Apparent motion distorts the shape of a stimulus briefly presented along the motion path

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We examined whether motion blur accompanying apparent motion (AM) affects the shape of a stimulus presented in the motion path. In a two-alternative forced-choice procedure, observers judged the shape of a Gaussian test stimulus flashed in the path of motion, relative to a reference stimulus, which was a circular Gaussian stimulus located away from the path of motion. In Experiment 1, we report that the test stimulus was affected by AM and its perceived width was wider than its actual width, and counteracting this distortion, shape discrimination thresholds coincided with a test stimulus that was physically "thinner" than the reference stimulus. Shape distortion correlated with the strength of AM (Experiment 2) and increased within the range of inter-stimulus intervals used to induce AM and with retinal eccentricity but was eliminated when the test stimulus was made "hard-edged" (Experiment 3) or when the stimulus does not overlap with the motion path (Experiment 4). In Experiment 5, we demonstrate that the effect is present for dichoptic presentations. These results can be accounted for by a process in which the neural representation of AM generated by higher cortical areas feedback to interfere with the coding of stimulus shape by units located along the trajectory of AM.

Keywords: apparent motion, shape, form, stereopsis, motion streaks


Introduction

When two stationary visual stimuli, separated by a fixed spatial distance, are viewed in rapid alternating succession, an illusion of movement is produced—a sensation of a single stimulus traversing the shortest path between the two points of stimulation. This illusory visual phenomenon is commonly known as “Stroboscopic” or “Apparent Motion” (AM) and arises not from a physical displacement of an object over time but through a process of perceptual interpolation in which visual motion is inferred from the spatiotemporal characteristics of inducing elements (Cavanagh & Mather, 1989; Kolers, 1963, 1972; Wertheimer, 1912). It has been proposed that the computation of AM is reflective of a perceptual “filling-in” process in which a sensation of movement is generated in the non-physically stimulated space between the two flashed stimuli (e.g., Clatworthy & Frisby, 1973; Kolers, 1963; Yantis & Nakama, 1998). Neural imaging studies have identified the locus of this operation in higher cortical areas, particularly in the motion sensitive area Middle Temporal (MT), and it is possible that AM arises from computation in high-level cortical areas, which is then directly fed back to lower cortical areas such as V1, to produce a neural representation of motion (Liu, Slotnick, & Yantis, 2004; Muckli, Kohler, Kriegeskorte, & Singer, 2005; Muckli et al., 2002).

The percept of AM arising from perceptual filling-in is thought to resemble motion blur, or motion smear, that would normally accompany an object physically traversing space over time. Previous research has shown that AM resembles motion smear since a comparison between both shows that the perception of AM coincides with the point at which real motion is blurred (Kaufman, Cyrlunik, Kaplowitz, Melnick, & Stoff, 1971; Kolers, 1963). Additionally, a spatial path can be used to imply motion smear, biasing the trajectory of AM. Shepard and Zare (1983) demonstrated that when a gray curved path (a spatial cue) is briefly flashed in the space between two alternating stimuli, apparent movement appears to follow the gray path rather than the most direct route. Presumably, the gray motion path is treated by the visual system as motion smear generated by actual movement along the path.
direction, and therefore, perceived motion follows this path. Moreover, this perceptual bias can occur with paths that are many times longer than the most direct route between elements. This finding is significant as it implies that motion smear is treated as a spatial signal resembling a line stimulus orientated along the axis of motion.

Research has also shown that, under appropriate stimulus conditions, illusory motion smear associated with AM can interfere with the appearance of a stimulus presented along the motion path. This can happen in a number of ways. First, AM can affect the detectability of an object. For example, Yantis and Nakama (1998) reported that the ability to identify a target stimulus was impaired when placed on the path of motion (relative to performance when the stimulus was off the path of motion), and this finding is indicative of a process in which the neural representation of AM disrupts the coding of another stimulus. Second, AM can bias the spatial registry of an object—the perceived position of an object briefly flashed along the motion path is shifted in the direction of AM with larger distortions noted at shorter temporal intervals. Originally noted by Brigner (1984), this observation has since been extensively reported in a number of studies (e.g., Eagleman & Sejnowski, 2007; Shim & Cavanagh, 2004, 2006; Watanabe, Nijhawan, & Shimojo, 2002; Whitney, 2002) and mirrors the same effect with real motion (see De Valois & De Valois, 1991; Tsui, Khuu, & Hayes, 2007). This effect likely occurs because the neural representation of AM disrupts the spatial registry of an object and its position code is shifted in the motion direction. Single cell recording studies lend support to this suggestion and show that the receptive field profile of position coding cells in primary visual cortex of the cat, when exposed to image motion, undergoes displacement in the motion direction (e.g., Fu et al., 2002). Third, AM can affect the appearance of an object briefly presented on the path of motion. MacFarland (1965) demonstrated that a square briefly flashed in the motion path of AM is not perceived as complete at the point of presentation, but instead appears to be sequentially revealed over time from the leading edge of motion. Together these studies reveal that AM is compelling (see Fahle, Biester, & Morrone, 2001), and that, under specific stimulus conditions, the neural representation of AM can interfere with the coding of objects overlapping with the motion path. However, current understanding of this process is limited, particularly regarding the degree to which form and AM interact, the nature of this interaction, and the conditions under which this interaction occurs.

With the aim of contributing to the understanding of this process, the present study questions whether the neural computation of AM also distorts the perceived shape of an object presented on the motion path. This question stems from the observation that motion smear accompanying AM also provides a spatial signal (an oriented line stimulus: Shepard & Zare, 1983), and previous studies have shown that the orientation of motion smear can affect the form of moving objects (see Or, Khuu, & Hayes, 2007; Ross, 2004; Ross, Badcock, & Hayes, 2000). As an example, Li, Khuu, and Hayes (2009) showed that motion smear produced by background dots moving along radial expanding trajectories distorts the apparent shape of a superimposed Kanizsa triangle. Thus, if the neural representation of AM (motion smear as a spatial line oriented along the axis of motion) affects the coding of shape, an expectation is that a briefly presented object overlapping with the motion path will be distorted and will appear elongated in the direction of motion. The aim of the present study was to investigate this possibility.

It has been reported that shape change accompanies AM. For example, if the stimuli inducing AM have different shapes, the percept is one in which the first shape appears to transform or “morph” into the second shape (e.g., Kolers, 1972; Kolers & von Grunau, 1976). Additionally, in the phenomenon of “representational momentum,” in which perceptual extrapolation occurs with the last element in an AM sequence (Freyd & Finke, 1985), the size of the last element may differ from the first element (see Freyd & Johnson, 1987). The present study differs from these previous investigations in that it is not concerned with the shape of stimuli inducing AM, but rather the extent to which motion smear accompanying AM distorts the shape of a stimulus that does not directly contribute to the generation of AM.

The present study comprises a series of experiments that quantify the degree to which the ability to discriminate the apparent shape of a briefly presented Gaussian-profile circle is affected by AM. We examine this as a function of temporal (Inter-Stimulus Interval: ISI) and spatial (eccentricity) parameters of the AM illusion in Experiment 1. In Experiment 2, we measure the strength of apparent motion for the range of ISIs used in Experiment 1 and compare these data with our observations of shape distortion in Experiment 1. Experiment 3 repeated the procedures of Experiment 1 using a well-defined “hard-edged” circle, rather than a Gaussian-profile circle, to determine whether any distortion observed in Experiment 1 is due to the spatial ambiguous nature of the Gaussian stimulus. In Experiment 3, we used a gray path to deflect the path of motion to investigate whether shape distortion is dependent on the proximity of the stimulus to the path of motion. Finally, in Experiment 5, shape discrimination thresholds were measured under monocular, binocular, and dichoptic viewing conditions to determine whether shape distortion is dependent on the ocular origin of the stimulus.

**Experiment 1: Distortion of apparent shape by AM**

As mentioned, previous studies have reported that AM can distort the perceived position of a briefly flashed...
stimulus, and that this distortion arises from an interaction between the neural representation of AM and the coding of stimulus position. This observation reveals a malleable relationship between form and motion, making it reasonable to suggest that the neural representation of AM may also distort the shape of a stimulus presented along the motion path. We examined this possibility by quantifying the ability of observers to discriminate the shape of a circular Gaussian stimulus presented in temporal sequence with AM. This observation was made in two conditions in which the temporal interval between the presentation of stimuli eliciting AM and the retinal eccentricity (relative to central fixation) was systematically varied. We predicted that, since compelling AM is generally observed with brief temporal presentations, any shape distortion would be most noticeable at short intervals but would decrease with longer intervals at which the illusion may not be compelling. Additionally, because illusions of spatial form are more apparent in the periphery (e.g., Khuu, Kidd, & Errington, 2010) due to coarser spatial acuity at large retinal eccentricities (coupled with the fact that AM is more compelling in the periphery, Kolers & von Grunau, 1977), we expect that a shape distortion effect would be larger with increasing eccentricity.

Methods

Observers

Six experienced psychophysical observers (aged between 21 and 33 years of age) with normal or corrected-to-normal visual acuity participated in the experiment. Two were authors on this study, while the others were naive to the purpose of the study.

Stimuli

Stimuli were movie sequences depicting AM (on a gray background set to a luminance of 40 cd/m²) induced by briefly presenting two identical black bars (luminance: 4 cd/m², length: 2°, width: 0.5°, Weber contrast = −0.9) sequentially at two spatial locations horizontally separated by a distance of 6° of visual angle (see Figure 1). The AM sequence commenced with the presentation of a bar to the left location followed by the second bar presented to the right location. Each bar was displayed for 0.1 s and separated by a period in which the screen was blank and set to the background luminance. The temporal duration of this period was the ISI, which was set to different values depending on the experimental condition (see below). In the middle of this temporal sequence (but in temporal order, thus after the presentation of the first bar, but before the presentation of the bar to the right), a light increment Gaussian blob of the form: $L(x, y) = C_0 e^{-\sqrt{((x - x_0)/\sigma_x)^2 + ((y - y_0)/\sigma_y)^2}}$—where $C_0$ is the contrast of the stimulus (set to a Weber contrast of 1, maximum luminance at peak = 80 cd/m²), $x_0$ and $y_0$ are the center of the distribution, and $\sigma_x$ and $\sigma_y$ are the $x$ and $y$ standard deviations of the element in degrees (see below for exact values)—was briefly presented for 0.05 s midway in between the two physical positions of the bars generating AM (see Figure 1). Observers viewed the stimulus binocularly in a dark room at a distance of 60 cm. Stimuli were generated using MATLAB version 7 and displayed on a linearized 24-inch Mitsubishi Diamond Pro monitor with a frame rate of 100 Hz.

Procedure

The objective of Experiment 1 was to examine whether the ability to discriminate the shape of Gaussian stimulus is affected by AM. Object shape discrimination thresholds were measured using a two-alternative forced-choice procedure. Observers were presented with an AM sequence at a particular ISI and vertical eccentricity superior to a fixation point at the center of the screen. As illustrated in Figure 1, in the middle of the apparent-motion temporal sequence, the aforementioned Gaussian stimulus was presented. This stimulus was the test stimulus, and it was displayed simultaneously with a reference stimulus, which was a circular Gaussian spot presented below the point of fixation at the same eccentricity as, and in vertical alignment with, the test stimulus. The reference stimulus was displayed for 0.05 s and was similar in form to the test stimulus but was symmetrically circular with $x$ and $y$ standard deviations set to 0.42° and the stimulus was not accompanied by AM (see the central panel of Figure 1). The task of the observers was to indicate whether the test stimulus appeared wider or thinner than the reference stimulus by pressing one of two buttons on a computer keyboard. Dynamic pixilated noise (20 Hz) was presented proceeding and preceding the presentation of the stimulus for half a second, to prevent a buildup of an image aftereffect.

A staircase procedure that converged on the 79% correct performance level (three correct responses to step down, one incorrect response to step up) was used to modify the width of the test stimulus (by changing $\sigma_x$, while $\sigma_y$ was the same as the reference stimulus at 0.42°) to reach the point at which the observer can reliably discriminate a difference in the shape between test and reference stimuli. The staircase began with the horizontal width of the test stimulus (standard deviation in degrees) physically wider than the reference stimulus at a value between 0.54 and 0.64°. The initial step size of the staircase was 0.08°. On the first and subsequent reversal, the step size was halved. After the third reversal, the step size was halved. After the third reversal, the step size was 0.01° and remained at this value until the end of the trial. The staircase lasted for 8 reversals and the average of the last 4 reversals provided an estimate of the shape discrimination threshold.

These procedures were repeated for two conditions in which stimulus eccentricity and ISI were systematically varied. A block comprised 24 staircase trials: six levels of
ISI (0.01, 0.02, 0.04, 0.08, 0.16, and 0.32 s, thus the duration of a trial varies with ISI) and 4 stimulus eccentricities of 2, 4, 6, and 8°. Additionally, for each eccentricity, observers discriminated apparent shape in which no AM was presented with the test stimulus. Importantly, these conditions provide an indication of thresholds removed of any potential distortion due to AM, and therefore they can be used as a baseline against which AM present conditions can be compared. Observers each completed 5 blocks and results were averaged over the 5
trials for each condition. Stimulus conditions were randomized within and between each block.

Results and discussion

The results of Experiment 1 are shown in Figure 2 as shape discrimination thresholds—expressed as the minimum difference (stimulus width, standard deviation in degrees) between the width of the test and reference stimuli required for observers to notice dissimilarity in shape—plotted as a function of the ISI of the AM sequence in log scale. Negative values on the y-axis correspond to a physically “thinner” test stimulus, while positive numbers represent a test stimulus that is physically wider than the reference stimulus. A zero value represents a test stimulus that physically matches the reference stimulus (i.e., both are circular). The results for all six observers were averaged and are represented in the figure as gray lines for different eccentricities (error bars represent one standard error of the mean and indicate variance between observers). Open symbols represent shape discrimination thresholds for conditions in which there was no AM for different eccentricities.

There are a number of data trends evident in Figure 2. First, when shape judgments between the test and reference stimuli are made without AM, shape discrimination thresholds are on average −0.025° and do not vary systematically with retinal eccentricity (open symbols). Though, as expected, there is greater variability for thresholds obtained at larger eccentricities of 6 and 8°. Second, when AM was presented in conjunction with the test stimulus, its perceived width was distorted, particularly at brief ISIs (e.g., 0.01 and 0.02 s), with the stimulus having to be thinner as compared to baseline conditions at threshold. These observations confirm that the perceived shape of an object presented along the motion path of AM appears perceptually longer than its veridical width, since the test stimulus is physically thinner at threshold (to counteract its perceptual elongation due to AM) for observers to no longer detect a difference in shape between the test and reference stimuli. Third, this distortion of shape is most evident when the stimulus was viewed at larger eccentricities, particularly at 6 and 8° with the average thresholds around −0.124 and −0.14° for the shortest ISIs (indicating a reduction in width of approximately 30%), respectively. For the smallest eccentricity of 2°, there was a marginal effect with thresholds no greater than approximately −0.07° for the shortest ISI. Fourth, for all eccentricities, as ISI increases, the extent of shape distortion gradually decreases. For the longest ISI, there is very little difference between these conditions and baseline, and therefore, no effect.

In summary, the results of Experiment 1 show that at brief ISIs, and at large stimulus eccentricities, AM interferes with the ability to judge the shape of an object overlapping with the motion path. This effect is consistent with the expectation that motion smear accompanying AM is treated by the visual system as a spatial stimulus orientated along the direction of motion, and that this spatial form interferes with the shape of the test stimulus. Greater shape distortion is observed at shorter ISIs as the percept of AM is stronger, and thus motion smear is more compelling and influences shape. Larger shape distortion effects found at greater eccentricities are the result of increased spatial uncertainty, due to coarser spatial acuity and or lower sensitivity to form information in the periphery (e.g., Gurney, Poirier, Bluett, & Leibov, 2006; Whitaker, Rovamo, MacVeigh, & Mäkelä, 1992). Concurrently contributing to and compounding the effect is the observation that AM is more compelling under peripheral viewing (Kolers & von Grunau, 1977), and thus motion smear is likely to exert a greater effect. These findings can be informally observed in the movie of the test stimulus provided in Figure 1B; with central viewing, there is minimal shape distortion, but if the stimulus is viewed in the periphery, the shape of the Gaussian stimulus appears elongated along the axis of motion.
In this experiment, the perception of motion is illusory, that is, the motion is a construct arising from the interpolation of motion from the spatiotemporal characteristics of stationary stimuli presented to discrete locations on the screen, not from a physical change in position between the two locations. However, the results clearly show that, despite the illusion of motion, the percept renders “real” distortion of object shape. It is important to point out that the polarity of elements used to generate AM (black bars) and the test Gaussian spot (a white spot) differed, but this did not disrupt the percept of AM, nor was it used as a cue for segmentation. These results are in agreement with previous findings (see, e.g., Shechter & Hochstein, 1990) demonstrating that the percept of AM is not luminance polarity dependent and occurs after information from On and Off pathways have been combined. On the issue of image segmentation, it is possible that the black bars generated a “darker” motion blur, which acting as the background, will enhance the apparent contrast of the test stimulus and thereby influence the shape of the stimulus. Alternatively, if the bars inducing apparent motion were white, and therefore the same polarity as the test stimulus, the contrast of the stimulus is reduced and therefore any shape distortion may not be evident. We addressed this suggestion in a control experiment in which one of the authors (SKK) and two experienced observers (NY and SH), who were naive to the purpose of the study, repeated Experiment 1 at an eccentricity of 8°, and ISI of 0.01 s with elements generating AM with the same polarity as the test stimulus. The result from this condition was similar shape distortion magnitudes (SD of the test stimulus, SKK: \( -0.18\), SEM = 0.0072, NY: \(-0.23\), SEM = 0.0132, SH: \(-0.14\), SEM = 0.0172) as those for the opposite polarity stimulus used in Experiment 1. These findings suggest that it is unlikely that our findings are due to a change in perceived contrast of the test stimulus due to a darker background arising from the motion blur. Additionally, we can discount a “contrast effect” since if a darker background (from a black motion blur) were to enhance the contrast visibility of the stimulus, a more likely outcome is that the stimulus will not be distorted but will be symmetrical and bigger in size. This is because the bars used to induce apparent motion are much longer than the Gaussian blob (approximately 3 times longer along the vertical axis), and thus the stimulus is wholly contained within and surrounded by the motion blur. Thus, according to the findings of Fredericksen, Bex, and Verstraten (1997), the perceived contrast of the entire edge of the stimulus will be enhanced producing a perceptually larger object that remains symmetrically circular in shape and would not be elongated along the axis of motion.

As mentioned, previous reports have shown that under conditions similar to Experiment 1, the position of the stimulus is shifted in the direction of AM (Shim & Cavanagh, 2004, 2006). Observers did indeed notice this effect and reported that test and reference stimuli, when presented, appeared out of alignment. While we did not measure this effect, it does not impact on the findings of the present study, as displacement of this type was small, and it is not obvious how perceived position along the motion path would modulate shape distortion. However, these studies and the present study are important in revealing concurrent effects arising from AM smear interfering with the spatial coding of a stimulus that is in close proximity to AM. It is possible that the shape distortion noted in the present study explains the effect of Shim and Cavanagh; a shape elongation may result in a centroid shift in the motion direction and thus resulting a perceived shift in position in the direction of motion. Previously, Tsui et al. (2007) have applied a centroid change explanation to account for the original demonstrations by De Valois and De Valois (1991) of a motion-induced position shift. Particularly, Tsui et al. noted that a stationary object containing internal motion appears to be perceptually longer, with the leading edge of motion, but not the trailing edge of motion, extended in the direction of motion. The consequence of this shape change is that the stimulus centroid is physically shifted in the direction of motion leading to a change in perceived position. Certainly, a future study carefully examining this issue would be fruitful.

The results of this experiment are similar to those of Suzuki and Cavanagh (1998) who reported an analogous shape distortion effect with spatial masking—the apparent shape of a briefly flashed test circle appears to be elongated perpendicularly to a line stimulus presented before the test stimulus, with the effect most noticeable for short presentations and at large stimulus eccentricities. Suzuki and Cavanagh accounted for their “shape-contrast effect” in terms of an interaction between different shapes coded in a continuum of shape structures in higher cortical form sensitive visual areas such as inferotemporal cortex (IT) and Superior Temporal Sulcus (STS). Priming to a particular shape structure results in a “repulsive after-effect” and the complementary form interferes with the shape representation of a subsequently presented stimulus. Note that this “shape-contrast effect” cannot account for the findings of Experiment 1 as this effect is localized, and requires that target and inducing stimuli overlap. Suzuki and Cavanagh examined directly the possibility that AM, particularly the phenomenon of “representational moment,” might be responsible for their shape distortion effect but eliminated this possibility by generating AM by rapid and successive alternations of a spatially separated line and circle. There was no distortion effect for this stimulus because the circle was at the end of the temporal sequence and did not overlap with the line mask. This is not a requirement for the present study as shape distortion arises from an interaction with the generated motion smear (arising from perceptual filling-in) and not directly from the shape of elements inducing AM.

In light of the above, we suggest that our findings are unlikely to be due to an interaction between the shape of
elements inducing AM and the target stimulus itself: such an explanation suggests that, at brief ISIs, both are in close temporal proximity, presenting the opportunity for one to affect the other. However, to completely rule out this possibility, we conducted a supplementary experiment to show that the generation of AM is necessary to achieve the shape distortion effect noted in Experiment 1. Three of the original 6 observers repeated Experiment 1, but for stimuli presented only at 8°. While in Experiment 1 elements were presented sequentially to generate AM, in the supplementary experiment these elements were presented together and simultaneously with the target stimulus for 0.05 s (condition 1), or before the target stimulus (with an ISI of 0.01 s, duration of elements and test stimuli were identical to Experiment 1, condition 2). For both of these conditions, because elements are presented together, AM was not generated, so it was predicted that shape discrimination thresholds would be unaffected. However, if the distortion effect were reflective of an interaction between the shape of elements inducing AM and the test stimulus because they are in close temporal proximity, shape distortion ought to be evident.

The results of this supplementary experiment showed that the average shape discrimination thresholds for conditions 1 and 2 were $-0.038 \ (SEM: 0.0095^\circ)$ and $-0.027 \ (SEM: 0.0081^\circ)$, respectively. These thresholds are similar to the baseline condition ($-0.025 \ (8^\circ)$), indicating no effect. These thresholds contrast greatly with those in which elements we presented sequentially to generate AM (Experiment 1: $-0.14 \ (8^\circ)$). We therefore conclude that the generation of AM is critical to the shape distortion effect reported in Experiment 1, and that the effect does not arise from an interaction in shape between the test stimulus and elements inducing AM.

**Experiment 2: The strength of apparent motion**

In the previous experiment, we make the interpretation that the perceived distortion of a Gaussian circle arises because of an interaction between AM and the coding of shape. However, the validity of this interpretation is contingent on the assumption that compelling AM was achieved with the ISIs and stimulus configurations used. While observers verbally report compelling AM with the brief ISIs and large eccentricities employed in Experiment 1, it is nevertheless important to formally confirm this as it allows direct quantification of the strength of AM, and thereby allow direct verification of the impact of AM on perceived shape.

With this in mind, we conducted a control experiment using the methods of Kolers and von Grunau (1977) and measured the strength of AM generated using the same stimulus configurations (ISIs and eccentricities) as employed in Experiment 1 but with AM presented vertically superior to the point of fixation and with test or reference stimuli omitted. Stimuli were presented following the procedures depicted in Figure 1 and the task of the observer was to judge whether they saw “smooth” and “continuous” motion between the two flashed bars. They indicated their response by pressing appropriate keys on the keyboard. Observers were instructed to give a negative response if they saw partial or incomplete AM. A block of trials consisted of 240 trials: six different ISIs (0.01, 0.02, 0.04, 0.08, 0.16, and 0.32 s) and for stimulus eccentricities of 2, 4, 6, and 8°, 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. The four of the same observers (one was the author while the others were naive to the aims of the study) as in Experiment 1 participated in this experiment.

The results of all four observers were averaged and are shown in Figure 3, which plots the probability of seeing AM as a function of ISI for different stimulus eccentricities (different gray symbols). These data show two obvious data trends. First, the probability of seeing AM (and hence indicating the strength of the percept) is the highest for short ISIs ranging from approximately 0.01 s to 0.08 s, thereafter the probability of seeing apparent motion decreases. This finding is in agreement with, and replicates, previous reports showing a dependency of AM on ISI (see, e.g., Kolers & von Grunau, 1977). Second, agreeing with the findings of Kolers and Von Grunau, the overall probability of seeing AM is highest for larger eccentricities (6 and 8°) than for smaller eccentricities (2 and 4°). Importantly, the implications of these findings is that they agree with the findings of Experiment 1; the ISIs and eccentricities in which AM was judged to be most

![Figure 3](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/933482/ on 11/12/2018)
compelling are largely comparable with those under which the largest shape distortion was noted in Experiment 1. Given the concordance between the conditions leading to shape distortion (Figure 2) and compelling AM (Figure 3), we are confident that the former effect is due to an interaction between the shape of the Gaussian stimulus and the generated AM path.

A noteworthy point is that while we show a gradual decrease in shape distortion as a function of ISI (in Figure 2), the probability of seeing AM is approximately “low pass” remaining initially constant (for ISIs of approximately 0.01 to 0.08 s, with greater probability of seeing AM in the periphery) and then decreases rapidly with ISI. An explanation for this difference stems from the task used to measure motion strength in Experiment 2. As mentioned, in this experiment observers were required to indicate whether they saw smooth motion, but not to directly judge the “quality” of the motion percept on a trial. Thus, it is possible that while smooth motion was equally noticeable for short ISIs, inherent differences in the quality of apparent motion exists. Such differences in the quality of the motion blur would directly impact on the shape of an object presented on the motion path, but only on the probability of seeing smooth apparent motion when ISI is sufficiently large at which the illusion is not compelling or breaks down.

Experiment 3: Spatial uncertainty leading to shape distortion

One of the salient findings of Experiment 1 was that shape distortion within AM is larger in the periphery. This may reflect a process in which the visual system is resolving the form of an ambiguous stimulus. In this case, the form of the stimulus is ambiguous for a number of reasons. First, the Gaussian luminance profile of the test stimulus has smooth edges, meaning that the spatial border of the stimulus is not clearly defined (e.g., Fredericksen et al., 1997). Second, its presentation is very brief (0.05 s), meaning that there is insufficient integration time to render a clear percept of the spatial form of the stimulus. Moreover, this shape uncertainty is magnified in the periphery where the ability to resolve spatial detail is coarse, where perceptual filling-in is most likely to occur, and where AM is most compelling (De Weerd, 2006; De Weerd, Desimone, & Ungerleider, 1998; De Weerd, Gattass, Desimone, & Ungerleider, 1995; Ramachandran & Gregory, 1991). Accordingly, a potential explanation of our findings is that, in the absence of a clear indication of shape, the test stimulus is susceptible to motion smear, leading the visual system to resolve its shape as one that is elongated along the axis of motion. Given this, it is logical to expect that the extent of distortion might be reduced if the shape of the stimulus is more clearly defined.

Previous studies have shown that the distortion in position of an object by image motion can be removed or minimized by using a stimulus for which the object border is “hard-edged,” and the shape well defined, particularly when presented in the periphery (De Valois & De Valois, 1991). In Experiment 3, we used a hard-edged stimulus to repeat Experiment 1, examining whether this stimulus is susceptible to distortion by AM. We hypothesized that since the shape of this stimulus is definitive, it would not be affected by AM, and that shape discrimination thresholds would be similar to baseline conditions.

The same observers as in Experiment 1 participated in this experiment, which repeated the procedures of Experiment 1 with the stimulus presented only at 8° (where the largest distortion effect was noted) and with ISIs of 0.01, 0.02, 0.04, 0.08, 0.16, and 0.32 s. The test stimulus was a hard-edged circle with a radius of 0.5° and set to a luminance of 60 cd/m². These parameters approximately matched the apparent size of the Gaussian stimulus used in Experiment 1. As in the previous experiment, a two-alternative forced-choice paradigm, in conjunction with an adaptive staircase procedure, was used to measure the ability of observers to discriminate the shape of the test stimulus. Observers performed this task for conditions in which the test stimulus was presented with or without AM. In a block of trials, observers completed a staircase for each ISI. The order of ISI was varied within the block of staircases both within and between each block. Observers each completed five blocks such that each ISI condition had five staircases from which thresholds were estimated. Results were averaged over the five thresholds for each ISI condition.

Results and discussion

The results of Experiment 2 are shown in Figure 4. As in Experiment 1, shape discrimination thresholds are indicative of the difference in the width of the test and reference stimuli required for a just noticeable difference in shape, and they are plotted as a function of ISIs (on log scale). For the purpose of comparison, results from Experiment 1 are also shown in this figure. The dark solid line (squares) illustrates data from Experiment 1 in which the test stimuli was a Gaussian spot, and the gray dashed line (circles) illustrates data with a hard-edged circle. Different open symbols indicate thresholds for conditions in which there was no AM and the test stimulus was hard-edged (circle) and Gaussian-edged (squares). These data show a clear trend: when a hard-edged stimulus is used, the distortion of shape noted in Experiment 1 is greatly reduced at short ISIs (0.01–0.04 s). For ISIs of 0.08 to 0.32 s, shape discrimination thresholds did not systematically deviate from baseline conditions. These results contrast with those obtained with a smooth-edged circle. For this condition, shape distortion due to AM was noticed (as shape discrimination thresholds resulted...
in a test stimulus that was physically thinner than the reference stimulus) for ISIs except for the slowest interval (0.32 s). These findings affirm that the effect of AM on the perception of shape is most evident when the spatial form of the stimulus is not obvious, and that when the apparent shape of a stimulus is clearly defined, AM does not affect its percept. These results agree with previous reports showing that apparent position is not displaced by image motion if the form of the stimulus is clearly defined (De Valois & De Valois, 1991; Li et al., 2009). For example, Li et al. (2009) demonstrated that the apparent shape of a Kanizsa triangle is distorted by AM such that illusory contours are displaced in the direction of background motion. However, this effect is negated if the triangle is constructed with “real” luminance-defined edges, which provides an obvious cue to position and shape.

Experiment 4: Motion distortion on the perceived path of AM

In the previous experiments, we showed that AM distorts the perceived shape of an object, increasing as a function of ISI and eccentricity. We believe that a requirement for this shape distortion is that the Gaussian stimulus must be presented along the motion path, overlapping with the motion smear accompanying AM. We therefore expected that if the test stimulus was not overlapping with the motion path, but was rather placed away, it would remain undistorted. We tested this prediction in Experiment 4.

Yantis and Nakama (1998) examined the degree to which AM, generated between two spatially separated and temporally alternating stimuli, interferes with the perceived form of an object presented between the stimulated locations. They reported 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, but this effect was negligible if it was perceived away from the path of motion. To ensure that their stimulus did not overlap with the motion path, Yantis and Nakama did not physically shift its position (that is, the Landolt C stimulus was always physically placed on the shortest path in between stimuli), but rather diverted the trajectory of AM around the stimulus by presenting a gray luminance arc path with the stimulus. Shepard and Zare (1983) noted that the brief presentation of a curved gray path between the first and second elements could be interpreted as motion blur, reflecting a process in which the visual system attributes this spatial path as a product of actual movement of a single element along the path trajectory. In Experiment 4, we use a similar stimulus paradigm to Yantis and Nakama—a gray curved path was presented simultaneously with the test stimulus to “guide” the trajectory of AM around the test stimulus. As in the previous experiments, shape discrimination thresholds were measured with this stimulus. We predicted that since the trajectory of AM given by the gray path does not overlap with the test stimulus, there would be no shape distortion.

Methods

The same observers as in the previous experiments participated in Experiment 3. In Experiment 3, we repeated Experiment 1 with stimuli presented at 8° of eccentricity at ISIs of 0.01, 0.02, 0.04, 0.08, 0.16, and 0.32 s in two separate conditions. In the first condition, the test Gaussian stimulus had an accompanying gray arc path (luminance: 15 cd/m², length: 9°, width: 1.5°) presented directly above it, connecting the two AM-inducing elements. This path trajectory was a 180° arc of a circle. In condition 2, no gray path was presented, making this condition similar to Experiment 1 (for the purpose of comparison). In addition, a control experiment was also conducted for both conditions in which observers made judgments of the shape of the test stimulus without AM. A block of trials comprised 12 staircases: observers judged the apparent shape of a Gaussian circle for each of 6 levels of ISIs and for both the “path” and “no path” conditions. Stimulus conditions were randomized within and between each block. Observers each completed...
5 blocks such that thresholds were calculated for each condition five times. These thresholds were then averaged for each condition.

Results and discussion

The results of this experiment are shown in Figure 5, which plots shape discrimination thresholds for conditions in which a gray path was presented with (gray circles) and without (black squares) the test stimulus, as a function of ISI. Open symbols denote thresholds for baseline conditions in which no AM accompanied the test stimulus. As shown, in the condition in which a gray curved path was presented with the test stimulus (the “path” condition), there was no systematic shape distortion as a function of ISI despite the fact that the stimulus was located on the most direct path between elements. For this condition, shape discrimination thresholds were similar to the baseline condition. By contrast, the outcomes of the “no path” condition replicate those of Experiment 1, in which shape distortion did occur and was most evident for presentations at the shortest ISI (where shape discrimination thresholds were approximately 30% “thinner” relative to the width of the reference stimulus). These results are consistent with the idea that a gray path simultaneously presented with the test stimulus is interpreted as motion smear arising from the movement of a single element traversing a curved path around the test stimulus. Confirming our expectations, as there was no perceptual overlap, there was no effect. These findings reinforce the perceptual nature of AM, and that the visual system is likely to incorporate additional external cues, which influence the interpretation of the illusion.

Experiment 5: Inter-ocular interactions in the effect of AM on the perception of shape

Previous studies have reported compelling AM when inducing elements are presented to each eye individually (Anstis & Duncan, 1983; Anstis & Moulden, 1970; Georgeson & Shackleton, 1989). Georgeson and Shackleton (1989) demonstrated that dichoptic presentations of out-of-phase sinusoidal gratings generate a compelling sensation of AM, and that its perception is consistent with the operation of “long-range” mechanisms that infer motion from spatially separated elements (though see Carney & Shadlen, 1992 for an alternative interpretation implicating short-range motion mechanisms). Additionally, Anstis and Moulden (1970) noted that it is possible to elicit a Motion Aftereffect (MAE) through adaptation to AM generated by flickering gratings presented dichoptically. Together, these findings provide evidence that the perception of AM is cortical, occurring at a stage in the visual processing hierarchy after binocular integration. Additional evidence for binocular integration in the perception of AM comes from the observation that AM presented to one eye will exhibit inter-ocular transfer and affects the perception of another stimulus presented to the fellow eye. In a classic study, von Grunau (1986) demonstrated that adaptation to AM (induced by spatial and temporal displacements of a grating patch) in one eye exhibited inter-ocular transfer such that a MAE was generated in a counterphasing grating test stimulus presented to the other eye. While it has been shown that binocular interactions occur in the perception of AM, it is not clear whether, and to what extent, inter-ocular interactions occur between AM and object shape. In this experiment, we asked whether AM presented to one eye elicits inter-ocular transfer and distort the apparent shape of a test stimulus presented to the other eye. Resolving this question not only informs about the neural locus of interaction but also about binocular summation in AM generally, providing insight into the degree to which the perceptual filling-in accompanying AM affects the perception of stimulus form.

Methods

The same observers who participated in the previous experiments participated in Experiment 4. In Experiment 4, we repeated Experiment 1 for stimuli presented only at an
Results and discussion

The results of Experiment 5 are shown in Figure 6. Different gray lines represent the averaged data for different viewing conditions. Open symbols represent data for monocular and binocular baseline conditions in which no AM was present with the test stimulus. A number of data trends are noteworthy. First, for baseline conditions, shape discrimination thresholds for both monocular and binocular viewing conditions were close to zero. Second, for conditions containing AM, regardless of the viewing condition, shape distortion was observed at brief ISIs, but decreased as a function of ISI. At the longest ISI, there was no distortion of shape; shape discrimination thresholds were similar to those obtained in baseline conditions.

The condition producing the biggest effect was binocular viewing, while results for monocular, dichoptic, and AM dichoptic were very similar and comparatively smaller: shape discrimination thresholds for binocular conditions are approximately 1.5 times greater than monocular conditions for all ISIs. It is likely that this larger effect in the binocular condition is a consequence of binocular summation in which the integration of information from both eyes results in greater visual enhancement (relative to vision from one eye: see Frisen & Lindblom, 1988), producing a stronger effect. A smaller effect may arise for dichoptic conditions because binocular integration of AM produces a comparatively weaker percept of illusory motion due to the fact that this process requires a minimum integration time to render a clear percept (e.g., Wolfe, 1983). Third, for the dichoptic condition in which AM is presented to one eye and the test stimulus to the other, shape distortion was evident with thresholds greater than baseline conditions (for brief ISIs).

The results of Experiment 5 demonstrate binocular interaction: motion blur associated with AM distorts apparent shape regardless of ocular origin. Thus, the perception and interpretation of AM must arise after binocular integration in which ocular origin is no longer considered. This observation is further supported by the findings of condition 4 in which AM elements were presented dichoptically—shape distortion was reported regardless of the ocular origins of elements inducing AM. In summary, these data are consistent with previous reports of binocular integration of AM and together affirm...
that the perception of this motion illusion has its cortical origins high in the visual processing hierarchy, beyond the stage at which binocular integration occurs.

**General discussion**

The present study reports a series of experiments examining the degree to which AM interferes with the perceived shape of objects. Particularly, we questioned whether motion smear (which is a spatial stimulus) accompanying AM interferes with the judgment of the shape of a stimulus presented on the motion path. In Experiment 1, we showed that, under specific stimulus conditions, a Gaussian stimulus presented on the motion path is distorted by AM, such that its perceived shape appears elongated along the axis of motion. This effect increases with shorter ISIs where AM is more compelling (verified in Experiment 2), and at larger eccentricities where coarser visual acuity results in a spatially ambiguous stimulus rendering it susceptible to distortion by AM. The latter observation well supported the finding of Experiment 3, which demonstrated that shape distortion is largely reduced if the test stimulus has well-defined edges. In Experiment 4, we confirmed that shape distortion is evident when the test stimulus is perceived to be along the path of motion, but not when a non-overlapping curved gray path is used to substitute and divert the AM path around the stimulus. Finally, in Experiment 5 we showed that the shape distortion occurs regardless of the ocular origins of the test stimulus and AM, suggesting that the effect is cortical in origin, occurring beyond the stage of binocular integration.

Given that AM involves spatiotemporal processing, the locus for AM is likely to be motion area Middle Temporal (MT). Indeed, area MT feeds back to earlier cortical areas such as V1, and previous studies have shown that MT is important in the perception of AM (Liu et al., 2004; Muckli et al., 2005; Pascual-Leone & Walsh, 2001; Tong, 2003). For example, Muckli et al. used neural imaging to show that AM activates extrastriate areas as well as areas in V1 along the motion path. It is therefore feasible that the percept of motion smear from AM arises from higher level processes and actively feeds 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 smear. In terms of the present study, this neural representation would also interfere with the neural coding of the shape of a stimulus presented within the two sites of stimulation. Indeed, this was our finding, and this is a possible explanation for the effect. An alternative explanation is that this interaction may reflect mutual activity in motion and form sensitive areas such as MT and the Lateral Occipital Complex (LOC), which are cortical modules beyond binocular integration, and which share reciprocal feed-forward and backward projections (Van Essen, Anderson, & Felleman, 1992). Thus, the determination of shape at LOC is directly modulated by activity signaling motion by MT (see Kourtzi & Kanwisher, 2000). This conclusion is well supported by the findings of Liu et al. (2004) who reported that neural imaging of AM reveals overlapping activation in areas MT and LOC, and that this mutual activation is suggestive of interaction. We cannot directly comment on this possibility because our investigation is behavioral in scope. However, the findings of these imaging studies are consistent with our observations.

The results of the study accord well with those of Khuu et al. (2010) who recently reported that the perceived position of elements in the Visual Saltation illusion is effectuated by the Motion Aftereffect (MAE). The visual salutation illusion is an illusion of movement elicited when multiple stimuli are presented first to one location, then to another, in regular and rapid succession. 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° of visual angle (Geldard, 1976). Khuu et al. demonstrated that a locally generated MAE in the middle of the two points of stimulation distorts the perceived position of only the middle element, which perceptually overlaps (but may not be physically overlapping) with the motion-adapted region. Thus, the saltatory path is disrupted by the MAE based on the illusory, rather than physical, position of the elements. This observation suggests that motion adaptation of local units interferes with perceptual filling-in and alters the neural representation of saltatory motion. Together with the findings of the present study, these data show that the generation of a coherent visual percept is a high-level malleable construction with the neural representation capable of affecting, and also being affected by, associated visual information.

Previous reports by Kolers (1972), Berbaum and Lenel (1983), and Deatheridge and Bitterman (1952) have shown that when a stationary object is presented in the motion path, AM appears to be “deflected” around the stimulus, and the form of this stimulus is unaffected. At first hand, this result differs from our observation in which the path of motion is perceived overlapping with the test stimulus. An explanation for this difference is that in our experiments the form stimulus is always briefly flashed in the motion path, while in the aforementioned studies, the form stimulus was continuously present in the display and the stimulus was viewed foveally. In the latter condition, the visual system has ample time to deduce the form of the stimulus, and thus, it is not susceptible to distortion. Moreover, the visual system may attribute the form stimulus as the “background” and therefore segregating any affect of AM on form. However, the observations of Kolers
(1972) are of significance to the present study as they show a complementary effect in that form information can distort the path of AM and mirrors the observations of Shepard and Zare (1983).

The findings of the present study also complement those of Li et al. (2009) who examined the impact of real motion on apparent shape (that of a Kanisza triangle defined by illusory contours). Li et al. reported that the perceived shape of an equilateral Kanisza triangle appears curvilinear if superimposed on a background of dots physically moving along trajectories conforming to expanding and contracting motion. Specifically, a Kanisza triangle superimposed on a contracting background appears “thinner,” while an expanding background results in a distortion in shape producing a “fatter” stimulus. Our results show a similar distortion effect to that of Li et al., but under converse stimulus conditions in which image motion is illusory and the form stimulus is real. Together these studies show that the interpretation of illusory stimuli, regardless of whether they are form or motion, is likely to engage similar neural processes to those dedicated to processing real stimuli.

The reported shape distortion effect cannot be explained in terms of an interdependence of space and time in the perception of AM. It is possible that, by changing ISI, the perceived space between tokens is expanded or compressed, making an object located in the path of motion similarly distorted. However, this is unlikely since previous reports of AM show that the perceived spatial distance between tokens increases with temporal duration—the Tau effect. If it were the case that the Tau effect accounted for our results, it would be expected that the stimulus would appear to be compressed at shorter ISIs. Our results clearly show the opposite trend: shortening the temporal interval (short ISIs) produces stronger spatial distortion such that the stimulus appears “wider” along its horizontal axis. Our results can be accounted for by the observation that AM and motion smear is most compelling at briefer ISIs, and that this spatial cue is likely to distort the shape of a stimulus presented along the path of motion. This finding accords well with previous studies examining the role of motion smear arising from real motion, particularly that motion smear affects perception under the conditions in which they are generated from fast object speeds (Geisler, 1999; Li et al., 2009; Or et al., 2007).

In conclusion, the present study has two clear findings. First, motion smear arising from the interpolation of motion from sequentially presented stationary stimuli can distort the perceived shape of a stimulus overlapping with the motion path. Second, this reflects a process in which the spatial information derived from motion smear directly interferes with the coding of a shape-ambiguous stimulus. This process is likely to be cortical, occurring at a stage subsequent to binocular summation.

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