The effect of motion adaptation on the position of elements in the visual saltation illusion

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The visual saltation illusion—illusory motion induced by presenting elements first to one peripheral location, then to another, in rapid and regular succession—belongs to a class of stimuli for which a difference exists between the physical and perceived positions of elements. Rather than being perceived at their physical location, elements are perceived as traveling smoothly across the area between the two locations. In separate experiments, we examined the distortion to the saltatory path caused by adaptation to an upward drifting grating presented between the two physically stimulated locations (where elements were nonetheless perceived), and at the first location of physical stimulation. Where adaptation occurred between the two sites of physical stimulation, the saltatory path was distorted as if elements had a physical origin at that location; elements perceived as arising from the central location were subject to a motion aftereffect (MAE). Where motion adaptation overlapped the first site of physical stimulation, the saltatory path was affected only for those elements perceived as arising from the first location; elements perceived at the central location (but physically presented at the first site of stimulation) were not subject to an MAE. Our results indicate that the impact of motion adaptation on position is dependent on the perceived, and not the physical, location of elements.

Keywords: visual saltation, motion adaptation, spatial position, form and motion

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Introduction

A primary goal of the visual system is to derive an estimate of the spatial position of objects in the retinal image. Previous research has shown that the visual system is well capable of registering the spatial position of features through cortical mapping in areas early in the visual processing hierarchy (see Fu, She, Gao, & Dan, 2004; Hubel & Wiesel, 1968; Livingstone & Hubel, 1988), and behavioral experimentation consistently reveals the capacity of this spatial map to allow fine discriminations in the relative position of objects (e.g., Westheimer & McKee, 1977). Despite the specialization of the visual system to detect the position of objects, this process is vulnerable to influence by a number of factors. Foremost among these is image motion (e.g., De Valois & De Valois, 1991; Kirschfeld & Kammer, 1999; Nijhawan, 1994; Whitney & Cavanagh, 2002).

In a classic study, De Valois and De Valois (1991) used a Vernier acuity task to demonstrate that the apparent position of a Gabor patch containing carrier motion appears shifted in the direction of the carrier motion relative to stationary aligned flankers. The extent of the reported misalignment was dependent on stimulus eccentricity and speed of grating motion. Whitney (2002) suggested that the misperception of position is a consequence of image motion directly influencing the coded location of the object (Berry, Brivanlou, Jordan, & Meister, 1999; Fu et al., 2002; Nijhawan, 1997; Nishida & Johnston, 1999; Snowden, 1998). However, more recent studies have noted that this example of motion–form interaction has been accounted for by differential activation of motion de-blurring at the trailing and leading edge of motion (Tsui, Khuu, & Hayes 2007; Whitney et al., 2003).

Previous research has also demonstrated that internally generated motion, elicited through motion adaptation, is also capable of distorting the apparent position of objects (McGraw, Whitaker, Skillen, & Chung, 2002; Nishida & Johnston, 1999; Snowden, 1998). Snowden (1998) demonstrated that if motion and form patterns are presented sequentially, that is, when motion is initially presented for a period of time to generate a motion aftereffect (MAE)

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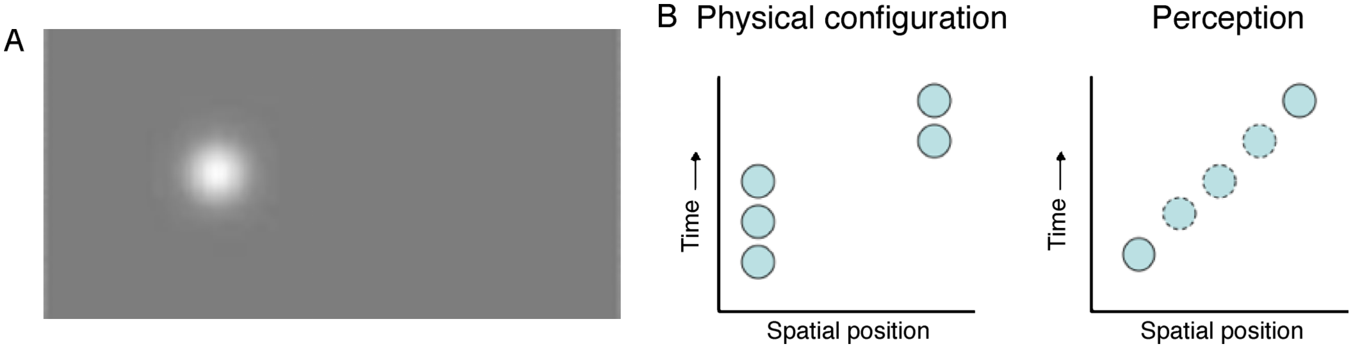

Figure 1. (A) A movie demonstration of visual saltation, in which five elements are sequentially presented such that three elements are presented to the first site and then two to the second site. When viewed at least 10 deg in the periphery, the stimulus elicits a compelling sense of saltatory motion. (B) A schematic of the spatio-temporal arrangement of elements corresponding to the physical configuration and perception of the visual saltation illusion. Dashed circles indicate elements that are perceptually mislocalized in space.

and is then followed by the presentation of a static test pattern, the apparent position of the test pattern appears shifted in the MAE direction. In an extension of this finding, McGraw et al. (2002) noted that the distortion of position elicited by the MAE is not limited to a particular set of stimulus parameters. Rather, it is a visual phenomenon independent of stimulus characteristics such as image contrast, spatial frequency, and orientation differences between the adapting and test stimuli.

It is important to note that, in the aforementioned motion adaptation studies, stimuli were configured such that the test pattern was presented within the adapted region after a period of motion adaptation. Thus the stationary test pattern *physically* overlapped with the adapted region and the distortions in position arose because the same mechanisms affected by motion adaptation are also responsible for the spatial registry of the test pattern. However, it is possible to generate a visual stimulus in which the phenomenological position of an object does not correspond to its physical position. An example is the “flash-lag effect”, in which an object that is briefly flashed physically adjacent to a moving object appears perceptually lagged behind the moving stimulus (Nijhawan, 1994). Another example is the “Fröhlich effect” (Fröhlich, 1923), in which the position of an object emerging from an occluded border appears displaced from the border along the axis of motion. For these stimuli, the perceived position of the object does not correspond to its physical position but is slightly displaced from it. Kanai and Verstraten (2006) demonstrated that, for such stimuli, both the physical and perceived locations are coded by the visual system. An important question thus arises: is the extent to which motion adaptation affects position contingent on adaptation at the physical location of the object, or at its perceived location? It is this question that the present study sought to investigate.

For both the flash lag effect and the Fröhlich effect, the difference between the perceived position and the physical position of the object is small, with typical offsets of less than half a degree of visual angle. These stimuli are therefore unsuitable for this study because it is difficult to generate a localized MAE and to ensure that the motion adaptation is selectively confined to either the perceived or physical positions of the object. Given their proximity, there is the potential that adaptation at one region may transfer to affect the other, rendering it impossible to reliably determine the locus of any motion-induced distortion effect. A solution to this problem is to use a stimulus that is characterized by substantial perceptual mislocalization of elements from their physical location, thereby ensuring that motion adaptation can be largely localized to either the physical or perceived locations of elements. In this study, we examined the degree to which motion adaptation affects the position of elements in the visual analogue of the saltation illusion—a compelling illusory motion percept characterized by the substantial and systematic mislocalization of a number of briefly presented objects from their veridical position between at least two points of stimulation.

Saltation was originally identified in the cutaneous sense (Geldard, 1975) and has since been observed in both audition and vision, though the latter is perhaps the least well documented. Saltation is typically elicited when multiple stimuli are presented first to one location, then to another, in regular and rapid succession (see Figure 1). Rather than being perceived one after the other at the sites of stimulation, stimuli are perceived as traveling, or jumping, in equidistant steps across the non-stimulated space between the two sites, up to as much as 5 to 10 deg of visual angle (Geldard, 1976). Geldard (1976) in quantifying the illusion, noted that visual saltation is most apparent when the stimulus is presented at least 10 deg in the periphery. Geldard (1976) and Lockhead, Johnson, and Gold (1980) both make the observation that the effect does not occur in central vision because spatial acuity at this location is particularly fine and observers are able to accurately resolve the spatial position of objects. This contrasts with peripheral viewing for which coarser spatial acuity leads to uncertainty in the apparent location of briefly presented objects. Eye movements therefore cannot account for saltation as the stimulus must remain in peripheral vision for the experience of positional displacement.

Saltation has been likened to well-known spatio-temporal apparent motion phenomena such as Phi, Tau, and Kappa (Brigner, 1984; Geldard, 1982; Geldard & Sherrick, 1986; Lockhead et al., 1980; Wiemer, Spengler, Joublin, Stagge, & Wacquant, 2000). However, saltation is unique in at least two ways. First, unlike Phi, for example, saltation is not a continuous motion illusion. Rather than appearing to move between the stimulated locations in a single step, stimuli are perceived at discrete equidistant sites between the two locations. Second, saltation arises from repetitive stimulation at at least one of the two locations (therefore, a minimum of three elements needs to be presented); alternative apparent motion stimuli minimally require only one presentation of the stimulus at each site (Geldard & Sherrick, 1986; Phillips & Hall, 2001). Therefore, despite commonalities with this class of illusion, saltation is phenomenologically different.

Given the sizable shift between the physical and perceived locations of objects in the saltation illusion, this stimulus is suitable for use with the MAE in that it allows for localized adaptation. This study therefore examines distortion to the trajectory of the saltation illusion induced by the MAE after adaptation separately to both the physical and perceived locations of objects within the saltation sequence. This analysis is informative in revealing whether the phenomenology and computation of the visual saltation illusion is reliant on the physical or perceived position of elements, and the degree to which motion adaptation is capable of distorting the position of elements for which the spatial registry does not correspond to direct physical stimulation of the visual map.

The degree to which motion adaptation will affect the position of elements is dependent on the mechanisms responsible for the perception of the visual saltation illusion. Some previous studies have argued that the illusion has its origins in early cortical processing areas where the visual system initially registers the physical position of elements at the two stimulation sites, but, because of factors affecting the ability of spatio-temporal sensitive mechanisms to process briefly presented stimuli, elements are localized non-veridically (see Wiemer et al., 2000). Consistent with the results of McGraw et al. (2002) and Snowden (1998), this explanation would predict that the MAE would distort the illusory path of saltation only where elements physically overlap with the motion-adapted region. This situation is illustrated in Figure 2A(i). As shown, if motion adaptation (to an upward drifting horizontal grating) occurred between the two stimulation sites (and elements therefore do not physically overlap with the adapted area), the illusory path will remain undistorted. Moreover, motion adaptation at one stimulation site would only affect the spatial registry of elements physically presented at that stimulation site (Figure 2B(i)). Elements presented at the second, non-overlapping site would remain at their veridical positions. Thus, following the subsequent mislocalization, the saltatory percept would resemble a distorted path in which the first few elements appear displaced in the MAE direction, with the elements at the end of the temporal sequence unaffected.

Other previous investigations have argued that, like apparent motion, the saltation illusion originates in higher stages of visual processing and reflects a process in which the visual system makes an interpretation of the possible nature of an ambiguous stimulus. A number of characteristics of visual saltation accord with this suggestion. For example, Geldard (1976) noted that visual saltation occurs for dichoptic presentations whereby the two stimulation sites are presented separately to the eyes. If stimuli at the two sites of stimulation were of different colors, the apparent color of mislocalized stimuli appeared to be a mixture of the two colors. Additionally, Lockhead et al. (1980) showed that visual saltation occurs across the blind spot (which is obviously devoid of receptors), and a high-level "filling in" process operates to complete the percept. Shore, Hall, and Klein (1998) proposed to interpret auditory saltation in terms of the Gestalt principle of grouping: where stimulus position is made ambiguous by temporal frequency, it is assumed that the rapidly presented stimuli arose from a single source moving from one spatial location to another. This is reflective of a process in which the illusion is generated in lower cortical areas due to feedback from higher cortical areas.

If the visual system adopts this strategy, the interpretation is made that elements arise from regular discreet spatial intervals between the two sites of stimulation. Under these circumstances, an opposite set of outcomes ought to be obtained from our use of the MAE. Specifically, as depicted in Figure 2A(ii), motion adaptation occurring between the two physical sites of stimulation will affect the position of the middle elements that perceptually (but not physically) overlap with the adapted area. Moreover, if motion adaptation occurred at one of the stimulation sites, only the element that is perceived to overlap with the adapted area (i.e., the first element) will appear shifted in the MAE direction; elements physically originating at this site, but perceived in an area removed from the adapted area (i.e., elements 2 and 3) would be unaffected (see Figure 2B(ii)).

The purpose of this study is to determine which of the outcomes outlined in Figure 2 accounts for the effect of motion adaptation on the perception of visual saltation, and, in so doing, to provide verification of the inherent mechanism by which the visual saltation illusion is produced. This study reports four experiments. In Experiment 1, we quantified visual saltation by directly mapping the spatial position of flashed elements (first, middle, and last) in the sequence to establish the range of ISIs for which the effect is most evident for our stimulus configuration. In Experiment 2, we examined the degree to which motion adaptation affects the path of saltatory

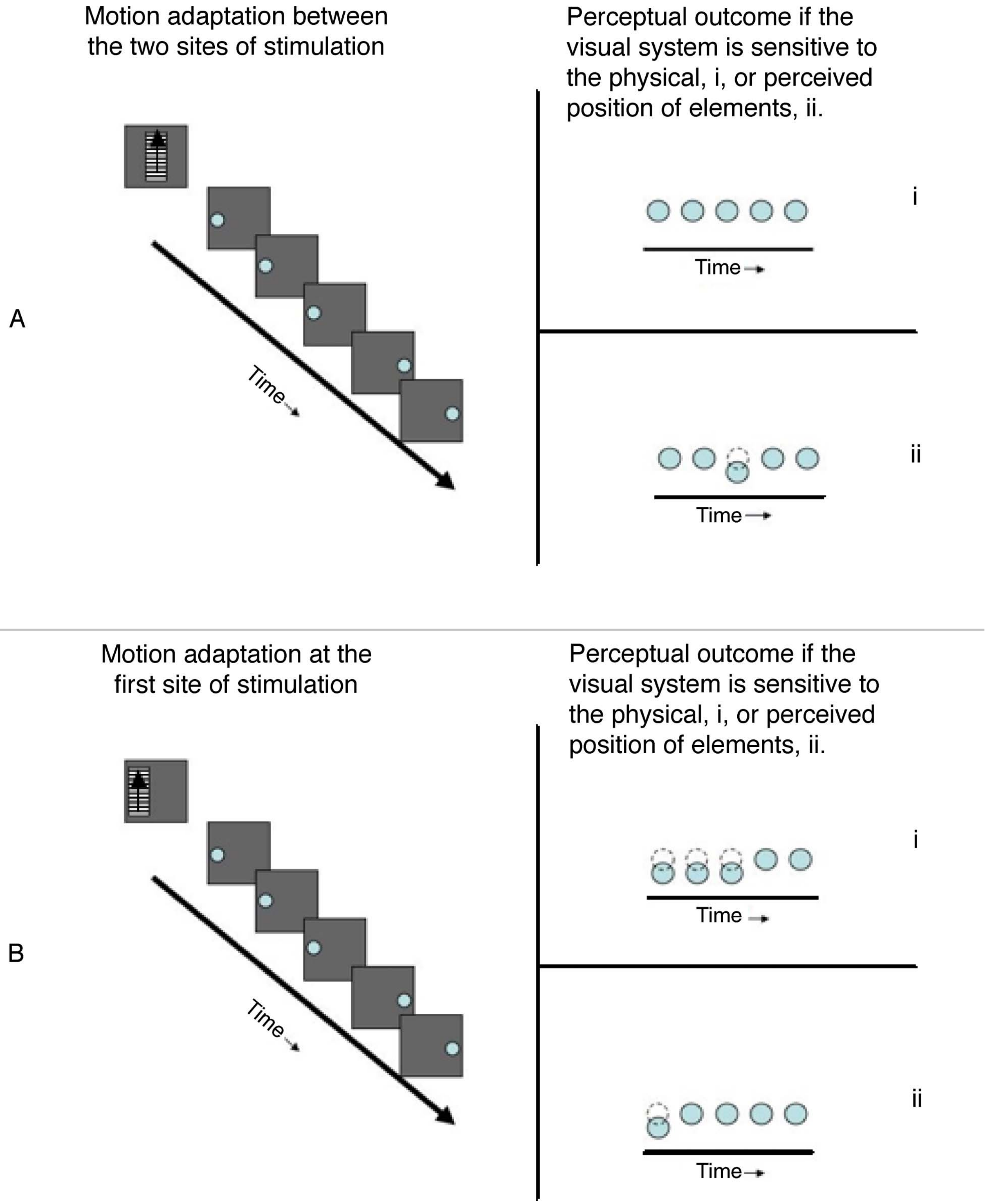

Figure 2. Possible outcomes from the impact of motion adaptation (generated by upward drifting motion) between the two sites of stimulation (A) and coinciding with the first site of stimulation (B), on the perception of the visual saltation illusion. In both (A) and (B), outcomes (right-hand panels) are presented consistent with the visual system being sensitive to the physical (top panels—i) or perceived position of the stimulus (bottom panels—ii). Dotted circles represent the position of elements in undistorted saltatory motion.

motion where elements perceptually, but not physically, overlap with a motion-adapted region. In Experiment 3, we examined the converse configuration in which the position of elements physically, but not perceptually, coincides with a region affected by motion adaptation. In Experiment 4 we considered whether the cursor used to record participant responses was itself subject to the MAE by opposing the polarity of the adapting stimulus and cursor.

Experiment 1: Quantifying the visual saltation illusion

Before the effect of motion adaptation on the percept of illusory saltation can be appropriately investigated, it is necessary to establish the stimulus parameters for which the illusion is most compelling. It has been convincingly shown that the most critical factor in the perception of visual saltation is ISI (e.g., Geldard, 1976). Therefore, the purpose of Experiment 1 was to establish the ISIs for which the illusion is most perceptible for our stimulus configuration.

Previous reports of saltation have employed measures that require observers to rate or verbally report their perceptual experience. These methods have obvious limitations, principal among which is an inability to quantify the extent of mislocalization and indicate the exact perceived location of elements in space (Kidd & Hogben, 2004). To overcome this limitation, observers in Experiment 1 were presented with a number of stimuli (Gaussian spots) first to one location in the periphery, and then to another adjacent site, also in the periphery. Using a spatial probe, observers were asked to indicate the spatial position of a single element within the sequence (either the first, middle, or last element in the sequence) for a range of ISIs. Because visual saltation is characterized by systematic displacement of elements between the two sites of stimulation, it was predicted that for optimal ISIs only the apparent position of the middle element will appear mislocalized exactly to the center, while the judged position of the first and last elements will remain unchanged. In addition to quantifying visual saltation, Experiment 1 also measured the ability of observers to judge the position of elements undergoing real motion (defined here as a situation in which perceived change in the position of the stimulus corresponds with an actual change in the retinal position of that stimulus) under similar stimulus conditions, so that the ISIs favoring a motion percept (whether illusory or real) could be compared.

Methods

Observers

Five observers (aged between 20 and 32 years of age) participated in Experiment 1. One was an author, and four were experienced observers who were naive to the aims of the study. All had normal or corrected-to-normal visual acuity.

Stimuli

Stimuli were sequences of five light increment Gaussian blobs of the form: $L(x, y) = C_0\exp(-(x - x_0) / 2\sigma_x^2) - ((y - y_0) / 2\sigma_y^2)$—where C_0 is the contrast of the stimulus, set to 0.3, and σ_x and σ_y are the x and y standard deviations of the element, both set to 0.125 deg—briefly presented (for 50 ms) on a blank gray screen set to a luminance of 30 cd/m^2. Where illusory saltation was elicited, stimuli were presented at two locations, three to the first location and two to the second. The locations were 15 and 20 deg of visual angle (respectively) immediately to the right of fixation, which was indicated by a black cross at the center of the screen. Observers viewed the stimulus monocularly (in a dark room) with their left eye at a viewing distance of 60 cm. This spatial separation of 5 deg was within the range of spatial separations sufficient to elicit compelling illusory saltation (Geldard, 1976). The inter-stimulus interval (a blank gray screen also set to 30 cd/m^2) was fixed throughout each stimulus sequence. Stimuli were generated using MATLAB version 7 and displayed on a linearized 24-inch Mitsubishi Diamond Pro monitor driven at a frame rate of 120 Hz.

The stimulus sequences used to elicit real motion were similar in design to those described above. However, rather than being presented at just two locations, the five elements were sequentially presented at equidistant intervals between and inclusive of the first and last sites.

Procedure

On each trial, observers were required to indicate the apparent position of either the first, last, or middle element in the sequence. To aid this judgment, the to-be-judged element was identified by increasing its contrast (to 0.9) so that it appeared "brighter" than the other elements in the sequence. Pilot studies revealed that this contrast change did not disrupt the perception of saltation, and observers were able to accurately identify the brighter "target element" for the range of ISIs employed in the present study. After each sequence ended, observers were asked to indicate on the screen, using a mouse cursor (a black spot with a radius of 0.15 deg of visual angle), the spatial position of the "perceptually brighter" spot. The cursor was not visible on the screen during the stimulus presentation, rather it appeared at a random location along the circumference of a non-visible circle (centered on the stimulus with a radius of 10 deg) at the offset of each sequence and disappeared immediately after the observer had pressed the mouse button. Observers were requested to respond as quickly and as accurately as possible.

A block comprised 420 trials: seven levels of ISI (0.1, 0.15, 0.2, 0.25, 0.3, 0.35, and 0.4 s) for each of three

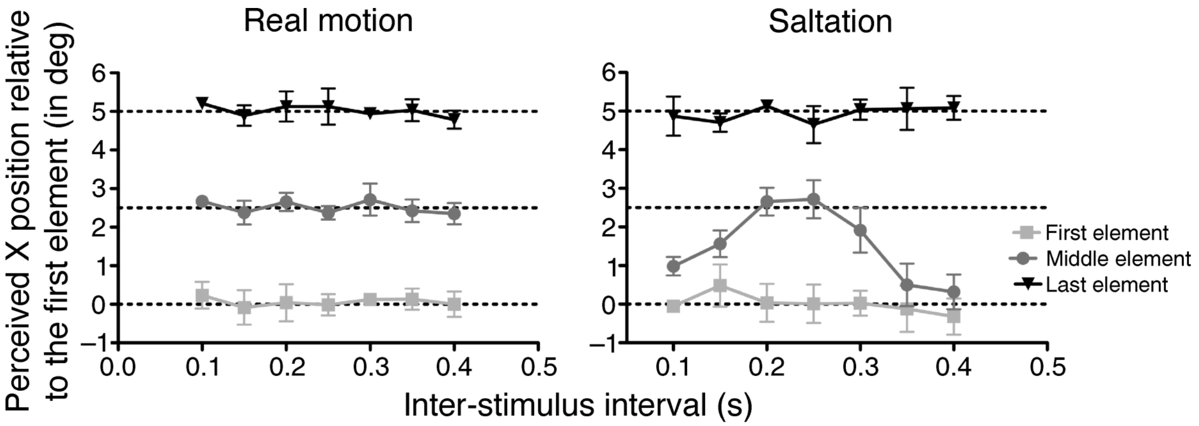

Figure 3. Average judged position of the first, middle, and last elements in the sequence (relative to the physical position of the first element) for real motion (left panel) and illusory saltation (right panel) plotted as a function of the inter-stimulus interval. Error bars represent one standard error of the mean. Dashed lines indicate the first, middle, and last spatial positions in the sequence.

position judgments (first, middle, and last) for both real motion and illusory saltation, repeated 10 times. Stimulus conditions were randomized within and between each block. Observers each completed 5 blocks such that each condition had 50 trials. Results were averaged across the 50 trials for each condition.

Results and discussion

The results of Experiment 1 are given in Figure 3. The judged position (in deg from the first site of stimulation) for the average of five observers is plotted as a function of ISI for real motion (left) and illusory saltation (right). In each figure, the judged position of the first (squares), last (triangles), and middle (circles) elements is plotted; error bars represent one standard error of the mean and horizontal dashed lines represent the veridical first, last, and middle positions of the sequence. As shown in the left-hand panel of Figure 3, position judgments for the "real-motion" conditions were extremely accurate regardless of ISI and despite the fact that the stimulus was viewed peripherally.

The results for the real-motion condition contrast with those obtained for the saltation illusion. As the right-hand panel of Figure 3 shows, while observers were able to accurately judge the position of the first and last elements in the sequence regardless of ISI, the judged position of the middle element was dependent on ISI. For short (less than 0.2 s) and long (greater than 0.35 s) ISIs, the judged position of the middle element was near its physical position corresponding to the first stimulation site. However, for ISIs between 0.2 and 0.3 s, the judged position of the middle element in the sequence appeared mislocalized approximately halfway between the first and last elements. Saltation as a function of ISI is therefore non-monotonic, best described as an inverted U-shaped function. This effect accords with previous reports (see Geldard, 1976; Lockhead et al., 1980). Comparison of results from the real-motion and saltation conditions shows that at an ISI of approximately 0.25 s the middle element of each sequence is judged to be in the same position. Moreover, an ISI of 0.25 s results in mislocalization of the middle element of approximately 2.5 deg, which is a much larger effect than that noted with the flash lag effect or with the Fröhlich effect.

Experiment 2: Motion adaptation at the perceived location of elements

In the previous experiment, we observed that saltation is most compelling, and most analogous to real motion, at an ISI of 0.25 s. In Experiment 2, we presented our stimulus sequences at that ISI to examine the effect of motion adaptation, generated by a moving sinusoidal grating, on the trajectory of saltation. Specifically, we examined the effect of motion adaptation at the location corresponding to the midway point between the two sites of stimulation on that trajectory. Thus this experiment examined the condition in which elements overlap perceptually, but not physically, with the adapted area. As outlined in Figure 2A, there are two possible outcomes. If saltation arises from the initial detection of elements at their physical locations, it would be expected that the path of saltation would be unaffected because there is no overlap of elements with the adapted region. However, if the illusory motion occurs because the stimulus sequence is interpreted as a single object undergoing saltatory motion, the middle element in the sequence will overlap with the adapted area (despite

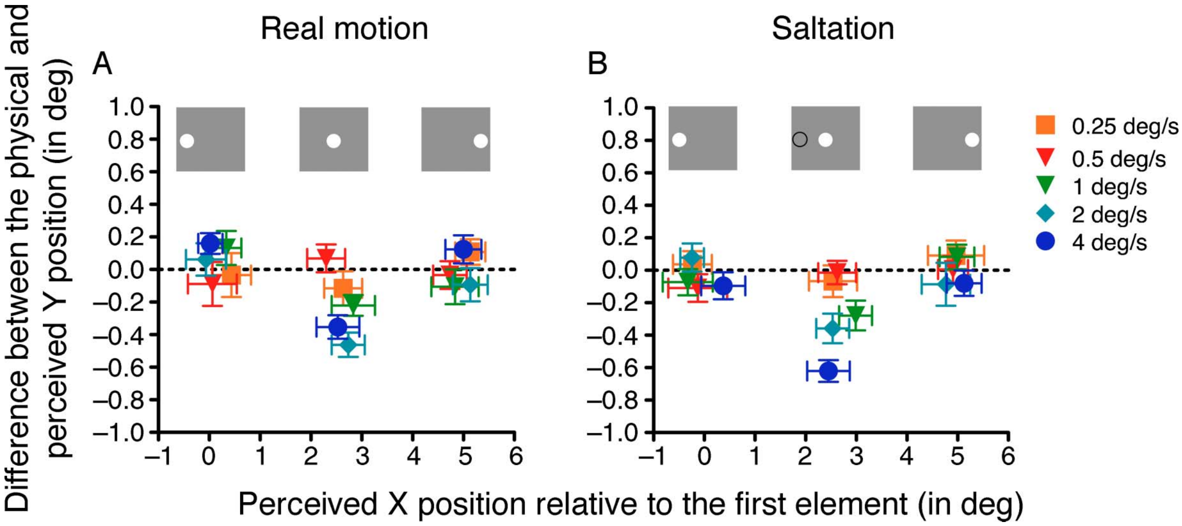

Figure 4. The perceived *Y* position (as a difference in deg from the actual position) of the first, middle, and last elements in the sequence (given by schematics above each data cluster) is plotted as a function of their perceived *X* position (relative to the first element, in deg). Note that in Figure 4B, for the middle element, an outlined circle is present to indicate the physical position. Colored symbols represent different adapting speeds. Error bars represent one standard error of the mean.

the fact that it physically originates from the first site of stimulation), and it would be expected to be distorted in the MAE direction. To provide an indication of the extent to which motion adaptation affects apparent position, we also varied the speed of the adapting stimulus in separate conditions.

As in Experiment 1, we repeated the experimental procedure with a stimulus undergoing real motion. Such a stimulus does present an element in the central position—an element that physically overlaps with the motion—adapted region. Therefore, an obvious expectation is that the middle element will be distorted in the MAE direction. Observer responses to this stimulus enables comparison to saltation in terms of the effect of motion adaptation on perceived position of elements.

Methods

The same observers as in Experiment 1 participated in this experiment. The stimuli and procedures were similar to Experiment 1 but were modified to include a period in which observers adapted to a horizontal, upward, drifting sinusoidal grating (spatial frequency of 6 cyc/deg; 1.5 × 3 deg of visual angle; Michelson contrast of 0.875, Lmin = 4 cd/m^2, Lmax = 60 cd/m^2).

Prior to each trial, observers were required to fixate on the central cross and were instructed to maintain fixation throughout testing. The drifting grating was presented exactly midway between the two sites of stimulation for 120 s to generate an MAE. Following adaptation, stimuli inducing either saltation or real motion were presented, and the task was to indicate the apparent position of the "target element" within the sequence. Motion adaptation was maintained across trials via "top-ups"—readaptation to the grating stimulus after every third trial for 20 s. Each block contained 300 trials: 10 trials at each of three judged positions of elements (first, middle, and last) for five adapting grating speeds (0.25, 0.5, 1, 2, and 4 deg/s) for both real motion and saltation. Each observer completed 5 blocks (i.e., 50 trials for each condition). To prevent order effects, stimuli were randomized both within and between blocks.

Results and discussion

The results of the five observers were extremely similar and were therefore averaged. These averaged results are given in Figure 4. Figure 4 plots judged position in terms of Cartesian *X* (relative to the first site of stimulation at 15 deg of visual angle to the right of fixation) and *Y* coordinates (as a difference between the perceived and physical *Y* positions) of the first, last, and middle elements (indicated by stimulus schematics directly on top of each data cluster) for real-motion (left panel) and saltation (right panel) stimuli as a function of the speed (different symbols and colors) of the adapting stimulus. The dashed line indicates the undistorted *Y* position of elements in the sequence. Error bars represent one standard error of the mean.

As expected, where observers judged the position of elements undergoing real motion (Figure 4A), motion adaptation midway between the two stimulation sites only affected the apparent position of the middle element in the sequence, displacing it in the MAE direction. Motion adaptation at this location did not affect the apparent position of the first and last elements in the sequence: the perceived position of these elements remained close to physical *Y* position of elements, as shown. This localized effect is consistent with previous reports of the interaction of position and the MAE, and additionally shows that the MAE in the periphery (where vision is mediated by comparatively larger receptive fields) does not extend beyond the adapted region. These findings are consistent with recent observations by McGraw and Roach (2008), who demonstrated that the MAE in the periphery is largely confined to the adapted area. Figure 4A additionally shows that the extent to which the MAE affects the apparent location of the middle element is dependent on the adapting speed. Increased speed of the adapting stimulus was associated with a notable increase in the extent of position offset, with a maximum offset of approximately 0.5 deg noted at the fastest speed (4 deg/s). This offset is similar to those noted by Snowden (1998) and accords well with the findings of De Valois and De Valois (1991), who reported that faster grating speed induces larger offsets in position.

Where saltation was elicited, a number of trends were evident (see Figure 4B). First, since the middle element was mislocalized to the central position, it would appear that motion adaptation does not break down the illusory percept. Second, motion adaptation within the region between the two stimulation sites does indeed shift the path of the illusory motion consistent with the prediction given in Figure 2A(ii). This shift is dependent on the speed of the adapting stimulus: at the slowest speed used in the study, there was no noticeable distortion in position, but as the speed of the grating increased, so did the positional offset in the MAE direction. Finally, comparison of results from the perception of real motion and saltation shows very similar trends, indicating similarities in the percepts of the two sequences under these conditions.

The results of Experiment 2 suggest a high-level, top-down, interpretation of the mechanisms of the saltation illusion. While the middle element in the sequence has its physical origin at the first site of stimulation, it is perceived to have originated from between the two physical stimulation sites. It therefore coincides with the adapted region and is shifted in the MAE direction. A high-level explanation of the saltation illusion is further validated by comparison of data given in Figures 4A and 4B. In both cases, motion adaptation effects were noted for the middle but not the first and last elements. This finding demonstrates that, like real motion, elements in the saltation illusion are perceived as being distributed across the space between the two stimulated sites, generating the conclusion that the elements must have arisen from a single moving object (note, though, that this does not necessarily indicate the equivalence of these two percepts). This result accords with previous findings showing that the visual system is sensitive to the perceived position of elements and not the physical position (e.g., Hayes, 2000).

It is important to note that the results of this experiment are dependent on the generation of a compelling percept of saltation. Where the optimal conditions (i.e., ISI) for saltation are not met, elements are obviously easily localized to their veridical locations. In this case, it would be predicted that motion adaptation in the region between the two stimulated locations will result in no distortion effect because the adapted region and the perceived location of elements are spatially separated. In a supplementary experiment, we tested this prediction by repeating Experiment 2 with one adaptation speed of 4 deg/s, but

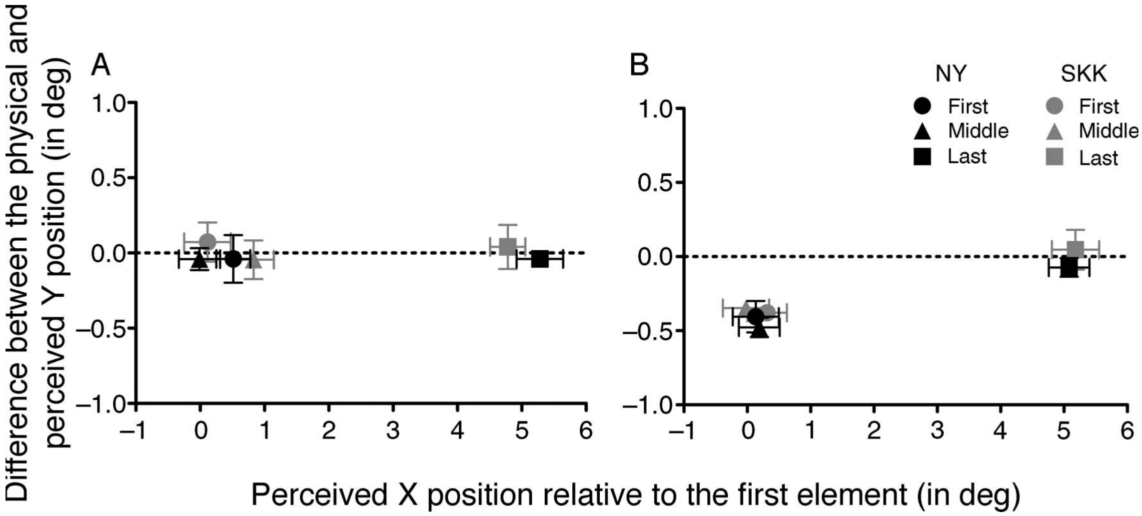

Figure 5. An ISI of 0.4 s was used to present stimuli for conditions in which adaptation occurred (A) between the two stimulation sites and (B) at the first stimulation site, plotted in the same format as Figure 4. The results, judged position of the first, middle, and last elements in the sequence, of two observers (NY and SKK), black and gray symbols, respectively, are shown. Error bars represent one standard error of the mean.

elements were presented at an ISI of 0.4 s, which produces veridical localization rather than saltation, as Experiment 1 verified.

Two observers (SKK and NY) participated in this supplementary experiment. Stimuli and procedures were the same as those previously described. Results are shown in Figure 5A, plotted in the same format as Figure 4. Figure 5A shows that the first, middle, and last elements in the sequence are perceived at their physical locations, confirming that the percept was not that of the saltation illusion. More importantly, in contrast to the aforementioned results obtained with an ISI of 0.25 s, the apparent position of the middle element was unaffected by the MAE. These findings confirm that the extent to which motion adaptation affects the position of elements is highly dependent on the visual system's interpretation of the origins of elements depending on ISI. At short ISIs, elements are mislocalized and are seen to originate at discrete spatial locations (due to a high-level interpretation of the stimulus as a single moving object) and the shifted middle element overlaps with the motion adapted area, but at long ISIs (in which the saltation illusion is not produced) objects are seen at their veridical positions, and there is no overlap between the adapted area and the position of elements.

Experiment 3: Motion adaptation at the physical location of elements

The findings of Experiment 2 indicate that the perceived position of elements is distorted by motion adaptation if elements are perceived to overlap with the adapted area, as indeed they are under conditions sufficient to produce the saltation illusion. These results can be accounted for by assuming that the visual system interprets the stimulus sequence as one in which elements are perceptually distributed evenly between the two sites of stimulation. In Experiment 3, we further examine the impact of motion adaptation on the trajectory of the saltation illusion by examining the effect of motion adaptation at one of the physically stimulated locations. This condition presents the complementary arrangement to Experiment 2 and tests the predictions outlined in Figure 2B.

The same observers and procedures as in Experiment 2 were used in Experiment 3, except that the adapting stimulus overlapped with the first site of stimulation. As in Experiment 2, we repeated the experimental procedures for both real motion and the saltation illusion, varying the speed of the adapting stimulus to determine the impact of motion adaptation on the apparent position of elements.

Results and discussion

The results of Experiment 3 are shown in Figure 6, plotted in a manner similar to those in Figure 4. Results for real-motion conditions are given in the left-hand panel (Figure 6A), while those for the saltation conditions are given in the right-hand panel (Figure 6B). As expected, in the real-motion condition, only the first element in the sequence is distorted in the MAE direction. Further, increase in the speed of the adapting grating produces a larger shift in the position of elements, with a reported offset of approximately 0.5 deg at the fastest adapting speed. That only the first element in the sequence was displaced as a result of motion adaptation is reflective of the fact that only this element physically overlapped with the adapted area; other elements in the sequence occupy

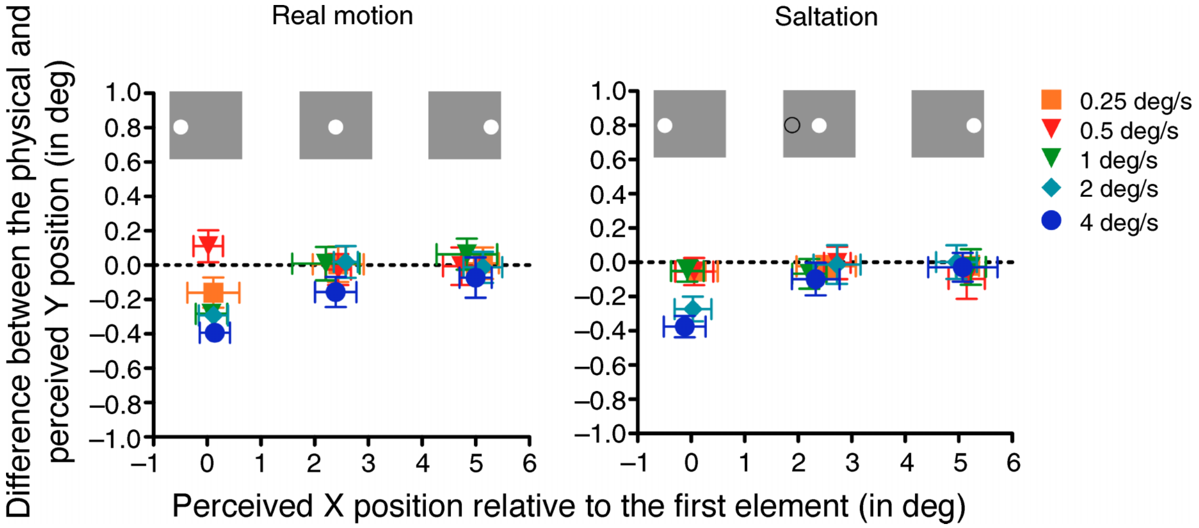

Figure 6. The perceived *Y* position (as a difference from their actual position) of the first, middle, and last elements in the sequence plotted as a function of their perceived *X* position (in deg from the position of the first element). Error bars represent one standard error of the mean.

positions that did not overlap with this area and thus were unaffected.

Interestingly, the pattern of results for the saltation condition is nearly identical to that obtained for real motion. As Figure 6B shows, only the first element in the sequence was affected by motion adaptation, with the extent of the offset in the MAE direction again dependent on the speed of the adapting stimulus. Importantly, the middle element remained unaffected (i.e., was localized to the central position) despite the fact that it had physically originated from the first site and was therefore physically overlapping with the adapting stimulus. The results of Experiment 3 are entirely in agreement with a high-level account of the saltation illusion: the visual system has judged the perceived position of the middle element as originating at a location removed from its actual physical position, rendering it unaffected by the MAE.

As in Experiment 2, we repeated Experiment 3 with a long ISI (0.4 s) at which saltation is not evident. The results of this condition (with the same two observers) are shown in Figure 5B. As shown, elements were perceived at their physical position (note that the middle element in the sequence is seen at its original location) and motion adaptation at the first site of stimulation affected both the first and (contrasting with the results with a shorter ISI) middle elements in the sequence; the last element is unaffected by adaptation.

Experiment 4: The impact of polarity-specific motion adaptation on the perceived position of the spatial probe

As discussed, our method in Experiments 2 and 3 was to have observers indicate the perceived position of the target stimulus via a mouse-controlled cursor after inducing an MAE. However, one might suppose that there is a potential confound in this method: perhaps the position of the cursor, in addition to the target, is distorted by the MAE. Where this is the case, it would not be clear whether the pattern of results we obtain is a genuine distortion of the saltatory path induced by the MAE, or an artifact of our measurement technique. To assess this possibility, we conducted an additional experiment in which we eliminated any potential MAE distortion of the cursor position by using an adapting stimulus and cursor that were of opposing contrast polarity. Previous research has shown that motion adaptation is polarity specific (Begg & Moulden, 1986; Mather, Moulden, & O'Halloran, 1991; Webb & Wenderoth, 1989). That is, if the adapting and test stimuli are of different contrast polarities, there is no (or at least very minimal) MAE as compared to same polarity conditions. This polarity-specific effect is presumed to be governed by independent polarity-tuned on and off cells in the visual processing hierarchy. In the present circumstance, we hypothesized that, if the adapting stimulus was of positive contrast polarity, and thus was a light increment like the target stimulus, while the cursor remained a light decrement (as in Experiments 1, 2, and 3), the generated MAE would selectively affect the perceived position of the target element but not the cursor.

This experiment repeated the procedures of Experiment 2 with the different adapting stimuli, but only measured the perceived position of the middle element in the sequence for adapting speeds of 0.5, 1, 2, and 4 deg/s. One of the authors (SKK) and two experienced observers who were naive to the goals of the experiment participated in the supplementary experiment. There were two stimulus conditions. In the first condition, the adapting grating and cursor were of opposite contrast polarity: the adapting grating was sinusoidal but was a light increment, representing a contrast modulation from the background luminance (34 cd/m^2) to a maximum luminance of 64 cd/m^2. The cursor was a black spot (4 cd/m^2). The second condition served as a replication of our original method to allow for comparison with the first condition and therefore had the same stimulus properties as Experiment 2 (i.e., the adapting grating and cursor were not of opposite contrast polarity). Because any potential distortion in the cursor position is eliminated through polarity-specific adaptation, in Condition 1 we hypothesized that similarity in results between the two conditions would suggest that the cursor is immune to the MAE in our experimental setup and that the results of Experiments 2 and 3 are not subject to this potential confound.

Results and discussion

The results are shown in Figure 7. The perceived *Y* position of the middle target stimulus (relative to its physical position) is plotted as a function of the speed of the adapting stimulus. Results for Condition 1 (solid symbols, average results indicated by the black dashed line) and Condition 2 (open symbols, average results indicated by the gray dashed line) are given for each observer at each of the four speeds. Three trends are evident in these data. First, the pattern of results is similar for all observers. Second, as the adapting speed increases, there is a systematic shift in the perceived position of the middle element in the MAE direction. Third, and most importantly, there is no difference in the judged position between the two contrast polarity conditions; results from both conditions are comparable to those of Experiments 2 and 3. These data indicate that, for our original experiments, the MAE did not distort the position of the cursor and that the reported results of the original experiments provide a good indication of the extent to which the MAE distorts the position of elements in the visual saltation illusion. The results of this study therefore allow us to rule

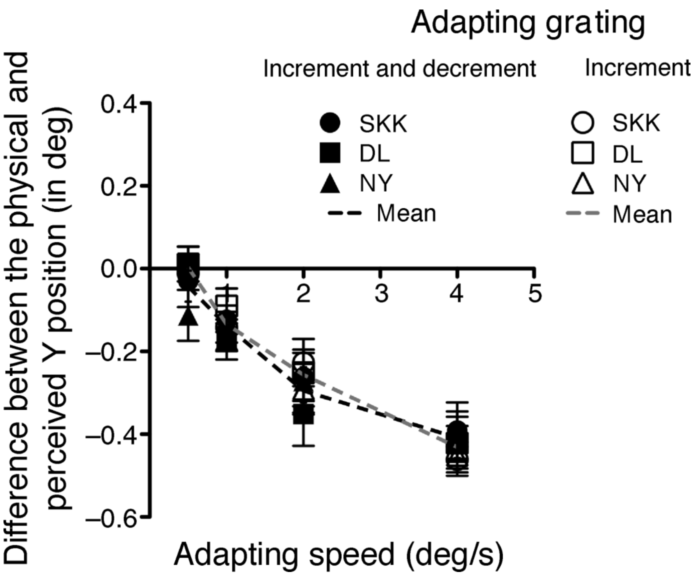

Figure 7. Perceived difference between the physical and perceived *Y* positions of the target stimulus plotted as a function of the speed of the adapting stimulus. Solid black symbols and open gray symbols depict data for conditions in which the adapting grating stimulus consisted of increment and decrement bars (averaged data indicated by black dashed line) and a light increment grating (averaged data given by gray dashed line), respectively. Error bars represent one standard error of the mean.

out the effect of the MAE on the cursor as a possible artifact in our experimental design. We suggest that the cursor was not affected by the adapting stimulus because it is present on the screen for only a brief period—observers responded as quickly as possible after the offset of the stimulus presentation. This explanation would certainly be consistent with Nishida and Johnston (1999), who noted that the extent of position distortion by the MAE is minimal for brief presentations, increasing with test stimulus duration.

General discussion

The present study sought to examine the extent to which motion adaptation distorts the position of elements (and therefore the perceived motion trajectory) in the visual saltation illusion. The visual saltation illusion belongs to a class of stimuli for which a discrepancy exists between the physical and perceived positions of elements; indeed the perceived positional shift created in this illusion is substantial by comparison to other examples of such stimuli. In separate conditions, the present study examined how motion adaptation at the physical and perceived locations of elements affects the perceived trajectory of motion, both real and illusory.

The results of both Experiments 2 and 3 showed that motion adaptation affects the judged position of elements if the elements are perceived to originate in the area at which motion adaptation occurs. That is, elements do not need to physically overlap with the adapted area to be affected by the MAE; the saltatory path is disrupted by the MAE based on the illusory, rather than physical, position of the elements. These findings are novel in showing that the original observation of position distortion by Snowden (1998) extends to the coding of illusory elements in which the percept is not exclusively derived from a physical representation on the retinal image. The present results provide for more informed conclusions about the mechanisms of the visual saltation illusion. The finding that the MAE distorts the illusory path of visual saltation strongly suggests a high-level interpretation of the illusion. As discussed, a low-level explanation would predict distortion in perceived position only at the physical location of the elements—a prediction that was not borne out in our results. Therefore, consistent with Shore et al.'s (1998) suggestion, in perceiving elements as misplaced in equal steps between the two stimulated locations, the observer is left with the compelling impression that a single object underwent motion.

The conclusion that the visual saltation illusion likely has a cortically high-level origin generates the question of what neural operations underlie the illusion. Some insights may be gleaned from our current understanding of how apparent motion is processed by the visual system. While apparent motion and the saltation illusion are fundamentally different (as discussed), they have commonality in that they arise from the visual system interpreting a sequence of stimuli degraded by temporal frequency as representing a single object undergoing motion. Particularly informative in this regard are the results of Yantis and Nakama (1998). Yantis and Nakama examined the degree to which apparent motion generated between two spatially separated and temporally alternating stimuli interferes with the perceived form of an object presented between the stimulated locations. They report that the detectability of the gap in a Landolt C stimulus was affected (that is, a higher stimulus contrast was required for detection) if the stimulus was presented at a location along the motion path. These results are very much analogous to those of our Experiment 2, in which it was demonstrated that motion adaptation between the two sites of stimulation distorted the perceived position of the middle element, which physically originated from the first site of stimulation. Yantis and Nakama (1998) postulated that their results are consistent with a process in which higher cortical areas feed back to lower areas to perceptually "fill-in" the area between the two sites of stimulation, and this neural representation interferes with the detectability of a stimulus presented within the path of motion.

In agreement with Muckli, Kohler, Kriegeskorte, and Singer (2005), Yantis and Nakama (1998) used neural imaging to show that the illusion of apparent motion activates extrastriate areas as well as areas in V1 along the motion path. It is therefore feasible that the visual saltation illusion follows a similar computation, with the percept arising from higher level processes and actively feeding back to influence the retinotopy at lower cortical areas. In this case, receptors coding information from between the two sites of stimulation (which do not receive direct physical stimulation) would be activated to produce illusory motion. In terms of the present study, if neural representation of this kind is affected by motion adaptation at a particular location, it follows that the MAE will distort the perceived position of elements overlapping with this location—indeed this was our finding. This explanation accords well with the model of Wiemer et al. (2000), who postulated that the saltation illusion arises due to reorganization of the topographical map in lower cortical areas in response to the temporal characteristics of the stimulus, in which the temporal interval between stimuli is directly transformed into a spatial offset, with the extent of separation dependent and proportional to ISI. Consistent with our findings, high-level processes may drive this remodification. While verification of this arrangement through direct investigation of the possible neural locus of the visual saltation illusion using imaging techniques would be most informative, it is beyond the scope of the present study.

Given that the visual saltation illusion involves spatio-temporal processing, the locus for the illusion is likely to be motion area Middle Temporal (MT). Area MT feeds back to earlier cortical areas such as V1, and MT has been shown to be important in the perception of similar high-level motion such as apparent motion (Liu, Slotnick, & Yantis, 2004; Muckli et al., 2005; Pascual-Leone & Walsh, 2001; Tong, 2003). Additional evidence for a possible locus at MT/V5 comes from McGraw, Walsh, and Barrett (2004), who showed that transcranial magnetic stimulation (TMS) to area MT/V5 appreciably reduces the extent to which motion adaptation affects apparent position, but disruption to V1 does not. Thus, it is possible that the results obtained in the present study reflect the activation at area MT/V5 in the mediation of position and in the perception of illusory motion. This is well supported by the findings of Kanai and Verstraten (2006) who used a novel transient motion stimulus to demonstrate that simultaneous perception of the veridical and distorted positions of an object is possible, suggesting a processing strategy in which veridical position is established at lower cortical areas, while position distortion is computed at higher cortical areas.

The results of the present study, and the high-level interpretation we have adopted, are also consistent with previous investigations showing that the visual system is sensitive to, and is reliant on, the perceived location of elements when judging the position of objects. For example, Hayes (2000) demonstrated that it is the perceived position of Gabor elements with internal motion that governs their binding to form contours. Additionally, Li, Khuu, and Hayes (2009) recently showed that the perceived position of illusory contours derived from the perceptual completion of a triangular Kanizsa figure is affected by image motion. Specifically, placement of the Kanizsa figure on a background of continuous contracting motion distorted the apparent position of illusory contours to produce a “thin” Kanizsa triangle, while expanding motion produced a Kanizsa triangle that appeared “fat” in shape. The findings of Li et al. (2009) are consistent with a processing strategy in which the visual system first perceptually completes the Kanizsa stimulus, with the neural representation then affected by the background motion.

To conclude, the results of this study converge on two clear findings. First, the extent to which the MAE affects the position of elements during saltation is contingent on the perceptual, but not necessarily the physical, overlap of elements with the adapted area. This strongly suggests that it is the visual system’s interpretation, rather than the physical properties of the spatial stimulus, that governs perception. Second, the MAE distorts the path of elements in the saltation illusion in a similar manner to that of real motion. This implies that the visual saltation illusion does indeed arise from a “grouping” mechanism in which the visual system assumes that the ambiguous sequence of elements arose from a single object moving smoothly across the area between the two physically stimulated locations. This interpretation is likely to occur in higher cortical areas.

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