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# Tilt aftereffects and tilt illusions induced by fast translational motion: evidence for motion streaks

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## **Abstract**

Fast-moving visual features are thought to leave neural 'streaks' that can be detected by orientation-selective cells. Here, we tested whether 'motion streaks' can induce classic tilt aftereffects (TAEs) and tilt illusions (TIs). For TAEs, participants adapted to random arrays of small Gaussian blobs drifting at 9.5 deg/s. Following adaptation to directions of 15, 30, 45, 60, 75, and 90 degrees (clockwise from vertical) subjective vertical was measured for a briefly presented test grating. For TIs, the same motions were presented in an annular surround and subjective vertical was measured for a simultaneously presented central grating. All motions were 50% coherent, with half the blobs following random-walk paths and half following a fixed direction. Strong and weak streaks were compared by varying streak length (the number of fixed-walk frames), rather than by manipulating speed, so that speed and coherence were matched in all conditions. Strong motion streaks produced robust TAEs and TIs, similar in magnitude and orientation tuning to those induced by tilted lines. These effects were weak or absent in weak streak conditions, and when motion was too slow to form streaks. Together, these results indicate that motion streaks produced by temporal integration of fast translating features do effectively adapt orientation-selective cells and may therefore be exploited to improve perception of motion direction as described in the 'motion streaks' model.

## **Keywords**

motion, evidence, streaks, translational, tilt, aftereffects, illusions, induced, fast

## **Disciplines**

Arts and Humanities | Life Sciences | Medicine and Health Sciences | Social and Behavioral Sciences

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# Tilt aftereffects and tilt illusions induced by fast translational motion: Evidence for motion streaks

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Fast-moving visual features are thought to leave neural ‘streaks’ that can be detected by orientation-selective cells. Here, we tested whether ‘motion streaks’ can induce classic tilt aftereffects (TAEs) and tilt illusions (TIs). For TAEs, participants adapted to random arrays of small Gaussian blobs drifting at 9.5 deg/s. Following adaptation to directions of 15, 30, 45, 60, 75, and 90 degrees (clockwise from vertical) subjective vertical was measured for a briefly presented test grating. For TIs, the same motions were presented in an annular surround and subjective vertical was measured for a simultaneously presented central grating. All motions were 50% coherent, with half the blobs following random-walk paths and half following a fixed direction. Strong and weak streaks were compared by varying streak length (the number of fixed-walk frames), rather than by manipulating speed, so that speed and coherence were matched in all conditions. Strong motion streaks produced robust TAEs and TIs, similar in magnitude and orientation tuning to those induced by tilted lines. These effects were weak or absent in weak streak conditions, and when motion was too slow to form streaks. Together, these results indicate that motion streaks produced by temporal integration of fast translating features do effectively adapt orientation-selective cells and may therefore be exploited to improve perception of motion direction as described in the ‘motion streaks’ model.

Keywords: motion streaks, 2-D motion, motion/form interactions, V1, awareness

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## Introduction

Human visual systems are remarkably accurate at discriminating fine differences in motion direction, with directional resolution generally reported to be in the region of 5 degrees (Ball & Sekuler, 1987; Gros, Blake, & Hiris, 1998; Krukowski, Pirog, Beutter, Brooks, & Stone, 2003). This directional acuity is achieved despite the fact that motion-sensitive neurons are tuned to a rather broad range of directions, both at the level of primary visual cortex (V1) (Sincich & Horton, 2005) and in more specialized motion-sensitive areas such as hMT+ (V5) (Born & Bradley, 2005). Single-unit studies show that the directional tuning curves of hMT+ neurons have a full width at half maximum of about 100° (Snowden, Treue, & Andersen, 1992). Individual motion units therefore have a relatively poor directional resolution. In response to this observation, most models of motion perception have assumed that direction of motion must be computed at the level of population response, possibly through a vector-averaging process whereby a population of motion-sensitive neurons responding to a moving stimulus provide a network of information from which motion direction can be extracted (Adelson & Movshon, 1982; Georgeson & Scott-Samuel, 1999; Koch, Wang, & Mathur, 1989; Reichardt & Schlögl, 1988; Snowden & Braddick, 1989; Wilson & Kim, 1994). These population models assume that this process occurs among

motion-specialized neurons in a stream that is functionally distinct from other visual properties such as color and orientation (Goodale & Milner, 1992; Livingstone & Hubel, 1988; Mishkin, Ungerleider, & Macko, 1983). However, in the years since the proposal for parallel and largely independent pathways for motion and for color and form was proposed, evidence has been accumulating to suggest that form and motion pathways do engage in significant interactions (Giese, 1999; Kourtzi, Krekelberg, & van Wezel, 2008; Lorenceau & Alais, 2001; Murray, Olshausen, & Woods, 2002; Ross, Badcock, & Hayes, 2000).

Phenomena such as biological motion and form-from-motion provide evidence that there are situations where information about the shape of an object is only available where there is motion in the stimulus (Cutting, 1978; Grossman & Blake, 2002; Grunewald, Bradley, & Andersen, 2002; Wallach & O’Connell, 1953). Conversely, there are cases where global motion from moving elements can only be computed if the elements form a coherent shape (Lorenceau & Alais, 2001). Thus motion and form interact strongly with each other, with cues from one enabling computation of the other. The particular relevance of form information in motion processing is highlighted by several recent neuroimaging studies which have shown that static images which imply motion, such as those of an athlete in motion, or a cup falling off a shelf, can produce significant activation in motion-sensitive brain areas, compared to static images which do not imply motion (Krekelberg, Vatakis, & Kourtzi,

2005). Similarly, viewing static patterns which induce illusory motion, such as the Enigma illusion and the rotating snakes illusion, also activate neurons in these areas (Kourtzi & Kanwisher, 2000). Further, it has been shown that viewing static photographs implying unidirectional motion can produce directionally opposite motion aftereffects (Winawer, Huk, & Boroditsky, 2008).

In the past decade, attention has turned to another possible kind of form/motion interaction, one that provides an alternative solution to the puzzle of high directional acuity despite the relatively crude directional tuning of cortical motion units. The proposal is based on the notion of “motion streaks” or “speed lines”. The suggestion is that, since the early cortical stages of the visual system integrate information over a period of about 100 ms (Burr, 1981; Snowden & Braddick, 1991), a fast-moving object should become spatially smeared and leave behind a blurred “streak”. For a translating object, such streaks would always be oriented parallel to the motion trajectory. Even though the streaks are not obviously seen under normal viewing conditions, and models have been proposed to account for such deblurring (Burr & Morgan, 1997), Geisler (1999) suggested that perhaps the visual system might utilize the orientation information that comes from spatial smearing to help judge the object’s direction of motion (see Figure 1). The advantage of this proposal is that orientation-sensitive units such as those commonly found in V1 (Hubel & Wiesel, 1962; Sincich & Horton, 2005) are known to be finely tuned, with a mean full bandwidth of about 30° (De Valois, Yund, & Hepler, 1982; Gur, Kagan, & Snodderly, 2005). This is much narrower tuning than that reported for specialized motion units. Geisler’s (1999) proposal is that the visual system

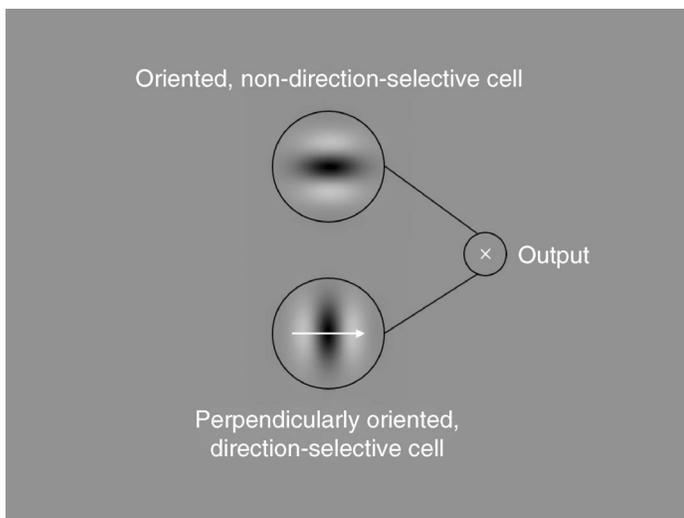


Figure 1. Geisler’s model of how output from a finely tuned “form” cell, selective for the orientation of the streak, might combine with that from a perpendicularly oriented direction-selective cell to help judge direction of motion when an object is moving fast enough.

might exploit this fine tuning for orientation to help refine its acuity for resolving motion direction. Thus, in contrast to the often assumed dichotomy between form and motion, the “motion streaks” model suggests that orientation and motion signals could be combined at an early level of visual processing to increase the acuity of the motion processing system.

Several studies have sought to support the motion streaks model by looking for evidence of greater motion acuity at high speeds, when spatial blurring would leave long streaks that could potentially be detected by the orientation system and combined with motion signals. Edwards and Crane (2007), for example, found that direction detection thresholds for fast global motion stimuli (above the streak speed threshold) were low when long dot lifetimes were used to produce elongated motion streaks, and were elevated when short dot lifetimes minimized streaks as an effective cue. Other studies have taken the complementary approach and tried to demonstrate degraded motion perception when oriented masks are used to render streaks unreliable (Burr & Ross, 2002). This approach was also adopted by Geisler (1999), whose psychophysical experiments showed that detection thresholds for motion of a single Gaussian blob masked by one-dimensional dynamic random noise were significantly higher when the orientation of the noise was parallel to the dot’s direction of motion (thus masking its trajectory) than when it was perpendicular. Importantly, this difference only became evident above a certain speed threshold, estimated to be around one dot width per 100 ms, consistent with the idea that the dot must move far enough in the neural temporal integration window to form an elongated “streak.” Further evidence is provided by several recent psychophysical and neuroimaging studies (Krekelberg, Dannenberg, Hoffmann, Bremmer, & Ross, 2003; Mateeff, Stefanova, & Hohnsbein, 2007; Ross et al., 2000) as well as by single-unit neural recordings (Geisler, Albrecht, Crane, & Stern, 2001). In the last study, neural recordings showed greater activation in neurons *parallel* to the direction of motion for fast, ‘streaky’ motion viewed by awake behaving monkeys.

Despite the evidence appearing to support a role for motion streaks in motion computation, there is still some dispute as to whether streaks are actually useful for direction discrimination (Matthews & Allen, 2005). To shed light on this debate, we adopt a more fundamental approach and focus on the first tenet of the motion streaks model: that fast translating motion produces spatial smearing that is encoded by orientation-selective mechanisms. Specifically, we will test whether fast, ‘streaky’ motion can induce two well-known orientation phenomena, the tilt aftereffect and tilt illusion (Clifford, Wenderoth, & Spehar, 2000; Gibson & Radner, 1937; Schwartz, Hsu, & Dayan, 2007; Wenderoth & Johnstone, 1988a). Although it can be assumed that streaks should arise as an inevitable consequence of temporal integration, it is less clear whether they are available to influence motion perception.

Several authors have noted that moving objects often do not look blurred, and may even look sharper (Bex, Edgar, & Smith, 1995), and thus motion-related smearing must be suppressed at some stage of visual processing (Burr, 1980; Burr & Morgan, 1997; Morgan & Benton, 1989). If the suppression of motion streaks were to happen very early in visual processing, then it is doubtful that they would be available to combine with motion signals. On the other hand, if it could be shown that fast ‘streaky’ motion in a surround was capable of inducing a tilt illusion on a central grating, or if adaptation to fast motion caused a subsequent grating to be repelled in orientation, as in the classical tilt aftereffect, then this would constitute solid evidence that motion streaks are indeed encoded by orientation-selective units, probably at a cortical level, and would very likely be available to be combined with signals from the motion system.

## Experiment 1: Tilt aftereffects from motion

If elongated streaks produced by fast translating patterns are encoded by orientation-selective neurons, it follows that prolonged exposure to such motion should cause adaptation in orientation-selective units whose preferred orientation is aligned with the motion streaks (i.e., parallel to the direction of motion). **Experiment 1** tests this prediction using the tilt aftereffect (Clifford et al., 2000; Gibson & Radner, 1937).

The magnitude of the TAE exhibits a characteristic angular tuning function, whereby adaptation to a given orientation causes nearby orientations (e.g.,  $\pm 15^\circ$ ) to appear repelled away from the adapting orientation, and more distant orientations (e.g.,  $\pm 75^\circ$ ) to appear attracted toward the adapting orientation (see **Figure 2**). Using

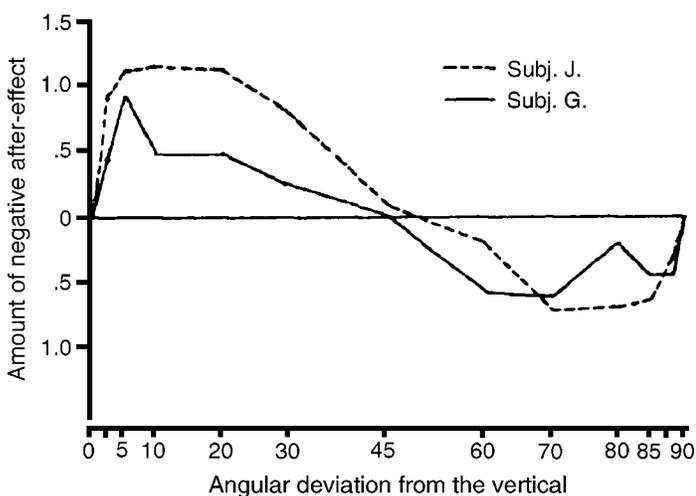


Figure 2. The classic TAE. Reproduced from Gibson and Radner (1937).

adaptation to a range of fast ‘streaky’ motion trajectories around vertical, we measured the TAE on a vertically oriented test grating and tested whether this characteristic angular tuning could be observed. No systematic TAE was expected following adaptation to patterns with short dot lifetimes, which should have reduced streak information.

## Method

### Participants

Participants were four experienced psychophysical observers, aged 27–40, three of whom were naive to the purpose of the experiment. All had normal or corrected-to-normal vision.

### Materials

Stimuli were programmed in Matlab version 7.4.0, using the Psychophysics Toolbox (Brainard, 1997), on a Mac Pro computer with dual 2.66 GHz dual-core Intel Xeon processors, running Mac OSX Version 10.4.10, and presented on a Trinitron Multiscan E400 monitor with a  $37 \times 28$  cm screen, a pixel resolution of  $1024 \times 768$  and a refresh rate of 75 Hz. To remove cues to vertical, participants viewed the stimuli through a circular viewing tube 20 cm in diameter and 57 cm in length, with a standard chin rest.

### Stimuli and procedure

Adapting motion stimuli frames were pre-computed in Matlab, and consisted of 320 Gaussian blobs with a diameter of 0.108 deg (given by  $4 \times$  the dot standard deviation) and Weber contrast of 0.95. Dots were dark on a gray background with a mean luminance of  $33.5 \text{ cd/m}^2$ , in a circular aperture  $9.74^\circ$  in diameter. All motion stimuli had a coherence level of 50%: that is, half the dots were ‘signal’ dots which always moved in the adapting direction and the other half moved in a ‘random walk’ manner in which the distance a dot moved was the same as that of the fixed-walk dots, but the direction of its motion was randomly determined. Streak length was determined by varying the number of ‘fixed-walk’ frames for an individual dot (see **Figure 3**). The initial position of each dot was randomly determined, and signal dots ‘wrapped around’ as they disappeared over the edge of the aperture. Dot speed was 9.5 deg/sec, and two ‘streak lengths’ were tested (using dot lifetimes of 8 and 2, giving ‘strong’ and ‘weak’ streak conditions respectively).

Initial motion adaptation period for each direction was 40 s, followed by top-up adaptations of 10 s. Directions tested were 0, 15, 30, 45, 60, 75 and 90 degrees clockwise from vertical and directions were blocked and presented in random order. The test stimulus was a sine-wave grating with a spatial frequency of 2.46 cycles/deg and Michelson contrast of 0.05, presented briefly for 50 ms. The subjects’

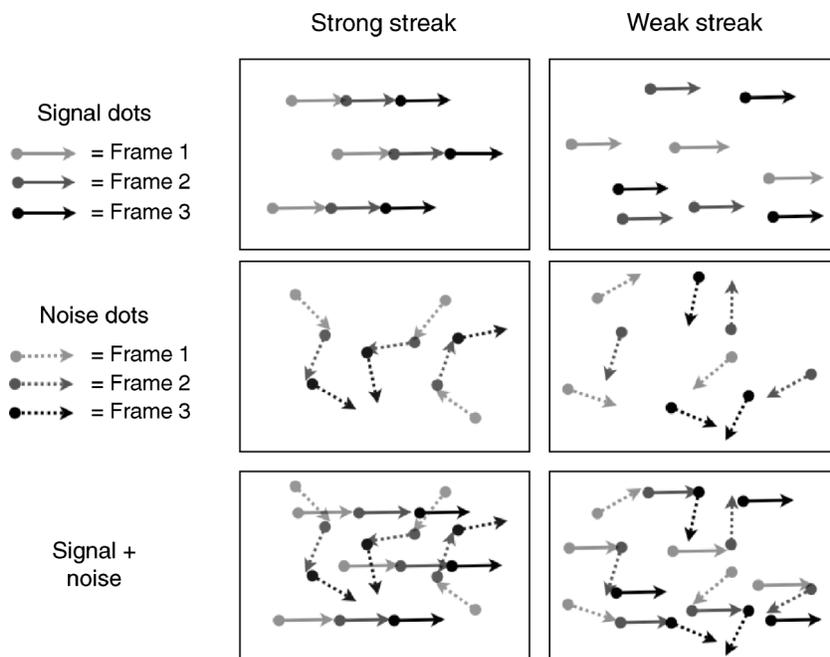


Figure 3. Schematic diagram of the “strong” and “weak” streak conditions. 40 dots were “signal” dots, and 40 were “noise” dots; noise dots moved in a random-walk fashion, while signal dots were fixed-walk. Streak length was controlled by the number of frames a dot remained fixed-walk before it became a random-walk dot.

task was to judge whether the test grating was tilted left or right of vertical. Test orientations were adjusted by two interleaved QUEST adaptive staircases (Watson & Pelli, 1983) which were driven by subjects’ responses and converged on an estimate of their subjective vertical for each condition (see Figure 4). Each QUEST contained 25 trials, and observers completed at least two trial blocks for each condition, giving a total of at least 100 data points for each direction of adapting motion and streak length. The QUEST data were pooled and fitted with a psychometric function using maximum likelihood estimation to obtain a threshold value for subjective vertical. A control condition was run in which the test grating was

presented without prior motion adaptation. This was used to determine each subject’s individual subjective vertical, and these baseline measurements were subtracted from the post-adaptation measurements.

### Results and discussion

Responses for each block of direction adaptation were fitted with a cumulative Gaussian function which gave a threshold measure for each participant indicating their subjective vertical following motion adaptation: that is, the grating orientation which appears vertical to the observer after adapting to a particular direction of motion. Control conditions measured the subjective vertical for each participant in the absence of adapting stimuli, and these measurements were subtracted from the post-adaptation results to determine the size of the aftereffect. These measures were then analyzed in a two-way ANOVA testing adaptation direction and streak strength. There were significant main effects of orientation,  $F(6, 18) = 20.065, p < 0.001$  and streak length,  $F(1,3) = 13.595, p = 0.035$ , and a significant interaction between orientation and streak length,  $F(6,18) = 5.384, p = 0.002$ . Polynomial contrasts showed that the interaction had a significant quadratic trend,  $F(1,3) = 87.165, p = 0.003$ , and the cubic trend approached significance,  $F(1,3) = 9.796, p = 0.052$ .

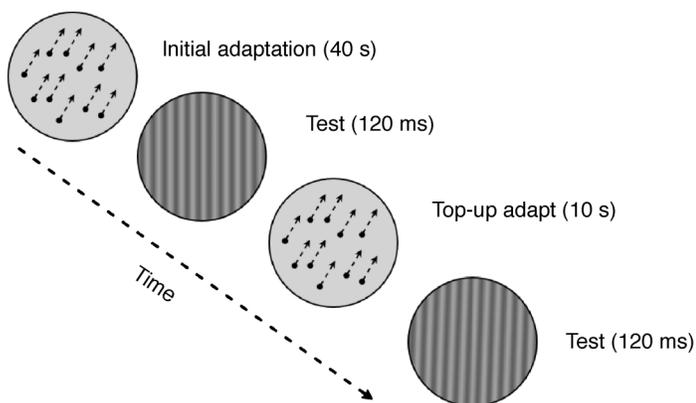


Figure 4. Schematic diagram of the procedure for the TAE from motion experiment.

Figure 5 shows the angular function of the aftereffect pooled across the four observers. For adaptation to strong

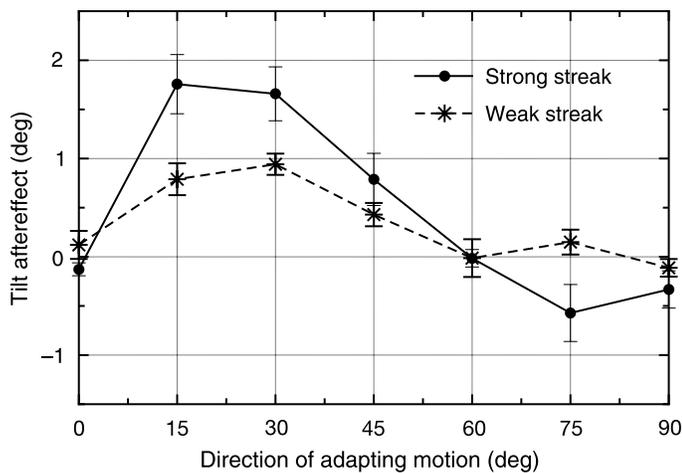


Figure 5. Pooled results across 4 observers. Error bars represent  $\pm 1$  SE of the mean.

streaks, there is a very clear pattern of results which is remarkably similar to the classic tilt aftereffect (Gibson & Radner, 1937). Importantly, the TAE produced by adaptation to strong motion streaks, although smaller in magnitude compared to those usually seen with briefly-flashed gratings (Wenderoth & Johnstone, 1988b; Wolfe, 1984), is closely comparable in orientation tuning to the classical TAE. These results confirm that oriented streaks were indeed present in the strong streak condition, and moreover, the near-identical pattern of tuning implies that they were encoded by the same orientation-selective mechanisms in early cortex thought to underlie the TAE (Clifford et al., 2000). Critically, TAEs were much weaker in the short-streak condition, although small positive effects are still seen at 15 and 30 degrees. Possible explanations for this phenomenon will be addressed further below.

## Experiment 2: Tilt illusions

A complementary approach to establishing the existence of oriented streaks in translating motion is to test whether they induce the tilt illusion (TI). The TAE and the TI have very similar and very well-researched angular functions, whereby, in both phenomena, nearby orientations cause “repulsive” aftereffects and illusions, and angular separations of around 75 degrees cause “attractive” effects, as observed in Experiment 1. The tilt illusion (TI) is a simultaneous version of the TAE, and is commonly ascribed to similar mechanisms (Magnussen & Kurtenbach, 1980; Wenderoth & Johnstone, 1988a). In the typical version of the illusion, the perceived orientation of a central stimulus is affected by the orientation of a surrounding stimulus (see Figure 6). Thus, if adapting to motion affects the perceived orientation of a subsequently-viewed grating, as shown in Experiment 1 (tilt aftereffects

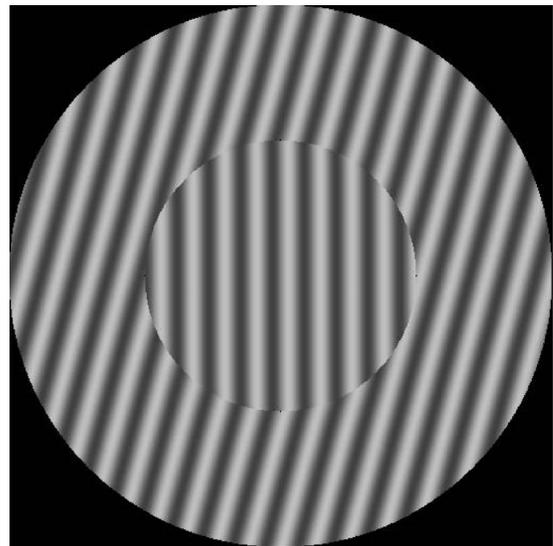


Figure 6. An example of the tilt illusion. Note that the inner grating appears tilted clockwise from vertical, even though it is, in fact, vertical.

caused by motion), then it should be possible to see a similar effect on a central grating of a surrounding motion stimulus (tilt illusions caused by motion). Given the close relationship seen in Experiment 1 between the classical TAE induced by gratings and the TAE induced by fast ‘streaky’ motion, we expect that replacing the surround grating by streaky motion will produce results very similar to the classical TI.

## Method

### Participants and materials

Participants were four experienced psychophysical observers aged 22–40, three of whom were naive to the purpose of the experiment. All had normal or corrected-to-normal vision. Materials were as above.

### Stimuli and procedure

Stimuli were again 320 Gaussian blobs appearing within a circular aperture 9.74 deg in diameter, with speeds, directions and dot sizes as above, but now the test stimulus was a small low-contrast grating (4.5 cyc/deg, Michelson contrast = 0.05) within a smaller, central aperture 1.5 deg in diameter, which ramped on and off smoothly in a Gaussian temporal window during the period of viewing the motion stimulus (800 ms), so that presentation was simultaneous (see Figure 7). Strong and weak streaks were again compared, and the participant’s task was again to judge the orientation of the test grating (left or right of vertical). QUEST was used to adjust the orientation of the test stimulus after each trial based on previous responses. Trials were blocked by direction of

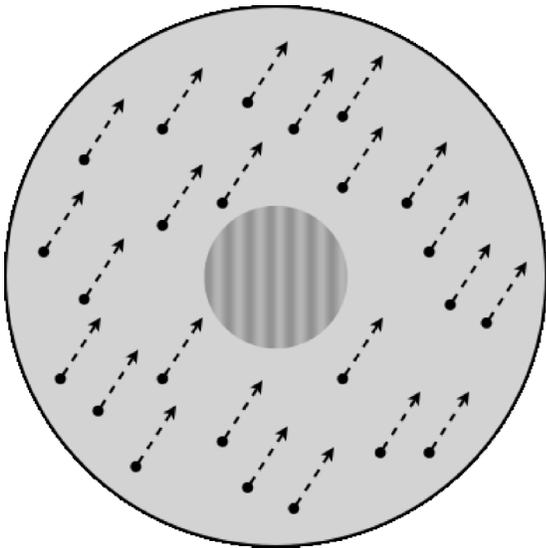


Figure 7. Schematic diagram of the procedure for the tilt illusion from motion experiment. Dots were 50% coherent, and the test grating ramped on and off briefly in the center of the display.

inducing motion and streak length, and presented in randomized order. Each session consisted of two interleaved QUEST staircases of 25 trials each. In the control condition, surrounding inducing stimuli were dots moving at the same speed, but with zero coherence (thus all dots moved in a random walk manner). Orientation thresholds from the control condition were presumed to represent the subject's subjective vertical, and this value was subtracted from thresholds obtained in the experimental conditions. These thresholds were then analyzed in a two-way ANOVA testing direction of motion and streak length.

## Results and discussion

Responses for each directional block were again fitted with a cumulative Gaussian function, which gave a threshold measure for each participant representing the angle of the test grating that appeared vertical in the presence of each direction of inducing motion. There were significant main effects of direction of motion,  $F(6, 18) = 2.987$ ,  $p = .033$ , and streak length,  $F(1,3) = 13.756$ ,  $p = 0.034$ , and a significant interaction between motion direction and streak length,  $F(6,18) = 1.968$ ,  $p = 0.001$ . Polynomial contrasts showed that the interaction had a significant cubic trend,  $F(1,3) = 80.139$ ,  $p = 0.003$ , but no other trends were significant.

Figure 8 shows the angular function of the illusion pooled across the four observers. The pattern of results is again similar to the classic tilt illusion (Wenderoth & Johnstone, 1988a); effects in the short-streak condition showed no significant difference from zero. Again, it is clear that there were both direct and indirect (repulsion

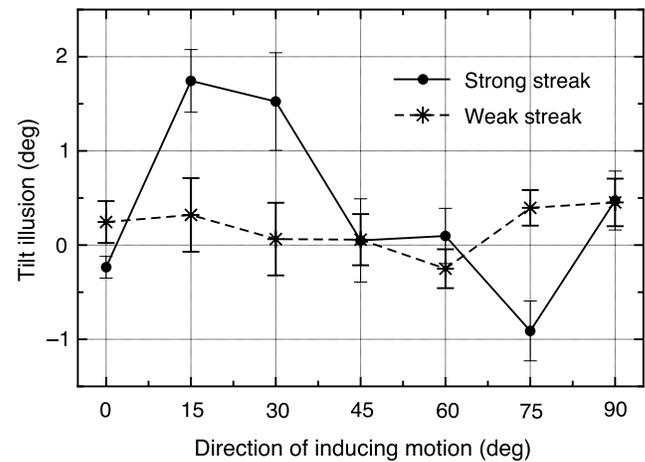


Figure 8. Pooled results for the tilt illusion experiment for 4 observers. Error bars show  $\pm 1$  SE.

and attraction) effects, suggesting a similar mechanism to that involved in the TI. Since it is usually assumed that the TI and the TAE are caused by the same neural interactions (Magnussen & Kurtenbach, 1980; Schwartz et al., 2007), it seems likely that the illusion seen here is caused by the same processes as those which caused the TAE in the previous experiment. This constitutes further evidence that effects once thought to be exclusive to the orientation domain can be induced by stimuli previously thought of as containing purely motion information, as the dots themselves do not contain oriented elements. Thus the tilt illusion was almost certainly induced by motion streaks.

## Experiment 3: Slow speed control

Although clear TAEs and TIs are seen for the “strong-streak” conditions in Experiments 1 and 2, there is a slight puzzle in the fact that the “weak-streak” condition produced a small TAE (although no TI). There are several possible explanations for this. First, lengthy exposure to an adapting direction in TAE trials could have provided observers with a frame of reference for making orientation judgments, which might have interacted with the static oriented test pattern to produce the small TAEs. If this were the case, motion streaks would not be the correct explanation for the data, and the smaller effects for weak streaks would be due to a weaker (noisier) reference. Second, there could have been an effect of adaptation in TAE trials whereby the oriented signal caused by the streaks builds up so that even very short streaks might, over time, accumulate enough to cause a tilt aftereffect.

The alternative accounts can be tested by using stimuli which are below the “speed threshold” for streaks. If the first possibility were true, then speed should not make a

difference, as motion direction signals would still be present to act as a frame of reference, especially in the strong-streaks condition. If the second possibility (accumulating adaptation) were true, then small effects could still result below the “speed threshold” for streaks provided the streaks were strong (i.e., long). In Experiment 3, using a slow speed, the TAE and TI experiments were retested for orientations of 15 and 30 degrees (where effect size is maximal).

## Methods

### Participants and materials

Participants were four experienced psychophysical observers aged 22–42, three of whom were naive to the purpose of the experiment. Three of the participants were the same as those in Experiments 1 and 2. Those observers who had not participated in the original experiment also performed the experiment at fast speed. All had normal or corrected-to-normal vision. Materials were as above.

### Stimuli and procedure

Stimuli were as above, with the exception that the step size for the dot motion was reduced so that dot speed was now 1.83 deg/sec, designed to be less than 1 dot width per 100 ms, so that dot motion was below the threshold for streaks.

## Results and discussion

Results for the slow speed conditions were fitted with cumulative Gaussian functions, and thresholds were determined by the mean of each function. Results for TAE and TI controls are shown in Figure 9. For both the illusion and aftereffect experiments, a two-way repeated-measures ANOVA was conducted. In the aftereffect experiment, there was no significant main effect of adapting angle,  $F(1,3) = .712, p = 0.461$ , or of streak length,  $F(1,3) = .273, p = .637$ . The interaction between angle and streak length approached significance,  $F(1,3) = 7.030, p = 0.077$ . For the illusion experiment, there was no significant main effect of inducing angle,  $F(1,3) = 1.829, p = 0.269$ , or streak length,  $F(1,3) = 3.171, p = .173$ . The interaction was also not significant,  $F(1,3) = 0.012, p = .919$ .

Since the main question of interest was whether any of the effects at slow speed were significantly different from 0 (i.e., no aftereffect or illusion), a set of four  $t$ -tests was conducted for the four slow conditions (strong/weak streaks  $\times$  15/30°) of the TAE and of the TI. For the TAE, although the 15-degree adaptation produced a small effect which approached significance (mean = 1.13,  $t(3) = 4.48, p = 0.084$ ), none of the conditions showed results

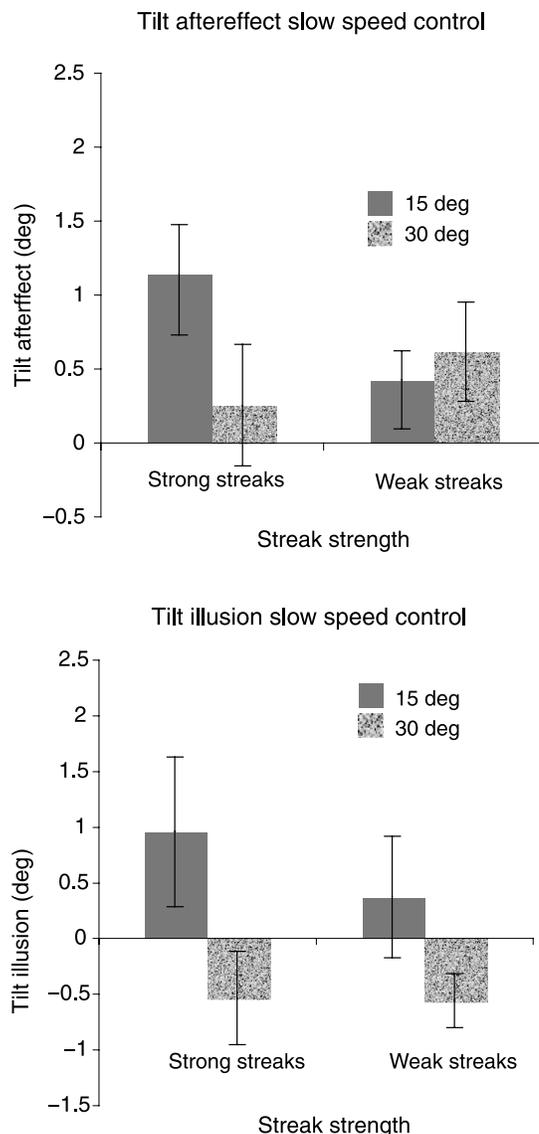


Figure 9. Results for the tilt aftereffect and tilt illusion control experiments. Slow speed results are shown for four observers. Error bars show  $\pm 1$  SE.

significantly different from 0 ( $p$ -values are Bonferroni-adjusted to control for overall error rate). For the TI, no effects were significantly different from 0 (see Table 1 for full results).

If the results in Experiment 1 had been due solely to motion direction information (as in the first possibility outlined in Introduction to Experiment 3) and not to

Condition	15, strong	15, weak	30, strong	30, weak
Aftereffect	4.48 (.084)	2.15 (.484)	0.75 (>.5)	2.27 (.432)
Illusion	1.94 (>.5)	1.21 (>.5)	-.38 (>.5)	-1.83 (>.5)

Table 1. Results of  $t$ -tests for the slow speed conditions of the tilt aftereffect and tilt illusion.  $P$ -values are shown in brackets, Bonferroni-adjusted to control for multiple  $t$ -tests in each experiment.

streaks, then running the experiment at sub-streak speeds should not have made a difference, since the same directional information was present at both speeds. Instead, the small (albeit non-significant) TAE seen at the slower speed suggests that a build-up of sub-threshold streaks over time (the second possibility) could have accounted for the pattern of small TAEs seen in the weak-streak condition of [Experiment 1](#). This is consistent with a motion-streaks account of the data presented in [Experiments 1](#) and [2](#), rather than one based purely on motion direction information.

## General discussion

The results of the tilt experiments ([Experiments 1](#) and [2](#)) showed that robust tilt aftereffects and tilt illusions can be induced by moving stimuli which do not contain explicit orientation signals. Critically, these effects were reduced or eliminated when “streak” length was reduced to a minimum in the inducing stimulus, using a manipulation which leaves the speed of individual elements constant, and which therefore rules out alternative explanations related to the motion content of the stimulus. This is further supported by the fact that presenting the same stimuli at sub-streak speeds did not produce significant aftereffects or illusions. This finding provides strong support for one of the key elements of the “motion streak” hypothesis ([Geisler, 1999](#)): that motion above the speed threshold for streaks will leave oriented traces that can be encoded by orientation-selective units. Thus, we conclude that although oriented motion streaks are not obviously visible, presumably due to motion deblurring ([Burr, 1980](#); [Burr & Morgan, 1997](#)), they are nonetheless present in neural processing at early cortical stages where orientation is encoded.

The presence of motion streaks at the orientation encoding stage is revealed not only by the TAEs and TIs they induce but by the highly similar orientation tunings of streak-induced and grating-induced TAEs and TIs ([Clifford et al., 2000](#); [Schwartz et al., 2007](#); [Wenderoth & Johnstone, 1988a](#)). The neural substrate underlying the TAE and TI induced with conventional grating stimuli is presumed to be the columns of narrowly tuned orientation-selective neurons found in primary visual cortex ([Gur et al., 2005](#); [Hubel & Wiesel, 1962](#); [Sincich & Horton, 2005](#)). The angular tunings of these effects are attributed to interactions between these narrowly tuned channels which vary with the orientation difference between the inducing and test gratings. The close similarity of the angular tuning functions implies that gratings and streaks are indeed encoded by the same mechanisms. Had we found a broader tuning for streak-induced effects, it might have pointed to streak orientation being encoded at a subsequent cortical stage, where tunings to features such

as orientation are broader than in V1. Since orientation is not generally thought to be encoded prior to V1, the evidence points to streaks and gratings being encoded by the same early cortical mechanisms, presumably orientation-selective neurons in primary visual cortex.

Although the angular dependency of the streak-induced TAEs and TIs was very similar to classical effects, the magnitudes of the streak-induced effects (slightly less than  $2^\circ$  at peak) are smaller than is generally reported for classically induced effects ( $3^\circ$  to  $4^\circ$ ). This can probably be explained by contrast differences between the inducing stimuli. Because motion streaks are formed by spatial smearing of the blobs over the temporal integration period they must inevitably have low contrast, since the luminance energy in the blob is averaged over the distance that it translates during the 100 ms or so that it is integrated. Although there is some debate over the effect of contrast on the TI and TAE ([Harris & Calvert, 1989](#); [Smith & Wenderoth, 1999](#); [Westheimer, Brincat, & Wehrhahn, 1999](#)), it is generally found that lower contrast of the inducing stimulus reduces both effects. Thus the lower magnitude of our effects, while still highly significant, is consistent with this known contrast dependency, as if the motion streaks formed the equivalent of a low-contrast grating. This underscores an important point about streaks: that they will inevitably be a low-contrast feature even in a high-contrast moving image. Spatial frequency might also be a factor in the reduced magnitude of streak-induced effects, as the TI and TAE are spatial-frequency ([Georgeson, 1973](#); [Ware & Mitchell, 1974](#)). The spatial frequency content of the motion streaks image is likely to be complex, and the peak frequency may not have been optimal to produce maximal effects.

The current results also shed light on the process of motion deblurring. If the oriented streaks caused by fast motion are not perceived, they must be suppressed at some stage of visual processing ([Burr, 1980](#); [Burr & Morgan, 1997](#)). From the TAEs and TIs reported here we can conclude that streaks are still present at the stage of early orientation encoding and that deblurring must therefore occur at a subsequent stage. The reason streaks are not suppressed before the first stage where they can be detected may be because they are useful to the visual system, and are exploited in combination with motion signals to improve directional acuity. An alternative to the motion deblurring ‘suppression’ account is that motion ‘sharpening’ arises from non-linear compression of local contrast responses, thus removing the need for any special ‘deblurring’ process ([Georgeson & Hammett, 2002](#); [Hammett, Georgeson, & Gorea, 1998](#)). If this were the case, there would be no oriented trail left by a moving object, as it would be attenuated at a very early, possibly pre-cortical stage. This account seems inconsistent with the results reported here, that motion streaks produce robust TIs and TAEs, presumably by activating orientation mechanisms in early cortex. Overall, the results we report here favor the ‘suppression’ account of motion

deblurring, and suggest that this process must occur at a stage subsequent to early orientation encoding.

A final observation on our tilt experiments concerns visual awareness of orientation. In effect, our findings demonstrate that adaptation to orientation can occur despite the absence of awareness of the adapting orientation. A number of recent studies have shown similar results using different approaches. For example, He and MacLeod (2001) showed that tilt aftereffects, as well as orientation-specific elevations in contrast thresholds, could be produced by gratings which were too fine to be perceived; also, Vul and MacLeod (2006) showed a McCulloch effect for gratings which were alternating too fast for the colors to be seen. Pearson and Clifford (2005) found that, during binocular rivalry, the orientation of the image in the dominant eye was systematically affected by the orientation of the image which was suppressed from awareness. Further, Clifford and Harris (2005) used backward-masking to suppress a surround grating from awareness, and found that a tilt illusion could still be produced on a central grating. Our results add to the growing body of evidence that classical orientation effects can occur without awareness of the inducing stimuli.

In summary, the robust tilt aftereffects and illusions shown here from adaptation to fast, “streaky” motion (and absent or reduced when streak information is attenuated), and the strong direction aftereffect caused by adapting to a tilted grating, add support to the growing body of evidence that oriented signals left by fast motion are an important component of direction processing in the human visual system. One possible explanation for the delay in realizing the impact of streaks on motion perception is that, for much of the history of motion research, experimenters have relied on stimuli such as orthogonally-moving gratings and plaids, based on early physiological evidence that V1 neurons maximally respond to orthogonally-moving stimuli (Hubel & Wiesel, 1962). As Geisler et al. (2001) point out, the contrast of these stimuli averages out over the period of motion to a contrast of zero, so, unlike moving natural scenes or blobs, they will not produce motion streaks at any speed. Recent work suggests natural scenes contain an abundance of “streak” information (Barlow & Olshausen, 2004; Zanker & Zeil, 2005), so it is likely that these signals are useful to the visual system over a wide range of speeds. However, it is likely that complementary motion analysis systems exist for slower-moving objects and components of a visual scene; it is of great interest to explore how these two systems might optimally combine to allow accurate motion perception.

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