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Grouping Inhibits Motion Fading by Giving Rise to Virtual Trackable Features

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After prolonged viewing of a slowly drifting or rotating pattern under strict fixation, the pattern appears to slow down and then momentarily stop. The authors show that grouping can slow down the process of "motion fading," suggesting that cortical configural form analysis interacts with the computation of motion signals during motion fading. The authors determined that grouping slows motion fading because it can give rise to trackable features, such as virtual contour terminators not present in the image, that possess stronger motion signals than would occur in the absence of such trackable features. That a continuously rotating stimulus will eventually be perceived to stop, despite the presence of such trackable features, suggests that the motion-from-form system itself can be fatigued. The finding that stationary form can remain visible even after the motion signal has faded suggests that the neural bases of motion visibility and form visibility arise from different neuronal populations.

Keywords: grouping, motion fading, trackable feature

After prolonged viewing of a slowly drifting or rotating pattern under strict fixation, the pattern appears to slow down and then momentarily stop, even though the stationary form of the pattern remains visible. This "motion fading" has been reported to occur over rotating gratings and spinning sector disks (Campbell & Maffei, 1979, 1981; Cohen, 1965; Hunzelmann & Spillmann, 1984; Lichtenstein, 1963; MacKay, 1982). Several factors, including retinal eccentricity, number of sectors, and speed of rotation, have been shown to affect the time required for motion fading when using slowly spinning sector disks as stimuli (Hunzelmann & Spillmann, 1984).

Motion fading is an example of a diverse class of phenomena in which an object appears to vanish from visual consciousness although still present in the stimulus. Past examples of visual fading involve the subjective disappearance of a stationary object, as in the Troxler effect (Hsieh & Tse, 2006a; Livingstone & Hubel, 1987; Troxler, 1804) or motion-induced blindness (Bonneh, Cooperman, & Sagi, 2001). In motion fading, however, only the motion component appears to vanish from consciousness, while the form component remains visible. Motion fading is not likely to be reducible to other classes of visual fading involving the subjective disappearance of a stationary object. Perceptual fading (Troxler, 1804), for example, occurs when a stationary object, though present in the stimulus and continually casting light upon the retina, vanishes from visual consciousness. Perceptual fading is optimal when the stationary object is located peripherally, has blurred edges and a low luminance difference to that of the background, and has been stabilized upon the retina, as happens under conditions of visual fixation (Livingstone & Hubel, 1987), presumably in part because of bottom-up local sensory adaptation to edge information among retinal ganglion cells (Martinez-Conde, Macknik, Troncoso, & Dyar, 2005; Ramachandran, 1992). Because the target is continuously moving during motion fading, no local sensory adaptation to edge information should occur. Moreover, it has been hypothesized (De Weerd, Gattass, Desimone, & Ungerleider, 1995; Gerrits, de Haan, & Ventrik, 1996; Gerrits & Ventrik, 1970; Spillmann & DeWeerd, 2003) that during perceptual fading, the vanished target area is actively filled in with the information of the background (but see Hsieh & Tse, 2006a). However, during motion fading, only the motion component of the stimulus seems to slow and then vanish. Because the form of the stimulus remains visible, it is unlikely that information from the surround is replacing the stimulus. In short, motion fading is not perceptual fading and likely has nothing to do with filling in.

An alternative account is that motion fading is due to a decrease of luminance contrast of the target stimulus following neuronal fatigue. It has been shown that motion appears to slow down as luminance contrast decreases (Anstis, 2003; Stone & Thompson, 1992; Thompson, 1982; Thompson & Stone, 1997; Thompson, Stone, & Swash, 1996). However, in motion fading, the motion pattern will appear to stop even though the form and/or contrast of the stimulus are still visible and even if the stimulus has high contrast. Moreover, the contrast of the stimulus just before and after illusory cessation of motion does not appear to change. In a recent study (Hsieh & Tse, 2006b), we have shown that when systematically changing the luminance of the stimulus, the perceived speed decrement (and the time to full perceived cessation of motion) does not change, suggesting that motion fading is unlikely to be due to a decrease of luminance contrast or perceived brightness.

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A more plausible account is that motion fading arises because of adaptation or fatigue among cortical neurons that encode motion (Hsieh & Tse, 2006b). Such fatiguing or adaptation is presumed to play a role in the well-known motion aftereffect (MAE), in which illusory motion is perceived to occur over a stationary object or image following prolonged exposure to visual motion (Wohlgemuth, 1911). On the face of it, it would seem that the MAE and motion fading have opposite attributes. In MAE, motion is always perceived in a direction opposite that of the MAE-inducing stimulus. In addition, MAE is only seen after the MAE-inducing stimulus stops moving. In motion fading, in contrast, no motion is perceived in the presence of a real motion signal. However, it is plausible that the MAE and motion fading are caused by the same underlying neuronal mechanism. Namely, as neuronal responses indicative of motion in a given direction adapt, the population representation of motion magnitude and direction should indicate a decreased magnitude of response for motion in that direction. In the case of the MAE, adaptation combined with the opponent nature of motion units, induces a shift in the population response to a stimulus that is in fact stationary, causing an illusory perception of motion in the opposite direction. In the case of motion fading, adaptation may lead to the loss of motion signal in cells that underlie the perception of motion. For example, if motion signals were already near threshold, as would be the case for the slowly moving stimuli used in motion fading, the loss of signal may lower the sensitivity of cells below threshold, causing the loss of a motion percept.

Motion fading must be cortical and not retinal in origin, because there are no motion-tuned cells in the human retina. However, motion fading might still be an early effect that takes place before higher level nonlocal operations, such as those involved in grouping. In this study, we investigated this issue by examining whether Gestalt grouping could affect motion fading. In particular, the grouping procedure used here involved the linking of collinear dots into virtual lines. If Gestalt grouping can affect motion fading, then motion fading must occur after low-level, purely localistic processing and must occur at or after a stage in which global motion signals have been computed.

We designed two types of stimuli: Both types (the grouped and nongrouped stimuli) contained identical rotating disks in the sense that these disks traversed identical paths on the retina across time. The only difference was that the stimulus pattern for the grouped condition looked more like a cross shape and the stimulus pattern for the nongrouped condition looked more like a random pattern. In particular, the cross shape had more virtual lines generated by the collinear arrangement of multiple dots. Moreover, these virtual lines had virtual terminators, where the virtual lines appeared to end. If there is any difference found in the time it takes for motion fading to occur, then it must be due to the global organization of the stimulus, as the two conditions are identical at the retinal level and at the level of local processing.

We found that the time it took for a stimulus pattern to be perceived as stopped during motion fading increased significantly when the target stimulus could be grouped into the shape of a cross. Four hypotheses about the possible causes of the grouping effects on motion fading were further tested and pitted against one another.

Experiment 1: Grouping Hinders Motion Fading

In Experiment 1, we tested whether grouping can affect motion fading. Figures 1A and 1B show the grouped and nongrouped stimuli, respectively. The disks in both grouped and nongrouped stimuli were arranged in such a way that, in both cases, individual disks would traverse identical paths on the retina over time. The only difference between the two stimuli was in how they were perceptually grouped.

Method

Observers. Six participants (5 unaware of the hypothesis and 1 author) carried out all the experiments. All participants had normal or corrected-to-normal vision and were experienced psychophysical observers. Before each experiment, the participants practiced several training trials until they were accustomed to the experimental procedure and were capable of fixating while conducting hand movements.

Stimuli and procedures. The stimulus configuration for Experiment 1 is shown in Figures 1A and 1B. In the grouping (cross) condition (see Figure 1A), the target stimulus was composed of 12 white (150 lm/m^2) disks, subtending 0.2° of visual angle in diameter. The 12 disks were

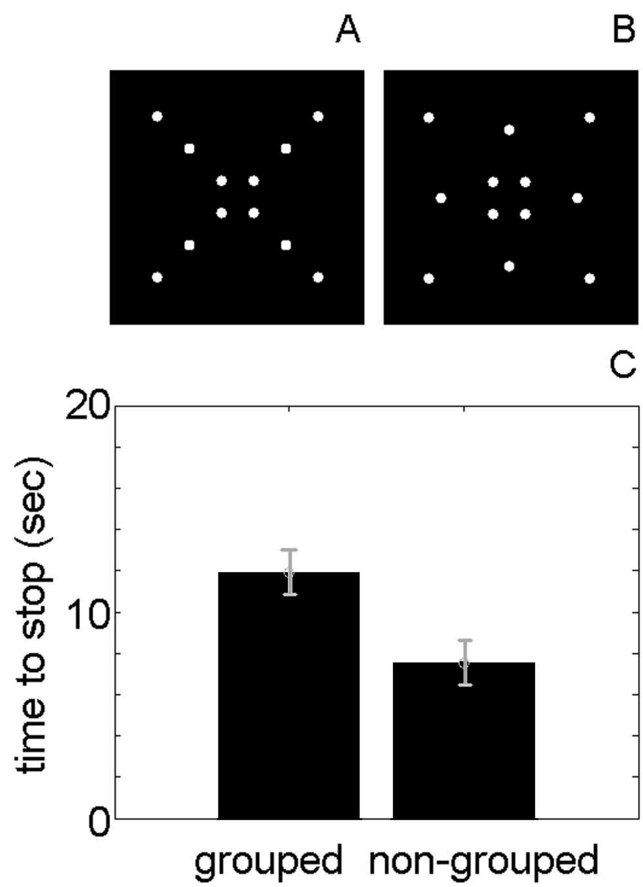

Figure 1. The time to stop during motion fading under different conditions (grouped vs. nongrouped). A: The stimulus configuration for the grouped pattern. B: The stimulus configuration for the nongrouped pattern. C: The time to stop is significantly longer for the grouped condition than the nongrouped condition. Error bars indicate the standard errors of the difference between conditions across 6 participants.

arranged to lie at three eccentricities from the center of the stimulus. The inner (middle, outer) ring was composed of 4 disks, located ±0.45 (±1.35, ±2.25) visual degrees horizontally and ±0.45 (±1.35, ±2.25) visual degrees vertically away from the center of the stimulus. The disks in the middle ring were aligned between the inner and outer layers to represent a grouped shape of a cross. In the nongrouping (control) condition (see Figure 1B), the target stimulus was composed of the same 12 white disks, but the 4 disks in the middle ring were rotated 45° so that the disks were not aligned. The speed of the target stimulus for both conditions was 0.025 rps (360° rotations per second). The two conditions were randomized and counterbalanced across 36 trials and presented in one of the four possible locations: 13.12 visual degrees left or right of the vertical midline and 8.25 visual degrees above or below the horizontal midline. All the stimuli were viewed with both eyes. The total size of the visual field was 40 cm × 30 cm, viewed from a distance of 57 cm. Participants had their chin in a chin rest. The visual stimulator was a 2 GHz Dell workstation running Windows 2000. The stimuli were presented on a 23-inch SONY CRT gamma-corrected monitor with 1600 × 1200 pixels resolution and 85 Hz frame rate.

Participants were required to press a button when the motion first appeared to fully stop. Eye movements were monitored with a head-mounted eye tracker (Eyelink2, SR Research, Ontario, Canada). Trials during which the participant's monitored left eye was outside a fixation window of 1.5 visual degrees radius were excluded and repeated later in the experiment. Thus, all data reported here were carried out under conditions of fixation.

Results and Discussion

Results in Figure 1C show that time to stop (TTS) increased significantly (two-tailed paired *t* test, $p = .0091$) when the target stimulus could be grouped. Thus, motion fading happens at or after a stage in which global form influences the computation of motion signals. Furthermore, because form remains visible even after the perception of motion has ceased, we conclude that different neuronal populations underlie the conscious perception of form and motion.

Experiment 2: Motion Fading Is Affected by Trackable Features but Not Illusory Contours

The cross configuration in Figure 1A possesses a number of different attributes than the control arrangement in Figure 1B, any of which might be responsible for the slowing of the onset of motion fading. The cross configuration appears to be grouped into intersecting lines that have a well-defined orientation. Moreover, the lines have apparent endpoints, which could be used as trackable features by a motion system sensitive to line terminators. Lastly, the cross configuration might be more salient for some other reason. To specify what properties of the cross configuration might underlie its effectiveness in hindering motion fading, we carried out Experiments 2, 3, and 4 to determine which of the following hypotheses is correct.

Hypothesis 1. First, it is possible that TTS increases for grouped stimuli because the grouped stimuli are more salient by virtue of having apparent endpoints, which can be more easily tracked by a salience-driven motion processing system sensitive to line terminators.

Hypothesis 2. The second possibility is that TTS increases for grouped stimuli because an illusory contour or shape can more easily be seen in the grouped stimuli than in the non-grouped stimuli. It is possible that the existence of illusory contour or shape in the grouped stimuli may activate more motion sensitive neurons, thereby making it harder to achieve motion fading.

Hypothesis 3. The third hypothesis is that TTS increases for grouped stimuli because the illusory contour or shape may increase the salience of global orientation in a way that could be used by the visual system to compute motion more easily than in the absence of such cues to global orientation.

Hypothesis 4. The fourth hypothesis is that TTS differs because the spatial frequency profile is different between the two stimuli. Corners and endpoints tend to have higher spatial frequency content than other regions of contour or shape. Because we hypothesized, in Hypothesis 1, that it is such information that hinders motion fading, we implicitly assume that high spatial frequency information play is responsible for the prolongation of TTS in the grouped condition. It is therefore necessary to control for the possibility that it is differences in the low spatial frequency domain that determine the differential stopping times for the grouped versus ungrouped stimuli.

Method: Stimuli and Procedures

The stimulus configuration and experimental procedure in Experiment 2A were identical to those used in Experiment 1 except for the following differences: In the trackable condition (see Figure 2A), the target stimulus was composed of one gray (64 lm/m^2) square subtending 4.5° of visual angle in width and height. Four more small white (286 lm/m^2) squares were superimposed onto the four corners of the gray square. The nontrackable condition (see Figure 2B) was identical to the trackable condition except that the four small white squares were absent from the gray square. If the increment of TTS observed in Experiment 1 was due to the illusory contour or shape, as suggested by Hypotheses 2 and 3, then TTS should be indistinguishable between the trackable and nontrackable conditions because neither contained illusory contour or shape. However, if the increment of TTS observed in Experiment 1 was due to the salience of the trackable feature as suggested by Hypothesis 1, then TTS should increase in the trackable condition.

Because a difference between luminances in Experiment 2A might affect the process of motion fading, we conducted Experiment 2B to test whether this was the case. The stimulus configuration and experimental procedure in Experiment 2B were identical to those used in Experiment 2A except that in the high luminance condition (see Figure 3A), the target stimulus was composed of a white (286 lm/m^2) square that had the same luminance as the four small white squares in Experiment 2A. The low luminance condition (see Figure 3B) was composed of a gray (64 lm/m^2) square, which was identical to the nontrackable condition in Experiment 2A. If any increment of TTS observed in Experiment 2A was due to the luminance difference, then TTS should also be higher in the high luminance condition in Experiment 2B.

The stimulus configuration and experimental procedure in Experiment 3 were identical to those of Experiment 1 except that in the grouped condition (see Figure 4A), the target stimulus was composed of four white (150 lm/m^2) disks, subtending 0.75° of visual angle in diameter. Two black (0.5 lm/m^2) rectangles, subtending 0.6° of visual angle in width and 4° of visual angle in height, were presented on top of the four disks so that two Kanizsa rectangles could be seen as a cross. In the nongrouped condition (see Figure 4B), the target stimulus was composed of the same 4 white disks,

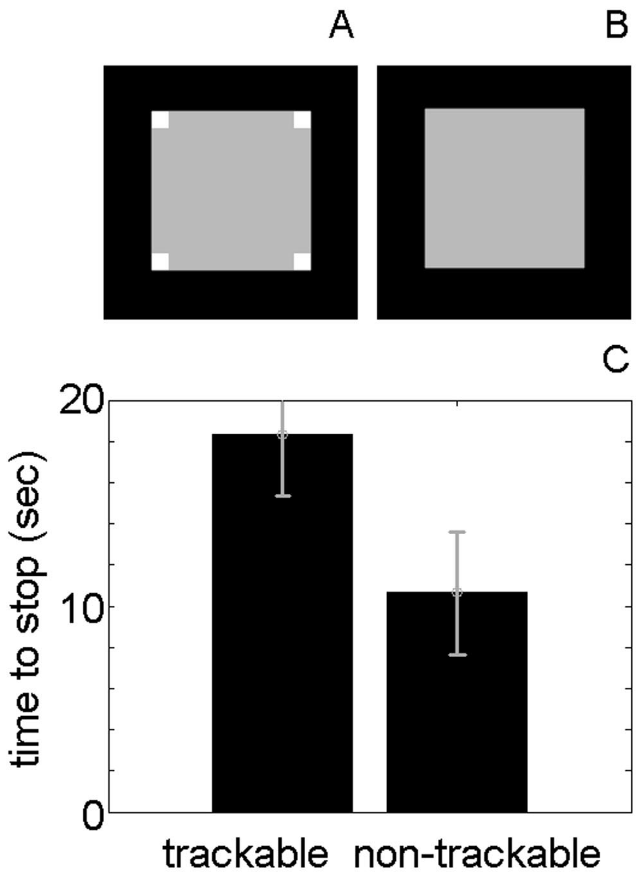

Figure 2. A: The stimulus configuration for the pattern with trackable features. B: The stimulus configuration for the pattern without trackable features. C: The time to stop during motion is significantly longer for the condition with trackable features than the condition without trackable features. Error bars indicate the standard errors of the difference between conditions across 6 participants.

but the 4 disks were rotated 45° so that no Kanizsa rectangles could be seen. If the increment of TTS observed in Experiment 1 was due to the influence of illusory contour or shape, as suggested by Hypotheses 2 and 3, then TTS should increase in the grouped condition. On the contrary, if the increment of TTS observed in Experiment 1 was due to the salience of trackable features, as suggested by Hypothesis 1, TTS should be indistinguishable between the grouped and nongrouped conditions because the trackable features (the four Kanizsa inducers) were identical in the two conditions.

The stimulus configuration and experimental procedure in Experiment 4 were identical to those of Experiment 1 except that the low spatial frequency content in both conditions was removed by replacing the white disks with contrast-balanced disks (Carlson, Anderson, & Moeller, 1980). We presented a smaller black disk (0.13° of visual angle in diameter) on top of each original white disk (see Figures 5A and 5B). The luminance of the white–black disk together was adjusted to become identical to that of the gray background (52.1 lm/m^2) so that the screen appeared a uniform gray when viewed from a distance. If the difference of TTS observed in Experiment 1 was due to the influence of low spatial frequency content, as suggested by Hypothesis 4, then TTS should be the same between the two conditions in this experiment because the low spatial frequency content was removed in both conditions.

Results and Discussion

Results in Figure 2C show that the TTS increased significantly (two-tailed paired *t* test, $p = .0098$) in the trackable condition. This increment of TTS was not due to its higher luminance because the results from Experiment 2B showed that the TTS did not increase significantly (two-tailed paired *t* test, $p = .4867$) in the high luminance condition (see Figure 3C). Results from Experiment 3 (see Figure 4C) showed that the TTS did not increase significantly (two-tailed paired *t* test, $p = .4962$) in the grouped condition. Because the grouped Kanizsa stimuli of Experiment 3 would appear to have more global orientation information than the nongrouped control, we concluded that it is not emergent global orientation that drives the results shown in Experiment 1. Rather, the most likely emergent features that can account for the results shown in Experiment 1 are the emergent contour terminators apparent in the cross configuration but not in the control configuration. These contour terminators arise as a byproduct of the formation of more virtual lines in the grouped versus nongrouped conditions. Results from Experiment 4 (see Figure 5C) further showed that TTS was still significantly longer ($p = .0189$) in the grouped condition then in the nongrouped condition, suggesting

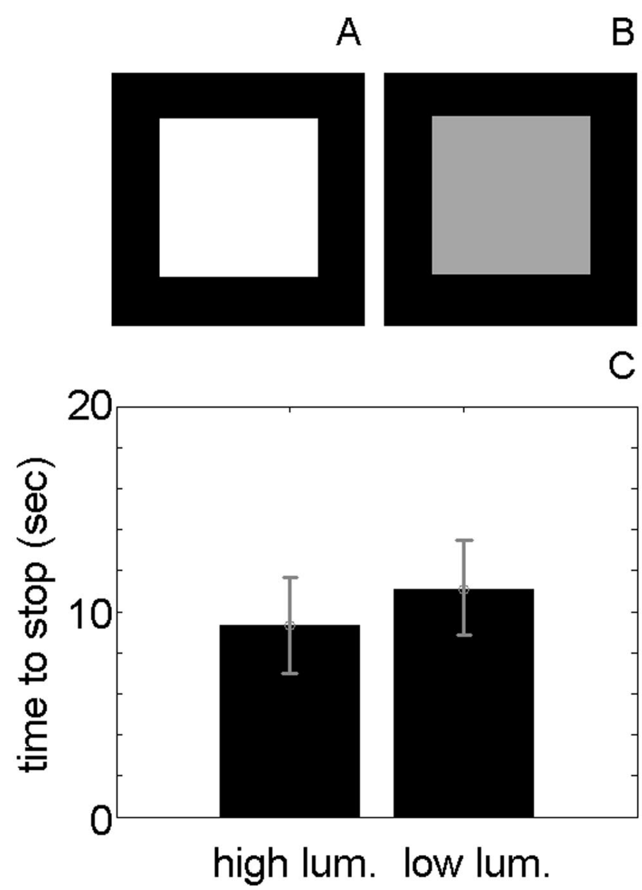

Figure 3. A: The stimulus configuration for the pattern with low luminance. B: The stimulus configuration for the pattern without high luminance. C: The time to stop during motion is not significantly different between two conditions. Error bars indicate the standard errors of the difference between conditions across 6 participants. lum. = luminance.

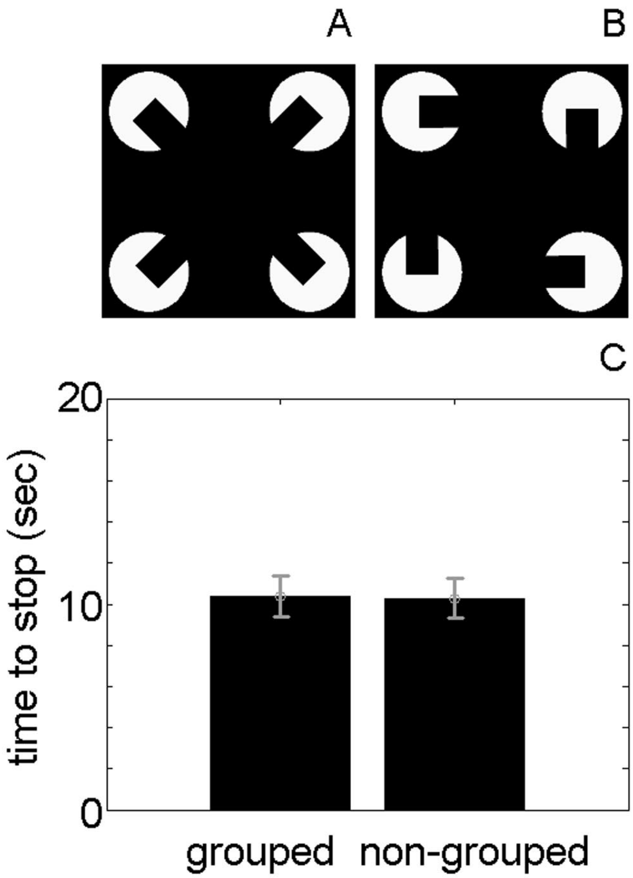

Figure 4. A: The stimulus configuration for the grouped condition. B: The stimulus configuration for the nongrouped condition. C: The time to stop during motion is not significantly longer for the grouped condition than the nongrouped condition. Error bars indicate the standard errors of the difference between conditions across 6 participants.

that the difference in TTS is not due to a difference in the low spatial frequency domain.

Figure 6 summarizes the results across experiments. It is interesting to note that the third condition (the trackable condition from Figure 2A) produced such long times compared to the fifth condition (the high luminance condition from Figure 3A). This result suggests that luminance-defined trackable features can counteract motion fading and that this effect is not due to luminance differences but is instead due to trackable feature per se. It is also interesting to note that the shortest TTS values seem to have come from nongrouped dots (the second condition from Figure 1B) and nongrouped contrast-balanced dots (the tenth condition from Figure 5B). This might be due the possibility that the trackable features defined by shape or contours are weaker in these conditions.

General Discussion

It is well known that motion perception can be derived directly from the analysis of retinal motion by dedicated motion sensors in cortex, or indirectly, by inferring motion from changes in the retinal position of objects, or their features, over time (Derrington, Allen, & Delicato, 2004). This latter process could be built upon motion signals derived from feature tracking (Del Viva & Morrone, 1998; Pack & Born, 2001; compare Lu & Sperling, 1995), which can overcome the ambiguity of motion signals arising from cells tuned to "motion energy" (Adelson & Bergen, 1985; Ullman, 1979; Watson & Ahumada, 1985). Our results show that the process of motion fading slows down with increased saliency of such trackable features, suggesting that salient trackable features help the motion system extract motion signals. When such trackable features are strong, motion fading is presumably hindered, because motion signals do not disappear as readily. We hypothesize that it is the emergent virtual terminators of the lines defining the cross that play a key role in increasing the motion signals in the grouped versus ungrouped conditions. What is surprising is that these terminators do not exist in the image. These virtual terminators are only defined after a stage of global visual form analysis in which the separate dots are grouped into contours and shapes. The dots comprising the virtual terminators in the grouped stimulus do not have more motion signal at the level of the image. They

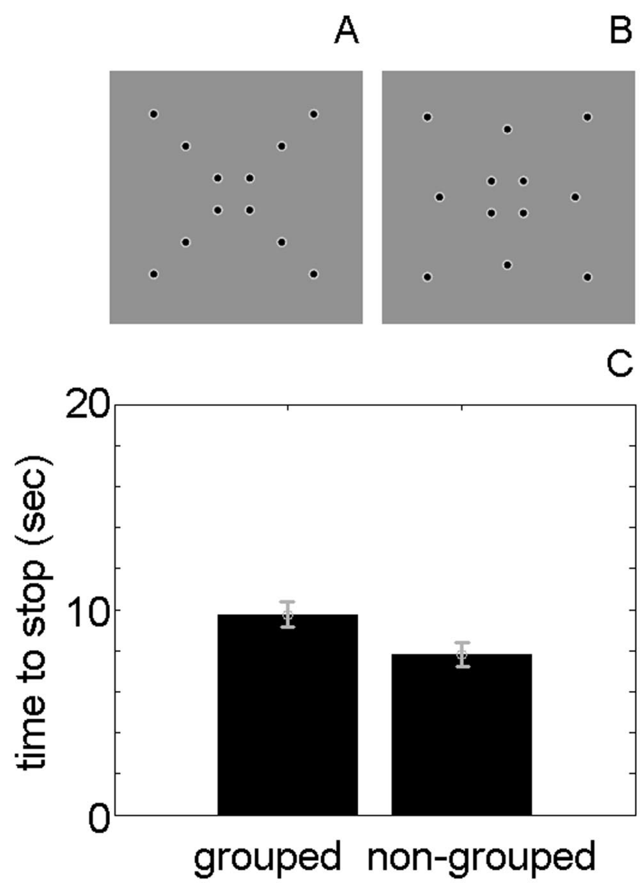

Figure 5. A: The stimulus configuration for the pattern identical to that shown in Figure 1A, except that the low spatial frequencies have been removed using contrast-balanced dots. B: The stimulus configuration for the pattern identical to that in Figure 1B with the low spatial frequency removed. C: As in Experiment 1, the time to stop during motion is significantly longer in the grouped (cross) condition than in the nongrouped (control) condition. Error bars indicate the standard errors of the difference between conditions across 6 participants.

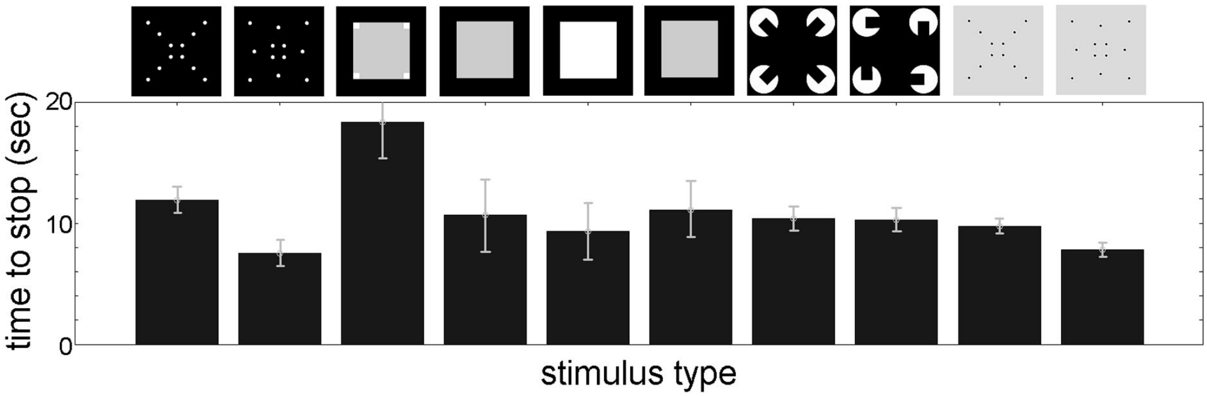

Figure 6. Data summary. Error bars indicate the standard errors of the difference between conditions across 6 participants.

only possess more motion signal after a stage of grouping that provides form information to a visual motion processing system that tracks them as salient trackable features, which presumably imbues them with more motion signal than they would have in a configuration in which they could not be treated as contour terminators.

Although our results show that the presence of trackable features alone may slow down the processes that lead to motion fading, trackable features might not be the only cause of the longer TTS in Experiment 1. For example, in the stimuli in Experiment 1, three concentric squares can be seen in the grouped condition, and two squares and a diamond can be seen in the nongrouped condition. This difference might also help increase the TTS for the grouped condition. Another possibility is that TTS increases when more groupings are possible in the display. Switching between different groupings may increase TTS by rejuvenating the adaptation, so that adaptation is slowed and illusory stopping is delayed.

Conclusion

In this article, we show that global form-based grouping can affect motion fading. We found that the time it takes for a stimulus pattern to be perceived as stopped (although in fact still continually moving) increases significantly when the target stimulus can be grouped into the shape of a cross than when it cannot. Four hypotheses about the possible causes of the grouping effects on motion fading were tested and pitted against one another. Our results show that the process of motion fading slows down with increased saliency of such trackable features, suggesting that salient trackable features help the motion system extract motion signals. We hypothesize that it is not spatial grouping per se that hinders motion fading but that grouping permits the emergence of salient trackable features, such as terminators or corners, which mitigate against the loss of motion signal. These trackable features need not be present in the image in a bottom-up sense. We conclude that motion fading is weaker in grouped stimuli because emergent trackable features provide a stronger motion signal than is present in ungrouped versions of the same stimuli that lack such emergent trackable features.

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