effects of varying adapting and test contrast for the first-order stimulus can be seen in Fig. 4, where perceived offset is plotted as a function of the ratio of adapting/test contrast. This ratio varies from 0.125 (adapting contrast 10.5%, test 84%) to 8 (adapting contrast 84%, test contrast 10.5%). When plotted in this way, data for all combinations of test and adapting contrast collapse to form a single function. The curve passing through the data has the same form as Eq. (5), i.e.:

$$\text{offset} = O_{max}/(1 + (R_{50}/\text{contrast ratio})) \quad (7)$$

Thus, O_{max} represents the perceived offset at very high adapt/test contrast ratios. Values were 21.8 pixels for DW and 21.6 pixels for PVM. The constant R_{50} represents the adapt/test ratio at which the perceived offset falls to half of its maximum. Corresponding values were 0.55 and 0.50.

Figure 5 presents alignment threshold data, as opposed to the location of the 50% response level which has been presented so far. Thresholds are plotted against the contrast of the test stimulus, and it can be seen that thresholds decrease somewhat as contrast is increased (the straight line represents a power function with an exponent of −0.44). Optimum thresholds are between 1 and 2 pixels, more than an order of magnitude less than some of the offsets induced by adaptation (Fig. 4). This helps to convey some impression of the large positional effects produced by adaptation. It is of further interest to note that, at any test contrast, thresholds for alignment are similar for all adapting contrasts. This occurs despite the fact that perceived offsets vary markedly as a function of adapting contrast for any given test contrast (Fig. 4). The implication of this finding is that psychometric functions for positional judgements at different adapting contrasts

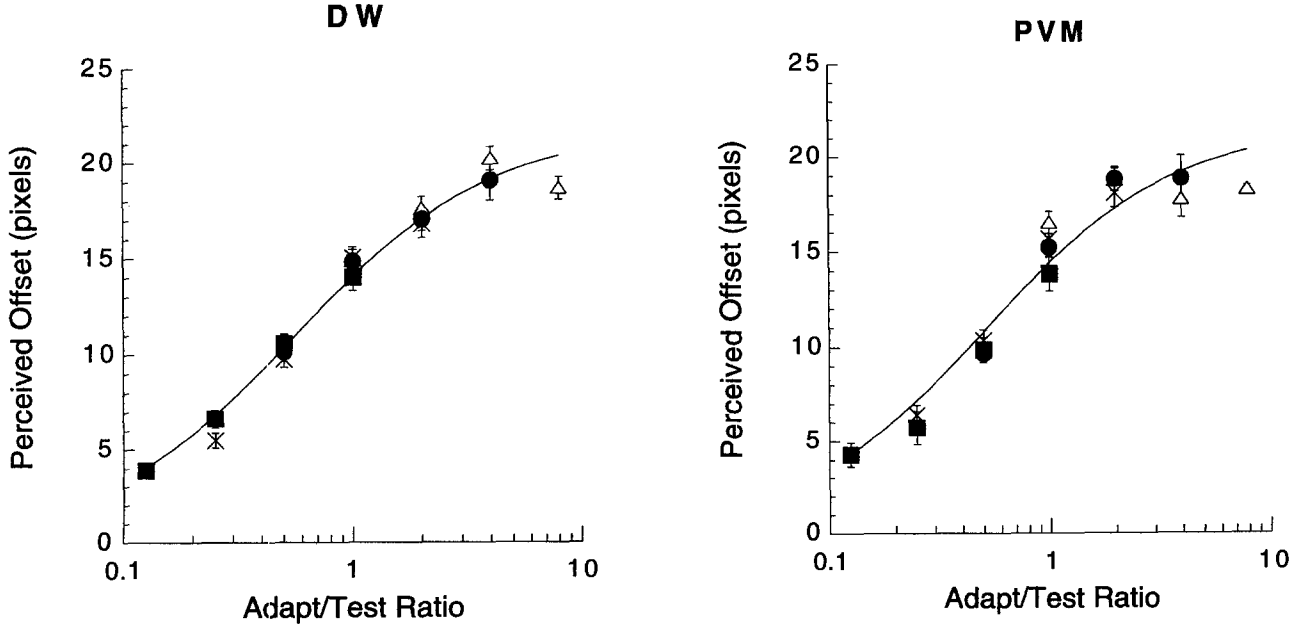

FIGURE 4. Perceived offset as a function of the ratio between the adapting and test stimulus contrast for the first-order stimulus. Different symbols represent different adapting stimulus contrasts: 84% (open triangles); 42% (filled circles); 21% (crosses); 10.5% (filled squares). The two figures represent data from the two observers. Standard deviations are shown. The data are fitted with a saturating function as described in the text.

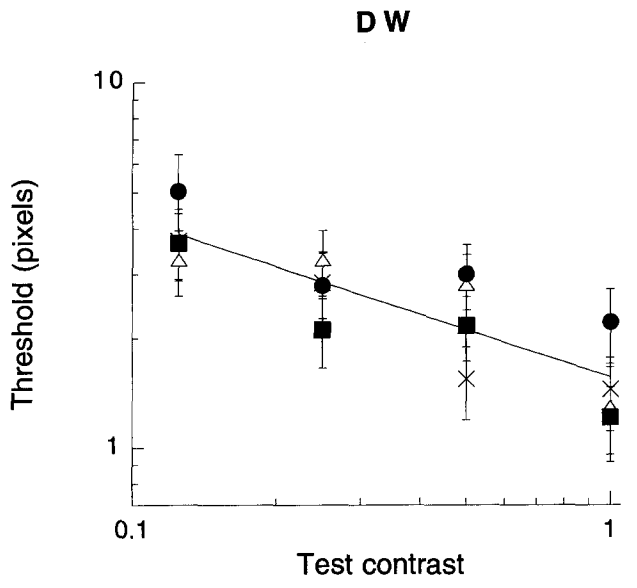

FIGURE 5. Thresholds from DW's data shown in Fig. 4, showing that performance improves with increasing test contrast. Symbols as for Fig. 4. The straight line is a best-fitting power function to the data as a whole and takes the form $y = 1.563*x^{-0.44}$. Standard deviations of the threshold estimates are shown.

are simply translated versions of one another, without any associated change in slope. The effect is, therefore, similar to the effect of flanking elements upon perceived location, where strong misperceptions of position occur without a marked change in precision (Badcock & Westheimer, 1985).

Figure 6 shows the effect of manipulating adapting and test contrast upon perceived offset for the second-order stimuli. As in Fig. 4, the whole data set is fitted with a single function depending only upon the ratio of adapt/test contrast. Values for O_{max} are 25.3 pixels for DW and 28.2 pixels for PVM, and corresponding values of R_{50} are 0.70 and 1.08. The range of adapt/test ratios is less than that in Fig. 4 owing to the reduced visibility of the second-order stimuli.

Crossover data

So far we have examined first- and second-order stimuli separately. Now we investigate whether crossover effects occur, i.e., does adapting to one type of stimulus result in a significant effect upon perceived position for a different stimulus type? One problem which immediately arises when comparing such different stimuli is what metric to use so that any comparisons made are valid. The metric of absolute contrast is clearly inappropriate, since one cannot assume that a first-order stimulus of one contrast is equivalent to a second-order stimulus of the same contrast. In an attempt to overcome this problem we adopt a solution which is prevalent in the vision science literature, that of equating the stimuli in terms of threshold contrast for detection. Contrast detection thresholds were measured for the first- and second-order stimuli as described in the methods. Since detection thresholds were higher for second-order stimuli we chose to fix this type of stimulus at 84% contrast and to adjust the first order stimulus to the same multiple of threshold contrast for detection. In this way DW and PVM's first-order stimuli were set at 29.6% (8.4 × detection threshold) and 43.6% (7.2 × detection threshold) contrast, respectively.

Figure 7 presents perceived offset found in each of the four possible adapt/test conditions for two types of stimuli. As expected from the previous results, adapting

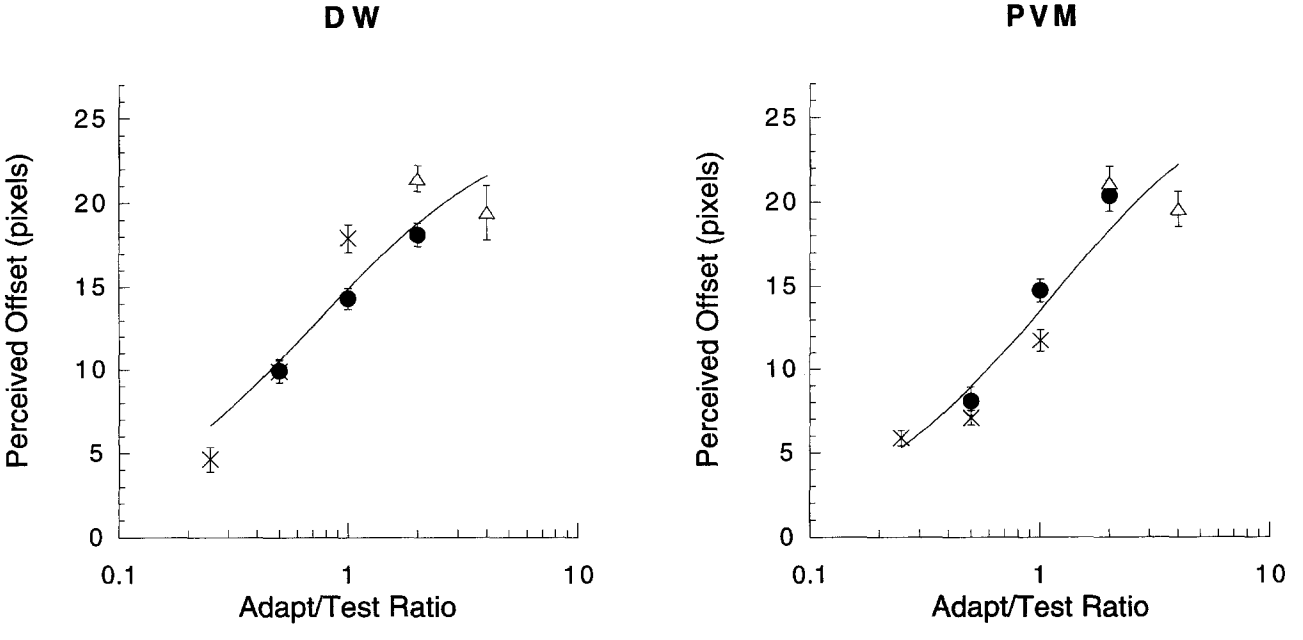

FIGURE 6. Data and symbols as for Fig. 4, but for the second-order stimulus. The two figures represent data from the two observers. Standard deviations are shown. The data are fitted with a saturating function as described in the text. The data range is more limited than in the first-order situation owing to the reduced visibility of the second-order stimuli.

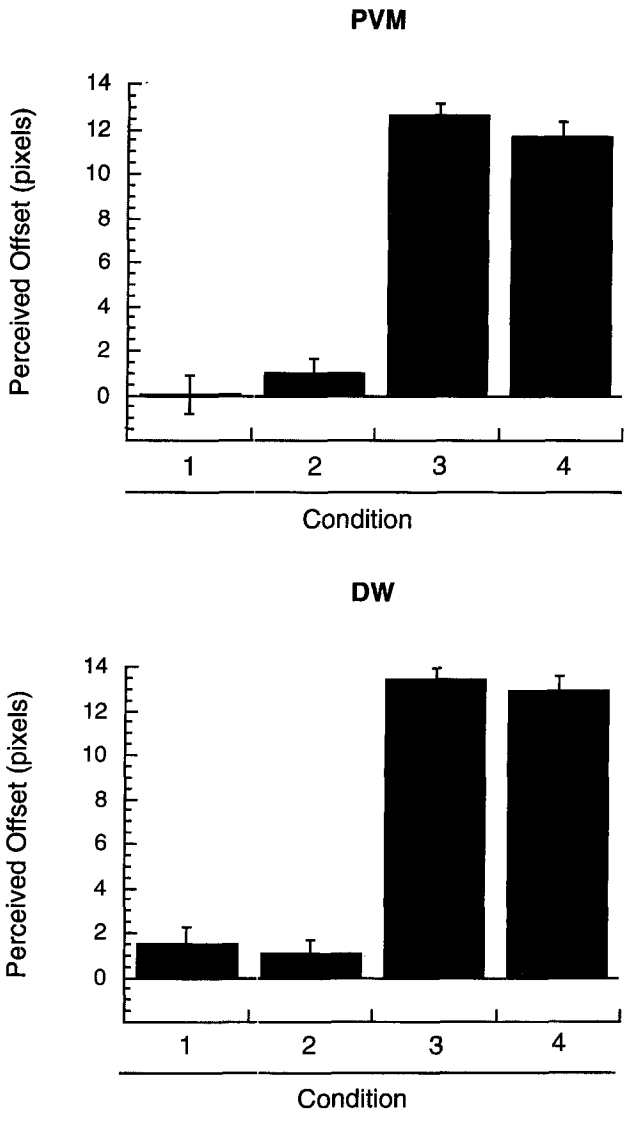

FIGURE 7. Perceived offset for each of the four possible combinations of conditions: Condition 1, adapt first-order, test second-order; Condition 2, adapt second-order, test first-order; Condition 3, adapt first-order, test first-order; Condition 4, adapt second-order, test second-order. Stimuli were equated for visibility as described in the text. The two figures represent data from the two observers. Standard deviations are shown. Note the lack of effect in either of the crossover conditions.

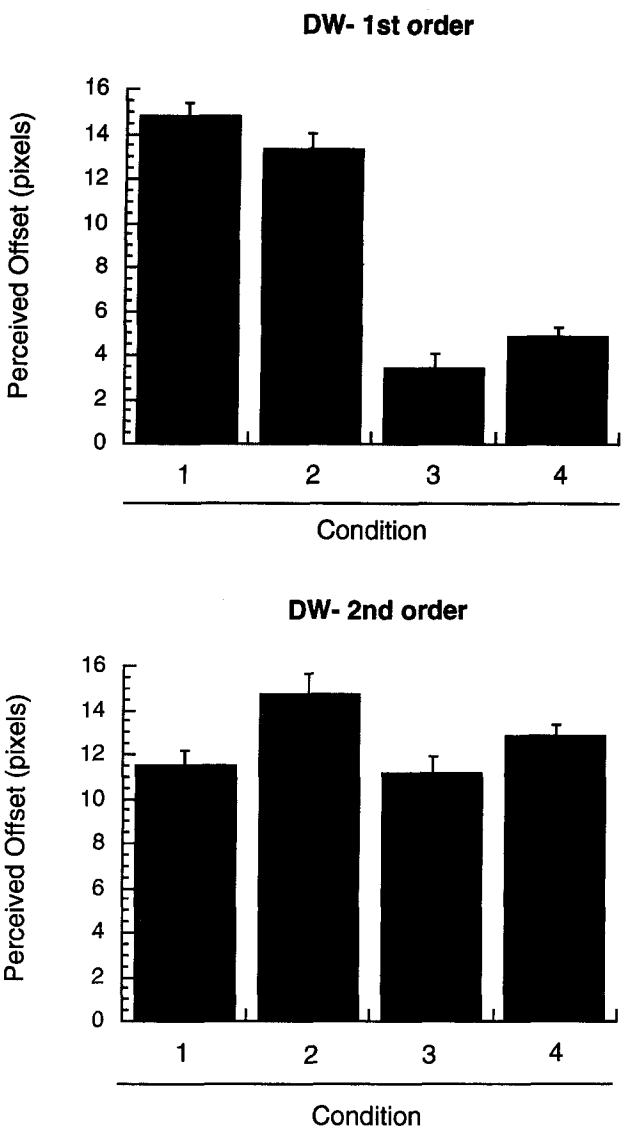

FIGURE 8. Interocular transfer of the perceived shift in position. Data are shown for all four possible combinations of conditions: Condition 1, adapt right, test right; Condition 2, adapt left, test left; Condition 3, adapt left, test right; Condition 4, adapt right, test left. The upper figure represents the effect for the first-order stimulus, whilst the lower figure shows the same data for the second-order stimulus. For both types of stimuli, contrast was fixed at 84%. Observer DW. Standard deviations are shown. Note the increased interocular transfer for the second-order stimulus.

and testing to the same type of stimuli results in large shifts in perceived offset. However, neither adapting to first-order and testing with second-order stimuli nor adapting to second-order and testing with first-order stimuli result in any significant perceived offset. Thus, the positional adaptation effects found for both first- and second-order stimuli appear to be restricted to their own domains.

Interocular transfer

The data so far have been gathered by presenting both the adapting and test stimuli to the dominant eye of the observers. Figure 8 shows the perceived offsets found for the fellow eye and for both interocular conditions where adapting and test stimuli are presented to different eyes. During the adaptation phase the unadapted eye viewed a uniform field of mean luminance, whilst during the test phase the untested eye viewed a uniform field of mean luminance. Adapting to first-order, luminance-defined stimuli produces only a small effect upon perceived offset when the adapting and test stimuli are presented to different eyes. The interocular effect amounts to only about 29% of the uniocular effect. For the second-order, texture-defined stimuli the situation is different, with considerably more interocular adaptation being produced (92% of the uniocular condition). Subject PVM showed similar results, although the difference between interocular transfer of the effect in the first- and second-order conditions was less marked (42% vs 73%).

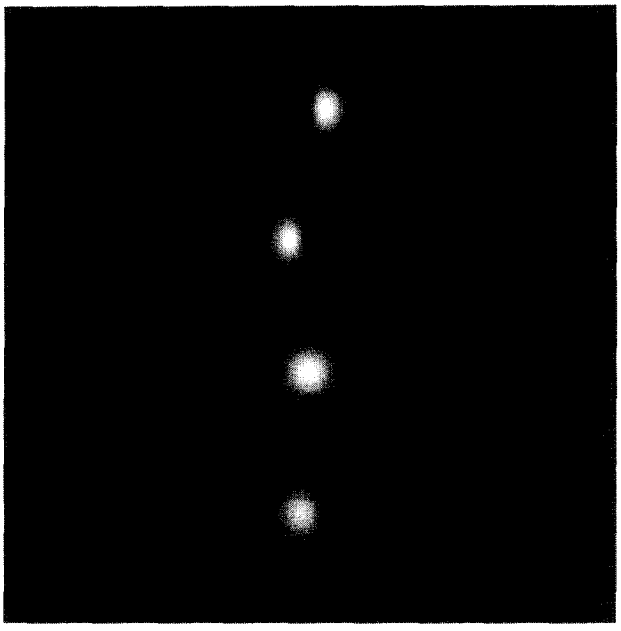

FIGURE 9. A schematic of the model used to explain the data. The top row shows the appearance (centre) and the profile (right) of the antisymmetric first-order stimulus. The second row shows the hypothesised after-image formed by this adapting stimulus. The third row shows the test stimulus. The bottom row depicts the linear combination of test stimulus and after-image. We then assumed that the centroid of this resulting image represents its perceived location.

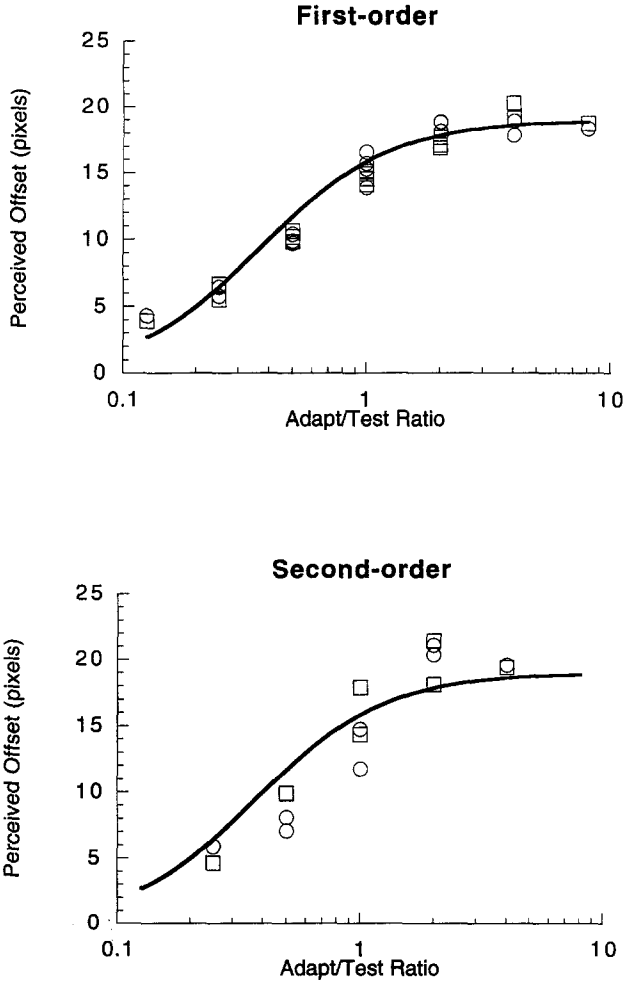

FIGURE 10. Predictions of the model fitted to the data of Fig. 4 (first-order, top) and Fig. 6 (second-order, bottom). Data are shown for the two observers DW (open squares) and PVM (open circles). Mean standard deviation is shown for both types of stimuli. The curve represents the prediction of the model, depicting the centroid of the linear combination of test and inverse of the adapting stimulus at each adapt/test contrast ratio. The prediction accounts for 95.6% of the variance for the first-order stimuli, but only 81.2% for second-order stimuli.

DISCUSSION

We have shown that adaptation can have marked effects on the perceived location of subsequently viewed objects. Importantly, these effects occur independently of any oblique orientational component to either the adapting or the test stimulus. The phenomenon is, therefore, unrelated to the well-known orientational illusions such as the tilt aftereffect, and represents a direct manipulation of perceived orthoaxial position. As further evidence against an explanation based upon global orientation, we performed a control experiment using the same test stimulus, but rather than alignment, the task consisted of a bisection judgement, i.e., was the central blob higher or lower than the mid-point defined by the outer blobs. The adapting stimulus again consisted of two antisymmetric gaussians, but with their asymmetry in the vertical, rather than the horizontal direction. The dark phase of both antisymmetric blobs was in the downwards direction. This resulted in a strong misperception of the subjective bisection judgement, of a kind which was quantitatively similar to that which we demonstrated for the alignment task.

A simple model, outlined in Fig. 9, can account for the change in perceived object location following adaptation. At the top of the figure is the asymmetric adapation stimulus which, following a suitable adaptation time, results in a negative after-image which is simply the inverse of the adaptation image. Note that we assume there is no contrast attenuation of the after-image, and that contrast is therefore not a free parameter of the model. We then assume that the negative after-image and the neural response elicited by the stimulus are combined by linear addition. A linear combination of stimulus and after-image has been suggested in previous studies (Burbeck & Kelly, 1984; Georgeson & Turner, 1985) although there is some evidence (notably the phenomenon of apparent phase reversal) to indicate the contribution of a non-linear, multiplicative mechanism prior to the linear process (Tulunay-Keesey *et al.*, 1987; Olson *et al.*, 1994). The final stage of the model represents the localisation stage, in which the centroid of the mean of after-image and stimulus (bottom row of the figure) is computed. Recent evidence has shown that the centroid of the luminance profile (for first-order stimuli) or that of the contrast envelope (for second-order stimuli) represents a stimulus characteristic which adequately describes the perceived location of objects (Whitaker *et al.*, 1996).

Centroid evaluations were performed using the macro capabilities of NIH Image™ for several combinations of adaptation and test contrast values. The predicted effect upon perceived localisation is shown by the bold curve in Fig. 10, and is compared with the data from the present experiments, as presented in Fig. 4 and Fig. 6. For the luminance-defined stimuli, the agreement between data and model is obviously excellent, and this parameter-free prediction accounts for 95.6% of the variance of the data. The agreement for the second-order, texture-defined stimuli is somewhat less impressive, with only 81.2% of the variance being explained. Whatever the reason for this discrepancy between data and model, it is not due to the fact that centroid evaluation is a poor predictor of localisation for second-order stimuli, since Whitaker *et al.* (1996) have shown excellent agreement between a centroid model and the type of texture-defined stimuli used in the present experiments.

The above model has its roots in early work on figural aftereffects (Köhler & Wallach, 1944; Osgood & Heyer, 1952; Ganz, 1966a,b). Both Köhler & Wallach (1944) and Osgood & Heyer (1952) explain the apparent repulsion of test contours viewed after an adapting contour on the basis of a linear, subtractive combination of cortical excitation produced by the adapting and test contours. Ganz (1966a,b) goes further, and suggests that figural aftereffects can be considered to be akin to simultaneous illusions, and occur because of the linear combination of test stimulus and after-image. Other similarities, such as the exponential time decay and the effect of the contrast of adapting and test contours, further strengthen the relationship between figural aftereffects and the shifts in perceived position which we report here.

Our results demonstrate important differences between adaptation effects involving first- and second-order stimuli. Recovery from adaptation to first-order stimuli is fairly rapid, and is almost complete within just a few seconds. On the other hand, recovery from second-order adaptation involves a comparatively slow second stage, which extends the recovery time considerably. No crossover adaptation effects were found between first- and second-order stimuli, suggesting that the visual pathways dealing with the two types of stimuli remain independent, at least up to the stage of localisation. Another difference is the larger extent of interocular transfer for the second-order adaptation effect, a finding which is consistent with the greater interocular transfer of subjective as compared to real contours (Paradiso *et al.*, 1989) and that of flicker- as compared to real-motion aftereffects (Nishida *et al.*, 1994).

The differences between first- and second-order adaptation effects can be viewed in relation to the dichotomy in the adaptation literature regarding luminance and contrast adaptation. Luminance adaptation is thought to be of retinal origin, and is likely to strongly contribute to the adaptation produced by our luminance-defined first-order stimuli. It is tempting to suggest that our second-order stimuli result in contrast adaptation, similar to that produced by adapting to drifting gratings whose motion avoids local luminance adaptation. It is easy to imagine that involuntary eye movements are sufficient to avoid local luminance adaptation to the type of texture-defined stimuli which we have used. Neurophysiological studies show that contrast adaptation is found first at a cortical level (Albrecht *et al.*, 1984; Sclar *et al.*, 1989; Saul & Cynader, 1989) and, as we have found for our texture-defined stimuli, contrast adaptation shows a large interocular transfer (Bjorklund & Magnussen, 1981; Maffei *et al.*, 1986). In addition, the rather lengthy time course of recovery from contrast adaptation (Blakemore & Campbell, 1969) corresponds to that found for our second-order stimuli (Fig. 3).

We have shown that adaptation to a second-order stimulus is quite capable of producing changes in the perceived position of a test stimulus, provided this is also second-order in nature. Similar findings occur in the motion domain, where contrast-modulated drifting stimuli produce direction-specific threshold elevation for similar patterns (Turano, 1991) and result in motion aftereffects for appropriate second-order test stimuli (McCarthy, 1993; Ledgeway & Smith, 1994; Ledgeway, 1994). An important difference, however, is that these motion phenomena demonstrate almost complete crossover effects between first- and second-order stimuli, provided the two types of stimuli are equated for visibility. This finding is obviously in marked contrast to the complete lack of crossover in the positional aftereffects of the present study and to the absence of crossover in the effect of flanks on vernier acuity when the target is luminance defined and the flanks motion defined, and vice versa (Banton & Levi, 1993). Taken together, the findings suggest that the processing mechanisms for the two types of stimuli remain separate until after the site at which positional information is extracted, but then combine to allow analysis by a common motion mechanism (Wilson *et al.*, 1992). The intriguing finding that the perceived position of a Gabor patch can be strongly influenced by motion of the carrier grating within its stationary contrast envelope (De Valois & De Valois, 1991) may also be viewed as evidence for an initial positional estimate which then becomes susceptible to a subsequent stage of motion analysis.

In conclusion, we have demonstrated that the perceived position of luminance- and texture-defined stimuli is highly dependent upon prior adaptation. For luminance-defined stimuli at least, the findings are accounted for by a model in which the adaptation-induced after-image and the luminance profile of the stimulus are added linearly, and the centroid of the resulting output is then used to determine perceived location.

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