



When do we know which way is up? The time course of orientation perception

Jennifer E. Corbett^{a,*}, Todd C. Handy^b, James T. Enns^b

^a Center for Mind and Brain & Department of Psychology, The University of California, 267 Cousteau Place, Davis, CA 95618, USA

^b Department of Psychology, The University of British Columbia, 2136 West Mall, Vancouver, BC, V6T 1Z4, Canada

ARTICLE INFO

Article history:

Received 22 June 2007

Received in revised form 22 September 2008

Keywords:

Orientation perception

Time course

Tilt illusion

Rod and frame illusion

ABSTRACT

There is evidence that global visual context affects orientation perception in later stages of processing than local context. We measured the relative time courses of two orientation illusions: The Tilt Illusion (TI) involves dense gratings in close proximity; the Rod and Frame Illusion (RFI) involves a solitary bar surrounded by a distant frame. We also varied whether the context was flashed briefly (Experiment 1) or remained visible (Experiment 2). Results showed that the TI (but not the RFI) occurs when the context is briefly flashed in advance of the test, that both illusions are strongest when the context and inducer appear simultaneously, and that the RFI frame must be visible for at least 800 ms to induce an illusion with asynchronous displays. Experiment 3 confirmed these patterns held for measures of illusion magnitude and discriminability. Results are consistent with an earlier effect of local spatial context and a later effect of global spatial context on orientation perception.

Published by Elsevier Ltd.

1. Introduction

Our sense of perceived upright is largely based on visual orientation cues. We perceive the orientation of objects relative to their local, spatially adjacent context, as well to their global, spatially more remote contexts. For example, a pilot must quickly determine the orientation of a needle on a dashboard meter, as well as the orientation of an approaching runway in a landing field. The Tilt Illusion (TI) and the Rod and Frame Illusion (RFI) are useful tools for examining the manner in which local and global visual context affect the perceived orientation of objects. TI displays generally consist of a test grating superimposed on a larger inducing grating, and RFI displays consist of a smaller test line surrounded by a larger, more spatially removed tilted square inducer (Fig. 1). A similar illusory outcome occurs in TI and RFI displays, with the test appearing to tilt away from the surrounding orientation context.

There is much evidence to suggest that the local interactions between the immediately adjacent gratings in TI displays originate earlier in the course of information processing than the RFI, which is driven by the orientation of the global visual environment. Yet, in contrast to the large literature cataloging the temporal dynamics of local tilt illusions, little is known about the time course of global context illusions. We therefore compared the time courses of these two types of visual context illusions in the present study. Specifically, we hypothesized that global visual context would have a later influence on behavioral measures of orientation discrimination than local context. Before describing our tests of this hypothesis,

we will briefly review what is known about possible dissociations between the TI and RFI, including the possibility that their effects occur on different time scales.

2. Spatial parameters of the TI and RFI

Although the magnitudes of the TI and RFI are each greatest when the context is tilted approximately 15° from vertical, the TI is generally greater in magnitude than the RFI (Beh, Wenderoth, & Purcell, 1971; Gibson & Radner, 1937; Over, Broerse, & Crassini, 1972). Manipulating the spatial parameters of these two illusions also produces markedly different effects:

- (1) TI displays are typically smaller and have multiple inducing elements that are immediately adjacent to the test element (e.g. Wenderoth & van der Zwan, 1989; Wolfe, 1984), whereas the RFI uses a large frame such that is spatially more remote from the test (e.g. Asch & Witkin, 1948; Dyde & Milner, 2002),
- (2) The magnitude of the TI decreases when there is a spatial gap between the center and surround (Antonucci, Fanzon, Spinelli, & Zoccolotti, 1995; Tolhurst & Thompson, 1975; Virsu & Taskinen, 1975; Wenderoth & Johnstone, 1989; Wenderoth, Johnstone, & van der Zwan, 1989; Wenderoth, van der Zwan, & Williams, 1993), whereas increasing the test-to-frame distance increases the magnitude of the RFI (Ebenholtz, 1977; Ebenholtz & Callan, 1980),
- (3) The outer-most of two or more frames governs the RFI, such that an upright rod appears tilted when surrounded by a small upright frame and a large tilted frame, but the same

* Corresponding author.

E-mail address: jecorbett@ucdavis.edu (J.E. Corbett).

rod appears upright when surrounded by a small tilted frame and a large upright frame (DiLorenzo & Rock, 1982; Spinelli, Antonucci, Daini, Fanzon, & Zoccolotti, 1995).

These findings are consistent with the hypothesis that the TI originates from local interactions between the spatially adjacent neural units, whereas the RFI originates via interactions among more distant neurons.

3. The time course of orientation illusions

Given the dissociations between the spatial parameters of the RFI and the TI, it is likely that these illusions also exhibit diverse temporal dynamics. While relatively little is known about the time course of global context effects, the following review summarizes a large literature on the time course of local tilt illusions.¹

- (1) Simultaneous presentations of the inducer and test result in larger magnitude illusions than asynchronous presentations (Durant & Clifford, 2006; Matin, 1974; Wolfe, 1984). When other cues allowed for the segmentation of the central test from the surrounding inducer, such as a spatial gap, contrast differences, or depth differences between the test and context, the magnitude of the TI decreased with simultaneous presentations (Durant & Clifford, 2006). However, the illusion resulting from asynchronous presentations of the inducing context and the test stimulus was relatively unaffected by these additional perceptual segmentation cues. Based on these findings, Durant and Clifford (2006) propose that when the test and inducer are segregated by a temporal gap (as in asynchronous displays) or a spatial gap, the effect of the inducing context is reduced. Without these cues, in simultaneous TI displays, the orientation of the test is more difficult to parse from the orientation of the inducing background, and the largest tilt effects occur.
- (2) When the central test and surrounding context are presented simultaneously, shorter stimulus durations yield larger TIs over the range from 10 to 100 ms (Calvert & Harris, 1985, 1988; Clifford & Harris, 2005; Wenderoth & Johnstone, 1988a; Wenderoth, van der Zwan, & Johnstone, 1989; but see also O'Toole, 1979).
- (3) Asynchronous presentations of test and inducer increase the TI: (a) when the inducer is visible for a relatively longer period of time (Harris & Calvert, 1989; Sekular & Littlejohn, 1974; Wolfe, 1984), (b) when the test is flashed for a proportionately shorter period of time (Harris & Calvert, 1989; Wenderoth & van der Zwan, 1989; Wolfe, 1984), and (c) when the stimulus onset asynchrony (SOA) between the inducer and test is decreased (Durant & Clifford, 2006;

Matin, 1974; Wolfe, 1984). Points (a) and (b) are consistent with the inducing context serving to adapt (or to condition) the system to establish a new, short-term reference for the perception of upright, and point (c) is consistent with rapid, forward-acting effects of the inducing context. Taken together, these results suggest that the test and inducing components may be perceived as part of the same temporal event when presented in contiguous rapid succession.

4. A later influence of global orientation context?

The literature on the time course of local tilt illusions stands in sharp contrast to the lack of corresponding research on the time course of the RFI. Nonetheless, studies of tilt effects involving single inducing lines, studies comparing the time course of direct (repulsion) and indirect (assimilation) tilt effects, and studies examining the effect of orientation context on visually-guided actions all support a later locus for the effects of global orientation context.

- (1) Longer exposure to an inducing global context results in larger Tilt Adaptation Effects (TAEs). Gibson and Radner (1937), for example, first adapted participants to a large (75° of visual angle) tilted line for a range of times from 1 s to several minutes. Then the experimenter asked participants to close their eyes, before adjusting the line back to vertical. When the experimenter asked participants to open their eyes again and adjust the line to vertical, the illusion increased along with adaptation time from 5 to 45 s, suggesting that the inducing global context had a relatively late influence on perceived orientation.
- (2) Studies comparing TI direct and indirect effects provide support a relatively late influence of global orientation context. Direct, contrast, or repulsion effects are measured in most TI studies: the orientation of the test appears repulsed from orientation of the inducing context when they are separated by 10°–20° in orientation. Direct effects are larger in magnitude and more frequently observed than TI indirect or assimilation effects: the orientation of test appears tilted in same direction as the inducing context with angular separations of 70°–85°. Introducing a spatial gap or a difference in spatial frequencies between the inducer and test decreases direct effects, but does not affect the magnitude of indirect effects (Wenderoth & Johnstone, 1989). Furthermore, when TI displays are surrounded by an upright global frame, direct effects persist but indirect effects are no longer observed (Wenderoth & Johnstone, 1988b). Taken together, these findings suggest that indirect effects are similar to the RFI in that they occur relative to the more global orientation context of the frame.

¹ Readers should note that what we refer to here as the TI is also called the Simultaneous Tilt Illusion (STI), which is the appropriate label when the test and inducer are presented at the same time. We are also examining the illusion with asynchronous presentations of the inducer and test, so we will use the more general label of TI. It is also important to distinguish the TI from the Tilt Adaptation/After Effect (TAE), typically used to study longer-term effects of orientation context (e.g., from seconds to minutes) with a range of stimuli. Research on the time course of the TAE is valuable to an understanding of the time courses of both local orientation context illusions (studies using spatially adjacent inducer and test gratings), and global orientation context illusions (studies using large spatially remote inducing lines). Also, the TAE may include effects attributable to neural fatigue and adaptation, whereas the focus of the present study is restricted to the immediate effects of orientation context. Any such long-term effects of neural fatigue will be averaged over the many trials in our experiments, where the orientation of successive stimuli is randomly determined. In reviewing the time course of orientation context illusions, we will consider evidence from TI, STI, and TAE experiments in an effort to gain the most complete picture of the known temporal dynamics of local and global context effects.

Wenderoth and Johnstone (1988a) reported that both direct and indirect effects increased as stimulus duration decreased. Yet, even at the shortest 25 ms durations, an upright frame reduced the magnitude of indirect effects by two-thirds, but did not modulate direct effects. In addition, whereas direct effects tapered-off with stimulus durations around 100 ms, indirect effects leveled-out later with stimulus durations of about 400 ms. Wenderoth and van der Zwan (1989) later confirmed these patterns held for direct and indirect TAEs composed of grating inducer and test stimuli. Furthermore, they showed that a surrounding upright frame affected the magnitude of indirect effects when presented simultaneously with the test, but not when it was presented with the inducer. This suggests that the frame modulates later response stages of processing, and not earlier input stages.

- (3) The TI affects visually guided actions, but actions are corrected online for the RFI. Dyde and Milner (2002) tested healthy human participants in both the TI and the RFI (illustrated in Fig. 1) using measures of perception and visually guided action. The main findings were that the TI influenced both manual adjustments of the perceived orientation of the test, and the end-result of visually guided reaching and grasping actions made toward it. In contrast, the RFI had an influence only on perceptual judgments, leaving visually guided actions to end in correspondence with the physical orientation of the test. These results were interpreted within the two visual streams theory (Milner & Goodale, 1995; c.f. Li & Matin, 2005), in which the dorsal visual stream carries information for visually guided action and the ventral visual stream carries visual information for perception. The authors propose that the TI originates during early stages of visual information processing before the bifurcation of the two visual streams, and the global RFI is manifest during later stages, in the ventral regions active after this division.

Also consistent with a later integration of global visual orientation cues, Li and Matin (2005) reported that the accuracy of manual pointing and reaching actions to a dot flanked by a large, pitched-from-vertical line increased as the distance from the hand-to-body increased. Actions were initially mislocalized to a similar degree as the illusory perception of eye level induced by the tilted line, but terminated in accordance with the physical position of the dot. Li and Matin propose that these results reflect a greater weighting of internalized, observer-based, proximal orientation cues during the initial stages of manual actions, switching to a greater weighting of distal, or environmental-based orientation cues as the distance from the hand-to-body increases.

5. The present study

The present study directly compares the time courses of the TI and the RFI for the first time. In Experiments 1 and 2 we measure the effects of the inducing context on the time observers need to correctly discriminate the tilt of a test stimulus. In Experiment 3 we confirm that the observed patterns hold for more explicit perceptual reports of perceived test orientation. In all three experiments, we varied the asynchrony (SOA) between the onset of the inducing context and the briefly presented test in TI and RFI displays, and measured the amount of time observers needed to correctly discriminate the orientation of the test. If local orientation context affects processing earlier than global context, when the inducing context appears briefly, larger forward-acting effects should occur for TI displays than for RFI displays. Second, with extended presentations of the inducing context, the global frame in RFI displays should need to remain visible for longer in advance of the test to induce an illusion than the local grating in TI displays.

To compare the time courses of the two illusions as closely and sensitively as possible, we did not use a traditional Point of Subjective Vertical (PSV) task, in which participants discriminate whether a test is oriented counterclockwise (CCW) (toward the left) or clockwise (CW) (toward the right), as our main dependent measure. Instead, we measured the time participants took to correctly discriminate whether the test was oriented CCW or CW. Whereas the PSV measure allows for an interpretation of the effects of the inducing context on the subjective percept of orientation, measuring reaction time and accuracy allows for a performance-based account of contextual effects on behavioral responses perhaps not manifest in consciously perceived differences of the magnitude of illusory tilt. Furthermore, as we were interested in the temporal dynamics of the two types of illusions, measuring reaction time

and accuracy allowed for a more sensitive and appropriate temporal measure of these illusions over time.

6. Experiment 1: Brief presentations of inducing context and test orientation

Experiment 1 compared the TI and RFI when the inducing context flashed briefly either before, during, or after a brief flash of the central test. On any given trial, the test could be tilted by 8°, either CCW or CW, and it could be surrounded by an inducing context that was tilted 15° CCW or CW. Congruent trials were those in which test and inducer were tilting in the same direction, and incongruent trials were those in which they were leaning in opposite directions (Fig. 1). Differences in the mean correct Response Time (RT) or mean Proportion Correct (PC) between these two types of trials indexed an illusory effect on the speed of orientation discriminations. Specifically, participants should take longer to respond, and have reduced accuracy on congruent displays (Fig. 1a and c) relative to incongruent displays (Fig. 1b and d). On congruent trials, the inducing context makes it appear as though the test is less tilted, or even slightly tilted in the opposite direction from the inducing context. On incongruent trials, the context highlights the mismatched orientation of the test.²

6.1. Methods

6.1.1. Participants

Twenty-nine undergraduate students from the University of British Columbia voluntarily participated in a 1-h session in exchange for extra credit in a department Psychology course. Separate groups of observers participated in TI and RFI sessions, and the illusions were never intermixed, such that TI inducers were never presented with RFI tests or visa versa. Fifteen observers (10 women and 5 men, aged 18–23) participated in the TI task and fourteen (8 women and 6 men, aged 18–23) participated in the RFI task. All had normal or corrected-to-normal vision and none reported any vestibular or proprioceptive disorders.

6.1.2. Task/instructions to participants

On each trial participants indicated whether the test stimulus tilted CCW (left) or CW (right) of gravity-defined vertical (upright) by pressing one of two lateralized response keys (“z” or “?”) on a keyboard with the left or right index finger, respectively. The experimenter instructed them to fixate on a 0.1° dot in the center of the display between trials, and that on each trial, a small grating (TI) or a short rod (RFI) would appear in the center of the screen. They were asked to indicate the direction in which the test grating or rod was leaning as quickly and accurately as possible, regardless of the orientation of any objects surrounding the test. Trials began at a fixed interval following each response and participants were instructed to respond even if they were uncertain.

6.1.3. Trial sequence

Each observer participated in four blocks of 64 trials for a total of 256 trials. We began by manipulating the SOA between the inducing context and the test stimulus and measuring the effects on the RT and PC for each type of illusion. On each trial, participants either saw the inducer followed by the test (positive SOAs), the inducer and test at the same time (simultaneous onset, 0 ms SOA), or the test followed by the inducer (negative SOAs). In each TI or RFI session, with equal probability in each trial, we tested five

² Note that a baseline measurement of test orientation discrimination without the surrounding inducer is not necessary with our task, as congruent and incongruent conditions can be collapsed over CCW and CW trials to average out any biases participants might have to respond in one direction when they are uncertain.

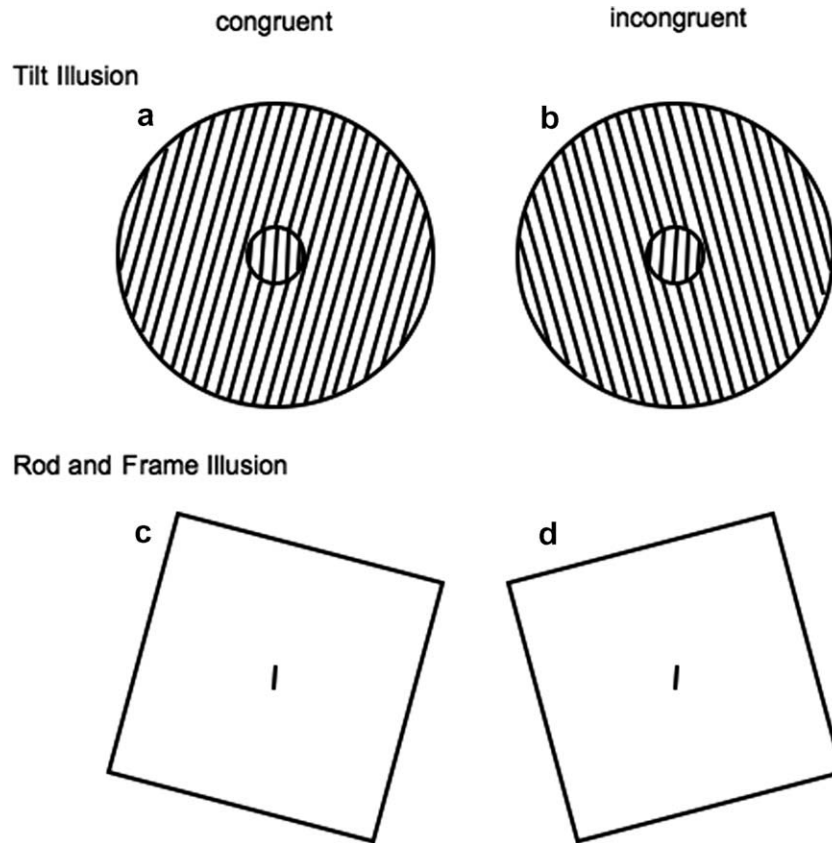


Fig. 1. Schematic illustration of the displays. The tilt illusion is shown in congruent (a) and incongruent (b) form for a counter-clockwise (right tilting) test. The clockwise version is not shown. The rod and frame illusion is also shown in congruent (c) and incongruent (d) form for a counter-clockwise (right tilting) test, with the clockwise version not shown. Participants perceive the orientation of the test as biased in the direction opposite to that of the surrounding context, such that the test in panels (b) and (d) appear to be tilted further away from upright than the identically tilted tests in panels (a) and (c).

positive SOAs (1600, 800, 400, 200, and 100 ms), a simultaneous 0-ms SOA, and two negative SOAs (−100 and −200 ms). We recorded RT and PC from the offset of the test in each trial. Fig. 2 provides a schematic diagram of the time course of a trial in each SOA in Experiment 1.

6.1.4. Displays

Stimulus displays were presented on 13" eMac computers (1024 × 768 resolution) controlled by VScope software (Enns & Rensink, 1995), and participants responded using the computer keyboard. All stimuli were presented on a 30 cd/m² background, viewed through a circular viewing window 20° of visual angle in diameter. From a viewing distance of 50 cm, the diameter of the surrounding frame in the TI was 12.4° of visual angle, and one side of the square RFI frame also subtended 12.4° of visual angle. All lines making up the frame and test in RFI displays subtended .25° of visual angle in width. Both TI gratings were composed of 5 cycle per degree square waves with light and dark bars of 30 and 0.1 cd/m², respectively. The refresh rate of the monitor was 89 Hz, with 11.2 ms display multiples of 143, 72, 36, 18, 9, and 0 yielding exposure durations or blank screen SOAs as close as possible to 1600, 800, 400, 200, 100, and 0 ms. To elicit the maximum illusions, the inducing frame or grating was tilted 15° CCW or CW, (Beh et al., 1971; Wenderoth & Beh, 1977), and the tests were oriented either 8° CCW or CW. We used tests that were as small as possible (2° of visual angle in diameter in TI displays and 1.15° of visual angle in RFI displays), to roughly equate the maximum range of possible spatial interactions in the displays, while maximizing potential short-range interactions for the TI and minimizing them for the RFI.

6.1.5. Procedure

In each display condition (TI and RFI), each combination of inducer (CCW or CW), test (CCW or CW), and SOA (1600, 800, 400,

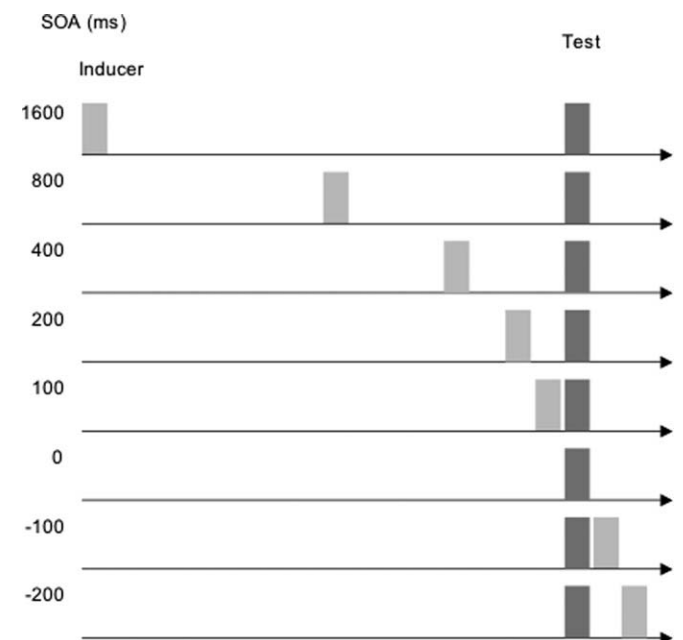


Fig. 2. Schematic diagram of the time course of a trial in Experiment 1 for each Stimulus Onset Asynchrony (SOA) in ms when the inducer was flashed for 100 ms.

200, 100, 0, –100, or –200 ms) appeared at random, with equal probability in each block. The lights remained off for the entire duration of each session to minimize the influence from the carpentered context of the experimental room, which has been reported to decrease tilt illusions (Purves & Howe (2004); Spinelli et al., 1995; Zoccolotti, Antonucci, Daini, Martelli, & Spinelli, 1997; Cian, Raphel, & Barraud, 2001; Ebenholtz & Utrie, 1982; Stoper & Cohen, 1989). To reduce the influence of the horizontal and vertical edges of the monitor, we affixed a black cardboard annulus 35° of visual angle in its outer diameter to the monitor casing to form a circular viewing window of 20° of visual angle. Viewing was binocular without restraint so as not to introduce any extraneous proprioceptive or vestibular influences on the perception of gravity.

Each participant completed four blocks of 16 practice trials. At the end of each practice block, a percent error rate was presented in the center of the screen. We were primarily concerned with the time needed for the inducing context to affect participants' correct orientation discriminations. Therefore, we required them to achieve an average accuracy of at least 80% in order to proceed to the experimental trials. Each trial was terminated when the participant made a manual response, or was timed-out after 5000 ms. No participant timed-out in more than 3% of the total trials.

6.2. Results

The mean correct RT and PC data are shown in Table 1. Fig. 3 shows the time course of the illusions, plotted as the difference between correct congruent and incongruent conditions as a function of SOA. This difference score involved a subtraction of Congruent–Incongruent for the correct RT data, and a subtraction of Incongruent–Congruent for the PC data. Positive values indicate faster response times and higher levels of accuracy for Incongruent versus Congruent trials, and negative values indicate faster response times and higher levels of accuracy for Congruent versus Incongruent trials.

The TI grew monotonically in both measures as the asynchrony between frame and test became smaller, with the largest effects occurring in the simultaneous condition (0 ms SOA). In contrast, the RFI showed no influence of the frame in any condition except the simultaneous one, where it was smaller than the TI.

These conclusions were supported by mixed analyses of variance (ANOVA) examining the between-participant factor of Display (TI, RFI), and the within-participant factor of SOA (1600, 800, 400, 200, 100, 0, –100, and –200 ms) on the difference scores shown in Fig. 3. Simple effect testing (Fisher's LSD) was used to compare selected conditions in each of the two display types,

and to compare the difference scorers in some conditions against zero (no illusion). Linear trend analysis was used to contrast the trends in RT and PC for the two types of illusions over time.

The main effect of Display was significant for both measures [RT: $F(1,27) = 19.52$, $p < .001$, $MSE = 12,519$; PC: $F(1,27) = 14.40$, $p < .001$, $MSE = .021$], indicating that the illusion was larger in the TI than the RFI condition. SOA was also significant [RT: $F(7,189) = 30.13$, $p < .001$, $MSE = 5,243$; PC: $F(7,189) = 48.79$, $p < .001$, $MSE = .009$], reflecting the generally larger illusion in the intermediate SOAs. Most importantly, the interaction of Display \times SOA was significant [RT: $F(7,189) = 17.23$, $p < .001$, $MSE = 5,243$; PC: $F(7,189) = 21.13$, $p < .001$, $MSE = .009$], indicating that the time course of the illusions differed for each type of display.

This interaction was examined in several ways. Fisher's LSD tests ($\alpha = .05$) comparing the difference scores with zero at each SOA indicated significant illusions in the TI displays at all SOAs from 800 ms to 0 ms, inclusive, in the RT data, and from 400 to 0 ms, inclusive, in the PC data. The data for the –100 and –200 ms SOAs were also significant, but opposite in direction to the illusion. We interpret this, in keeping with previous reports (Durant & Clifford, 2006; Matin, 1974; O'Toole, 1979), as evidence of a backward masking effect. The same statistical tests for the RFI displays indicated a significant effect for both measures only when the inducing context and test flashed simultaneously (0 ms SOA). A direct comparison of the effects of each illusion in the 0 ms SOA showed that the TI display yielded larger effects [RT: $F(1,27) = 15.95$, $p < .001$, $MSE = 15,799$, PC: $F(1,27) = 24.39$, $p < .001$, $MSE = .033$].

Finally, a trend analysis involving the 1600 to 0 ms SOAs showed a significant linear increase in the illusion for the TI that accounted for a vast majority of the systematic variance [90% for RT: $F(1,70) = 127.09$, $p < .001$, $MSE = 7,868$, 83% for PC: $F(1,70) = 29.14$, $p < .001$, $MSE = .030$], and no significant quadratic trends [$F_s < 2.0$]. In comparison, the same analysis for the RFI displays showed a significant quadratic effect (U-shape) over these SOAs [22% for RT: $F(1,65) = 10.45$, $p < .001$, $MSE = 2598$, 61% for PC: $F(1,65) = 25.74$, $p < .001$, $MSE = .005$], and a much reduced linear trend [25% for RT: $F(1,65) = 11.70$, $p < .001$, $MSE = 2598$, 28% for PC: $F(1,65) = 11.99$, $p < .001$, $MSE = .005$].

6.3. Discussion

Flashing the inducing context briefly and asynchronously with the test had very different effects on the time courses of the TI and the RFI. For the TI, flashing the context immediately before the central test led to the expected illusion, growing monotonically

Table 1
Mean response time (RT) and mean proportion correct (PC) in Experiment 1

SOAs	1600	800	400	200	100	0	–100	–200
<i>RT (ms)</i>								
Tilt illusion								
Congruent	608	621	650	731	728	983	655	690
Incongruent	571	552	560	558	570	703	708	721
Rod and frame illusion								
Congruent	504	497	485	465	466	603	521	513
Incongruent	532	491	473	467	495	510	511	511
<i>PC (proportion correct)</i>								
Tilt illusion								
Congruent	.98	.97	.93	.85	.78	.48	.97	.98
Incongruent	.98	.97	.97	.97	.98	.96	.77	.91
Rod and frame illusion								
Congruent	.95	.97	.95	.95	.94	.80	.95	.96
Incongruent	.96	.96	.94	.92	.89	.93	.91	.92

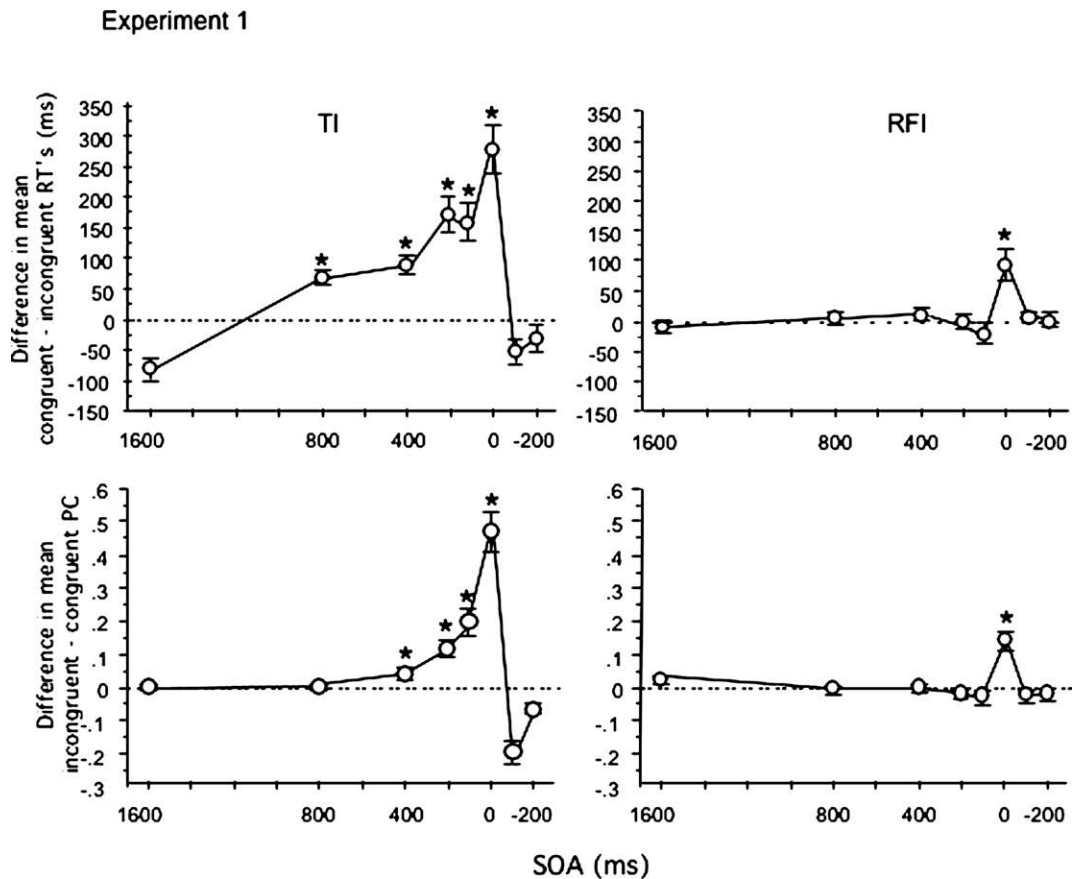


Fig. 3. Experiment 1 when the inducer was visible for 100 ms: Differences in mean congruent–incongruent RTs (top) and incongruent–congruent PC data (bottom) for the TI (left) and the RFI (right). Asterisks indicate a significant difference and error bars indicate ± 1 SEM. SOA = Stimulus Onset Asynchrony.

between 800 and 0 ms. This is consistent with the rapid forward-acting effects others have reported for TI displays (Durant & Clifford, 2006; Matin, 1974; Wolfe, 1984), and with the hypothesis that the TI is the result of local spatial interactions during early stages of processing. The RFI showed no similar rapid-acting effects of this kind. The largest TI, and the only significant RFI occurred with simultaneous presentations of the inducer and test (0 ms SOA). The absence of an illusion with brief asynchronous RFI displays supports our hypothesis that the RFI is manifest in later stages of visual processing than the TI, requiring longer exposures to the inducing frame to affect the speed and accuracy of orientation perception.

In addition to these differences in the illusions observed under asynchronous TI and RFI conditions, the illusion measured in simultaneous RFI displays was smaller than that measured for simultaneous TI displays. This finding is consistent with the literature, in that the RFI is generally smaller in magnitude than the TI (Beh et al., 1971; Gibson & Radner, 1937; Over et al., 1972). Yet, there are at least two different ways to interpret our results. One possibility is that a weaker baseline magnitude of the RFI than the TI hindered a thorough comparison of the two illusions. As such, the expression of the RFI in the asynchronous conditions was masked by the small baseline magnitude of the illusion under these display sizes and distances. However, another possibility is that an important theoretical distinction exists between illusions that occur with simultaneous and asynchronous presentations. For both RFI and TI displays, when the test and the context onset simultaneously they may be processed as part of the same perceptual event, making it more difficult to segment the test from the context. Yet, once the test and context onset asynchronously, the

test is easier to segment from the inducing background, thereby decreasing the influence of the slanted background on the perceived orientation of the test.

In the next experiment, we address these issues by allowing the inducing context to remain in view following its onset. This should result in an effect of the frame in RFI displays at least in longer SOAs if more viewing time is necessary for the global frame to have an effect. Testing the two types of displays with more similar-sized illusions should allow for an easier interpretation of any remaining differences in time course.

7. Experiment 2: Extended presentations of the inducing context

The method was identical to Experiment 1 with the exception that the inducing context remained visible until the end of each trial. Fig. 4 provides a schematic diagram of the time course of a trial for each SOA.

7.1. Results

The mean RT and PC data are shown in Table 2. Fig. 5 shows the difference between congruent and incongruent conditions at each SOA. There were several notable findings. First, as predicted, there was now a significant illusion at the longer SOAs for the RFI. In fact, the illusion was now greater at the longer SOAs (1600 and 800 ms) than at the intermediate SOAs (200 and 100 ms). The TI was weaker overall when the context remained in view, illustrated by comparing the scales of measurement in Figs. 3 and 5, but the RFI remained about the same at its strongest (0 ms SOA). Third, the

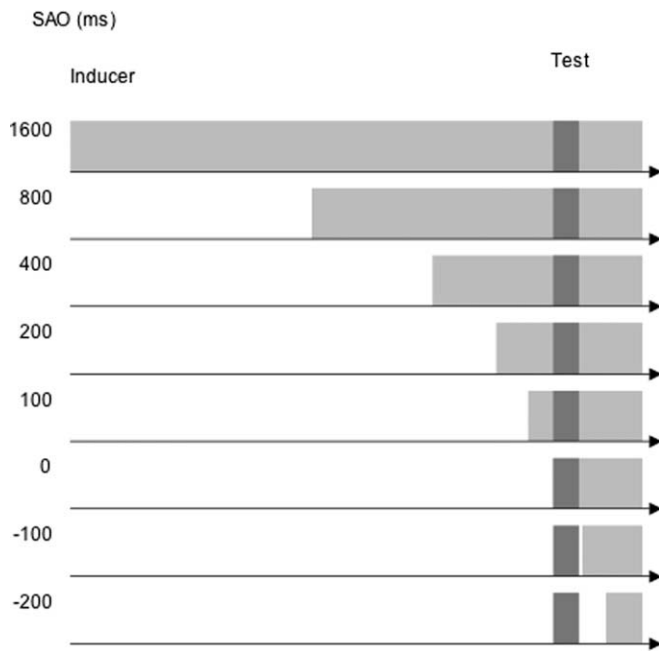


Fig. 4. Schematic diagram of the time course of a trial in Experiment 2 for each Stimulus Onset Asynchrony (SOA) in ms when the inducer was continuously visible until end of the trial.

size of the illusions in the two displays was more comparable in this experiment than in Experiment 1.

These conclusions were supported by mixed analyses of variance (ANOVA) examining the between-participant factor of Display (TI, RFI), and the within-participant factor of SOA (–1600, –800, –400, –200, –100, 0, 100, and 200 ms) on the difference scores shown in Fig. 5. In addition, an overall ANOVA compared Experiments 1 and 2. Fisher's LSD tests were again used to compare selected conditions and linear trend analysis was used to contrast the patterns of the illusions over time.

The main effect of Display was not significant for either measure [RT: $F(1,27) < 1.0$, $p > .10$, $MSE = 15,402$; PC: $F(1,27) = 3.00$, $p > .10$, $MSE = .082$], indicating that the effects of the inducing grating and frame were comparable in size in both conditions. SOA was significant [RT: $F(7,189) = 5.82$, $p < .001$, $MSE = 3,929$; PC: $F(7,189) = 16.98$, $p < .001$, $MSE = .018$], reflecting the generally larger illusion in the intermediate SOAs. Most importantly, the interaction of Display \times SOA was significant [RT: $F(7,189) = 2.85$, $p < .001$, $MSE = 3,929$; PC: $F(7,189) = 4.85$, $p < .001$, $MSE = .018$],

indicating that the time courses of the illusions differed for the two displays.

In addition, the analysis comparing Experiments 1 and 2 revealed a main effect of experiment [RT: $F(1,27) = 9.96$, $p < .01$, $MSE = 19,086$; PC: $F(1,27) = 10.18$, $p < .01$, $MSE = .054$], reflecting the larger illusions in Experiment 1. There was also an Experiment \times Display \times SOA interaction [RT: $F(7,189) = 12.05$, $p < .01$, $MSE = 3,995$; PC: $F(1,27) = 3.85$, $p < .01$, $MSE = .011$], confirming influences of both display type and experiment on the time course of the illusions. In particular, the TI was weaker in Experiment 2 than Experiment 1, whereas the RFI was similar in both experiments.

Fisher's LSD tests ($\alpha = .05$) comparing the difference scores in Fig. 5 with zero at each SOA indicated significant illusions in the TI displays for the 1600 to 0 ms SOAs inclusive in the RT data, and for the 400 to 0 ms SOAs inclusive in the PC data. The TI again showed evidence of backward masking for the –100 and –200 ms SOAs in RT, and in the –100 ms SOA in PC. The same comparisons for RFI displays showed a significant illusion when the inducing context and test onset simultaneously (0 ms SOA), in both RT and PC data, but now showed significant illusions at 1600, 800, and 100 ms.

Trend analysis involving the SOAs from 1600 to 0 ms in the TI displays showed only a significant quadratic trend for RT [55% of systematic variance, $F(1,70) = 3.89$, $p < .05$, $MSE = 6476$], but a significant linear trend for PC [82% of systematic variance, $F(1,70) = 25.14$, $p < .001$, $MSE = .030$] and no significant quadratic trend, $F_s < 1.2$. The same analysis for the RFI displays showed a significant linear trend for RT [30% of systematic variance, $F(1,65) = 4.11$, $p < .05$, $MSE = 2180$] and a significant quadratic trend [62% of systematic variance, $F(1,65) = 8.63$, $p < .05$, $MSE = 2,180$]. Most importantly for a demonstration of differences in the time courses of the two illusions, the quadratic trend in the RFI condition was in the opposite orientation (U-ape) to that in the TI data (inverted U-shape). The PC data in the RFI displays confirmed this pattern, showing significant linear [28% of systematic variance, $F(1,65) = 11.99$, $p < .05$, $MSE = .005$] and quadratic components [61% of systematic variance, $F(1,65) = 25.74$, $p < .01$, $MSE = .005$].

7.2. Discussion

The main finding in Experiment 2 was a moderate RFI when the frame was continuously visible for 800 ms or more in advance of the rod. As in Experiment 1, a comparison of the time course of the two display types revealed quite different effects, with the illusion building along with decreasing duration of the context in ad-

Table 2
Mean response time (RT) and mean proportion correct (PC) in Experiment 2

SOAs	1600	800	400	200	100	0	–100	–200
<i>RT (ms)</i>								
<i>Tilt illusion</i>								
Congruent	697	676	695	677	637	658	580	604
Incongruent	648	608	595	593	600	614	593	607
<i>Rod and frame illusion</i>								
Congruent	574	551	533	532	558	576	530	524
Incongruent	531	515	509	513	507	500	524	540
<i>PC (proportion correct)</i>								
<i>Tilt illusion</i>								
Congruent	.68	.65	.66	.55	.56	.52	.92	.91
Incongruent	.71	.72	.79	.84	.77	.80	.78	.90
<i>Rod and frame illusion</i>								
Congruent	.89	.90	.90	.90	.88	.78	.97	.97
Incongruent	.96	.96	.94	.93	.93.9	.95	.91	.94

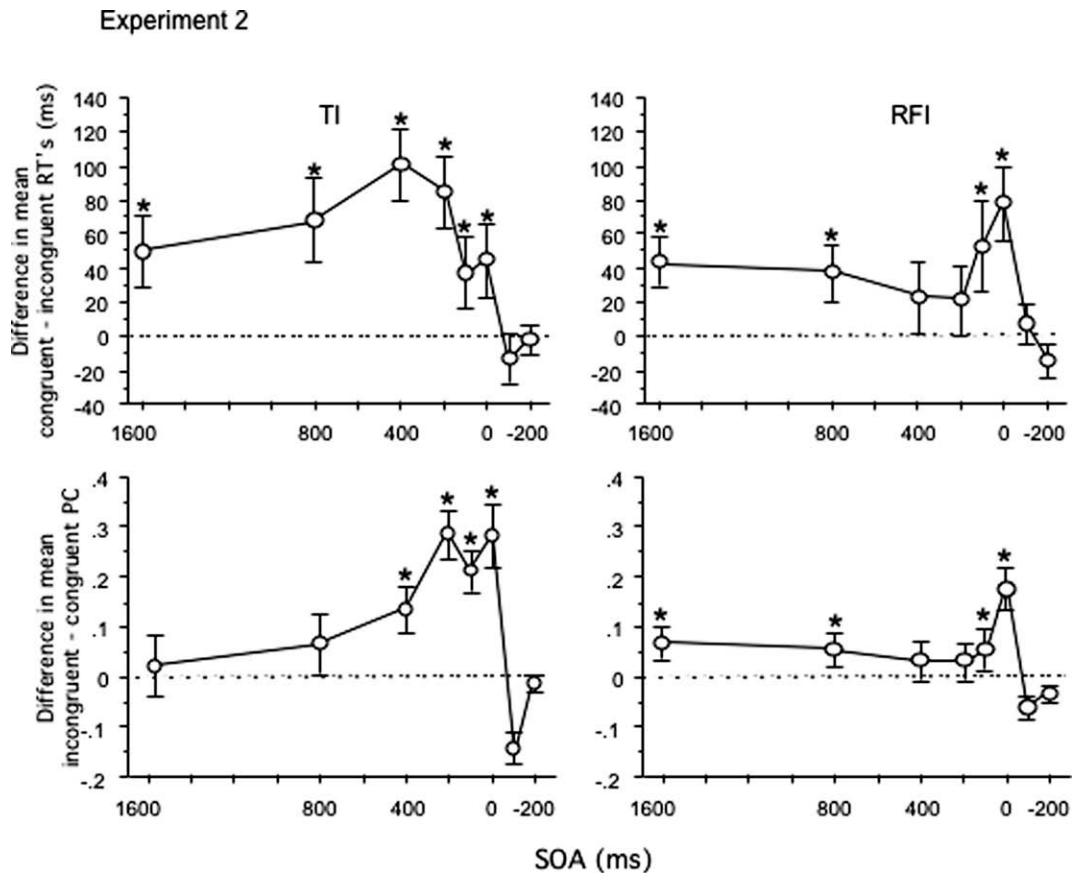


Fig. 5. Experiment 2 when the inducer remained in view until the end of each trial: Differences in mean congruent–incongruent RTs (top) and incongruent–congruent PC data (bottom) for the TI (left) and the RFI (right). Asterisks indicate a significant illusion and error bars indicate ± 1 SEM. SOA = Stimulus Onset Asynchrony.

vance of the test for TI displays, but dissipating in RFI displays when the inducing frame was exposed for less than 400 ms in advance of the test rod. Most importantly, our results are consistent with earlier local context effects in the TI exerting a forward-acting bias on the perceived orientation of the test grating, and a later influence of the more distant frame context in the RFI. In other words, the frame had to remain in view for at least 800 ms before it had sufficient time to bias the perceived orientation of the test rod, whereas the local inducing context in TI displays had a more immediate effect on the time needed to correctly discriminate the orientation of the test. The later effect of the distant frame supports Gibson and Radner's (1937) conclusion that the magnitude of the tilt illusion induced by a large line increases as adaptation time to the inducing line increases.

A second finding of Experiment 2 was that a relatively large illusion occurred again for both display types when the test and context appeared simultaneously. The similarity in the illusions with simultaneous presentations, and the differential time courses of the TI and RFI for asynchronous presentations in Experiments 1 and 2, suggest that different factors may be at work for asynchronous and simultaneous onsets. Specifically, the strong simultaneous illusion for both display types may reflect a perceptual grouping of the test and context that arises from their common onset. When a difference in orientation is the only segmentation cue to parse the test from the inducing background, the largest tilt effects of the inducer occur. When a temporal gap between the inducing context and test provides an additional segmentation cue, the test becomes easier to segregate and the influence of the tilted inducer decreases. These findings confirm previous reports that the TI is largest when the center and surround are presented

as part of the same temporal event, and fades as they are temporally segregated (Durant & Clifford, 2006; Matin, 1974; Wolfe, 1984).

Our results are also in accordance with Durant and Clifford's (2006) findings that when other cues allow for the segmentation of the central test from the surrounding inducer, such as a spatial or temporal gap, orientation is not as influential in discriminating the orientation of the test as when it is the only segmentation cue available in simultaneous displays. If participants perceive the stimulus and context as part of the same new visual event, they will be less able to discriminate the test orientation separately from the orientation context, leaving them vulnerable to the illusion. However, when the test and context are presented asynchronously, some conditions may reduce the perceptual influence of the context, allowing for easier discrimination of the test as a separate item. In the present study, these circumstances include when the test is spatially distinct from the context (RFI displays versus TI displays), when the context is briefly presented (Experiment 1 versus 2), and when the SOA between the context and test does not allow sufficient time for global context effects to occur (RFI at short versus long SOAs).

Finally, the TI was generally stronger with prolonged exposure of the context (Experiment 2) than with only brief presentations (Experiment 1). This is consistent with previous reports that the TI and TAE are maximal when the inducer is continuously visible versus briefly flashed (Harris & Calvert, 1989; Sekular & Littlejohn, 1974; Wolfe, 1984).

We therefore interpret the results of Experiment 2 as support for the hypothesis that local orientation context affects processing earlier than global orientation context.

8. Experiment 3: Magnitude and discriminability

This experiment examined whether our findings with regard to speeded responses and accuracy translated to the perceived magnitude of the two illusions. We therefore varied SOA using more traditional measures of both illusions: PSV and discriminability.

8.1. Methods

Observers attempted to discriminate whether the test stimulus was oriented CW of CCW from vertical as defined by gravity. Six graduate students (3 women and 3 men, aged 23–8) from New York University voluntarily participated, all with normal or corrected-to-normal vision. All aspects of the stimuli, task, temporal sequence of displays, and experimental setup were identical to those in Experiment 2. The key difference in Experiment 3 was that, instead of presenting the test stimulus tilted 8° CW or CW, we used the method of constant stimuli. We randomly varied the orientation of the test on each trial in 2° steps, from 6° in the same direction as the inducing context to 10° in the opposite direction, for a total of 9 test tilts. Each participant completed six blocks of 216 trials for each illusion. TI and RFI displays were tested in separate conditions, and the order of conditions was varied over observers. In each block, the 9 test tilts were randomly presented in two context orientations (–15° CCW and 15° CW), at three SOAs (0, 200, and 1600 ms). As in Experiment 2, the inducing context remained in view until the end of the trial. We tested these three SOAs because they illustrated the main differences in the time courses of the TI and RFI observed in Experiment 2, while allowing us to keep the duration of the experiment under an hour and a half for each participant.

8.2. Results

As in Experiments 1 and 2, the data were collapsed over congruent and incongruent context and test tilts for each subject. For each illusion, the probability of a response that the test was tilted in the same direction as the inducer was computed for each of the 9 rod tilts at each SOA. Participants' averaged responses for each illusion and SOA were fit to 6 separate logistic functions with upper bounds of 1.0 (All R^2 s > .923, all $F(1,7)$ s > 85.34, all ps < .001). The magnitude of each illusion at each SOA was defined by the PSV, or degree of test tilt in the same direction as inducer tilt for which responses were 50% correct. The slope parameter of each logistic function indexed discriminability/uncertainty, with smaller numbers indicating poorer discriminability of test orientation and greater response uncertainty (Table 3).

Overall, the TI was stronger than the RFI, and both illusions tended to be stronger with simultaneous onsets of the test and inducer (0 ms SOA). Within-subjects ANOVAs examining the effects of Display (TI, RFI), and SOA (0, 200, 1600 ms) on the PSV and slope parameters showed a significant effect of illusion type [PSV: $F(1,5) = 157.07$, $p < .001$, $MSE = 131.939$; Slope: $F(1,6) = 17.45$, $p < .01$, $MSE = .021$], with larger effects of the inducing context in TI displays than the frame in RFI. There was no evidence that the illusions differed over time, as neither measure showed a main effect of SOA, or an interaction between display type and SOA (F s < 1).

Fisher's LSD tests ($\alpha = .05$) indicated a larger effect of the inducing context in TI displays on the PSV at the 0 ms SOA compared to the 200 ms SOA, and a larger effect of the frame in RFI displays on the slope parameter at the 0 ms SOA compared to the 1600 ms SOA. Trend analysis of the SOAs from 1600 to 0 ms in each display showed only a significant linear trend for the slope parameter in the RFI displays [55% of systematic variance, $F(1,70) = 3.89$,

Table 3
Experiment 3

SOAs (ms)	1600	200	0
<i>Tilt illusion</i>			
PSV	5.5	5.1	5.9
Slope	0.2	0.2	0.2
<i>Rod and Frame Illusion</i>			
PSV	1.5	1.5	2.0
Slope	0.3	0.3	0.2

The Point of Subjective Vertical (PSV; the degree of test tilt in same direction as the inducer for which participants respond the test is tilted in the same direction as the inducer 50% of the time), and the slope parameter of the respective logarithmic functions (smaller values indicate weaker sensitivity to test orientation).

$p < .05$, $MSE = 6,476$], indicating increased discriminability as the frame was visible for longer in advance of the rod.

8.3. Discussion

The results of Experiment 3 were generally consistent with the results of Experiments 1 and 2. The TI was greater in magnitude than the RFI, and simultaneous onsets of the inducer and test tended to elicit the largest illusions for both TI and RFI displays. Specifically, the effect of the inducer was larger in magnitude and the tilt of the test stimulus was more difficult to discriminate in TI displays than in RFI displays. Furthermore, the magnitude (PSV) of the TI was larger at the 0 ms SOA than the 200 ms SOA, in line with findings that the largest TI occurs when the context and test onset simultaneously (Durant & Clifford, 2006; Matin, 1974; Wolfe, 1984). In RFI displays, the frame affected the discriminability of the rod more at the 0 ms SOA than the 1600 ms SOA, suggesting the largest RFI also occurred with simultaneous onsets. Therefore, the results of Experiment 3 regarding the relative levels of illusion magnitude and discriminability/uncertainty over time support our findings in Experiment 2 that the inducing context in TI displays affected the perceived orientation of the test more rapidly than the frame in RFI displays.

The one main finding of Experiment 2 not replicated in these results was a larger RFI when the frame was continuously visible for 800 ms or more in advance of the rod than when the frame was visible for shorter period. This result in our data distinguishes performance-based measures (RT and PC) from measures of the conscious experience of illusion magnitude (PSV), and suggests it is important for future studies to more carefully delineate implicit (unconscious) and explicit (conscious) aspects of these illusions.

9. General discussion

The main finding of this study is that the TI has a different time course than the RFI. With asynchronous onsets, the local grating in TI displays induced a rapid forward-acting bias, but the more distant frame in RFI displays only had an effect on the perceived orientation of the rod after 800 ms of concurrent sensory support. Early effects of local spatial interactions in the TI are supported by our findings that the inducing grating influenced the time needed to correctly determine the orientation of the test grating, regardless of whether it: a) flashed briefly up to 800 ms before the onset of the test grating (Experiment 1), b) appeared simultaneously with the test grating (Experiments 1 and 2), or c) remained visible up to 400 ms before the test grating (Experiment 2). The involvement of later global context effects in the RFI is supported by our findings that, aside from the simultaneous onset condition, the frame only affected the perceived orientation of the rod when it remained continuously in view for at least 800 ms prior to the onset of the test (Experiment 2). Experiment 3 confirmed that most

of these patterns held for measures of the magnitude of each illusion, as well as associated level of discriminability/response uncertainty. The one exception was there was not an increase in the PSV for RFI displays when the frame was continuously visible for 800 ms or more. This result stresses the need to examine the performance-based implicit measures of tilt illusions, which may be more sensitive than more explicit or conscious reports of the degree to which vertical is misperceived.

The consistently strong illusions at the 0 ms SOA suggest that when the inducer and test appear simultaneously, they are processed as a unitary perceptual event such that the inducing context involuntarily becomes the referent for the perceived orientation of the test. A temporal gap helps to segment the test from the inducing background, decreasing the influence of the inducer on the perceived orientation of the test. This interpretation is consistent with previous findings that the magnitude of the TI is largest when the inducer and test appear simultaneously (Durant & Clifford, 2006; Matin, 1974; Wolfe, 1984). The absence of an illusion for either TI or RFI displays in the negative SOA conditions (both in Experiments 1 and 2) confirms previous reports that a context that onsets after a test has disappeared does not affect the perceived orientation of the test (Durant & Clifford, 2006), even though it may mask or reduce the overall visibility of the test (Matin, 1974). Overall, the present results are consistent with dissociable time courses in the TI and RFI, with later effects of global than local orientation context.

Previously, researchers have proposed that distinct mechanisms underlie local and global tilt effects. Wolfe (1984) first hypothesized that one process adapted for brief durations underlies direct effects but another process adapted for longer durations mediates indirect effects. Although the RFI and TI/TAE indirect effects are not identical, as noted in the introduction, Wenderoth and Johnstone (1989a,b,c,d; 1988b) hypothesized that indirect effects arise from global interactions similar to those involved in the RFI. More specifically, Wenderoth and Johnstone (1988a) and Wenderoth and van der Zwan (1989) proposed that transient neural mechanisms underlie local direct TI/TAE effects and sustained neural mechanisms give rise to global indirect TI/TAE effects. Wenderoth and van der Zwan (1989) speculated that the transient mechanisms are mediated by classic receptive field inhibition between neighboring orientation-selective units in V1, and the sustained global mechanisms are the result of total receptive field responses of populations of orientation-tuned neurons responsible for global, orientation constancy mechanisms. Wenderoth and Johnstone (1988a) point to the slower buildup and later asymptote of indirect effect in support of their proposal that indirect effects arise later in sustained, parvocellular cortical pathways, including their feedback to V1, whereas direct effects involve the transient, and primarily feed-forward magnocellular mechanisms in V1.

However, it is also possible that separate mechanisms are not necessary to explain the main finding that global visual context has a later influence than local context on orientation perception. An alternative interpretation is that local and global tilt effects occur during different temporal stages of processing within the same mechanism, with the local effect occurring early and the global effect occurring later. Further research is needed to determine whether the local, fast acting effects of the TI and the more global, slower effects of the RFI are the consequence of different mechanisms or of distinct temporal stages in processing.

References

- Antonucci, G., Fanzon, D., Spinelli, D., & Zoccolotti, P. (1995). Visual factors affecting the rod-and-frame illusion: Role of gap size and frame components. *Perception*, 24(10), 1119–1130.
- Asch, S. E., & Witkin, H. A. (1948). Studies in space orientation: I. Perception of the upright with displaced visual fields. *Journal of Experimental Psychology*, 38, 325–337.
- Beh, H., Wenderoth, P., & Purcell, A. T. (1971). The angular function of a rod-and-frame illusion. *Perception & Psychophysics*, 9, 353–355.
- Calvert, J. E., & Harris, J. P. (1985). Tilt illusion decreases as presentation time increases. *Perception*, 14(1), A29.
- Calvert, J. E., & Harris, J. P. (1988). Spatial frequency and duration effects on the tilt illusion and orientation acuity. *Vision Research*, 28(9), 1051–1059.
- Cian, C., Raphael, C., & Barraud, P. A. (2001). The role of cognitive factors in the rod-and-frame effect. *Perception*, 30(12), 1427–1438.
- Clifford, C. W. G., & Harris, J. A. (2005). Contextual modulation outside of awareness. *Current Biology*, 15, 574–578.
- DiLorenzo, J. R., & Rock, I. (1982). The rod-and-frame effect as a function of the righting of the frame. *Journal of Experimental Psychology: Human Perception & Performance*, 8(4), 536–546.
- Durant, S., & Clifford, C. W. G. (2006). Dynamics of the influence of segmentation cues on orientation perception. *Vision Research*, 46, 2934–2940.
- Dyde, R. T., & Milner, D. (2002). Two illusions of perceived orientation: One fools all of the people some of the time; the other fools all of the people all of the time. *Experimental Brain Research*, 144, 518–527.
- Enns, J. T., & Rensink, R. (1995). *VScope(tm): Vision testing software for the Macintosh*. Vancouver: Micropsych Software.
- Ebenholtz, S. M. (1977). Determinants of the rod and frame effect: The role of retinal size. *Perception and Psychophysics*, 22(6), 531–538.
- Ebenholtz, S. M., & Callan, J. W. (1980). Modulation of the rod and frame effect: Retinal angle vs apparent size. *Psychological Research*, 42(4), 327–334.
- Ebenholtz, S. M., & Utrie, J. W. Jr. (1982). Inhibition of the rod-and-frame effect of circular contours. *Perception & Psychophysics*, 32(2), 199–200.
- Gibson, J. J., & Radner, M. (1937). Adaptation, after-effect, and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology*, 20, 453–469.
- Harris, J. P., & Calvert, J. E. (1989). Contrast, spatial frequency, and test duration effects on the tilt aftereffect: Implications for underlying mechanisms. *Vision Research*, 29(1), 129–135.
- Li, W., & Matin, L. (2005). Two wrongs make a right: Linear increase of accuracy of visually-guided manual pointing, reaching, and height-matching with increase in hand-to-body distance. *Vision Research*, 45, 533–550.
- Matin, E. (1974). Light adaptation and the dynamics of induced tilt. *Vision Research*, 14, 255–265.
- Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*. London: Oxford University Press.
- O'Toole, B. (1979). Exposure-time and spatial-frequency effects in the tilt illusion. *Perception*, 8(5), 557–564.
- Over, R., Broerse, J., & Crassini, B. (1972). Orientation Illusion and masking in central and peripheral vision. *Journal of Experimental Psychology*, 96(1), 25–31.
- Purves, D., & Howe, C. Q. (2004). The statistics of natural scene geometry predict the perception of angles and line orientation [Abstract]. *Journal of Vision*, 4(8), 40a.
- Sekular, R., & Littlejohn, J. (1974). Tilt aftereffect following very brief exposures. *Vision Research*, 14, 151–152.
- Spinelli, D., Antonucci, G., Daini, R., Fanzon, D., & Zoccolotti, P. (1995). Modulation of the rod-and-frame illusion by additional external stimuli. *Perception*, 24(10), 1105–1118.
- Stoper, A. E., & Cohen, M. M. (1989). Effect of structured visual environments on apparent eye level. *Perception & Psychophysics*, 46(5), 469–475.
- Tollhurst, D. J., & Thompson, P. G. (1975). Orientation illusions and after-effects: Inhibition between channels. *Vision Research*, 15, 967–972.
- Virsu, V., & Taskinen, H. (1975). Central inhibitory interactions in human vision. *Experimental Brain Research*, 23(1), 65–74.
- Wenderoth, P., & Beh, H. (1977). Component analysis of orientation illusions. *Perception*, 6, 57–75.
- Wenderoth, P., & Johnstone, S. (1988a). The differential effects of brief exposures and surrounding contours on direct and indirect tilt illusions. *Perception*, 17, 165–176.
- Wenderoth, P., & Johnstone, S. (1988b). The different mechanisms of the direct and indirect tilt illusions. *Vision Research*, 28, 301–312.
- Wenderoth, P., & Johnstone, S. (1989a). The differential effects of brief exposures and surrounding contours on direct and indirect tilt illusions. *Perception*, 17, 165–176.
- Wenderoth, P., Johnstone, S., & van der Zwan, R. (1989b). Two-dimensional tilt illusions induced by orthogonal plaid patterns: Effects of plaid motion, orientation, spatial separation, and spatial frequency. *Perception*, 18, 25–38.
- Wenderoth, P., & van der Zwan, R. (1989c). The effects of exposure duration and surrounding frames on direct and indirect tilt aftereffects and illusions. *Perception & Psychophysics*, 46(4), 338–344.
- Wenderoth, P., van der Zwan, R., & Johnstone, S. (1989d). Orientation illusions induced by briefly flashed plaids. *Perception*, 18, 715–728.
- Wenderoth, P., van der Zwan, R., & Williams, M. (1993). Direct evidence for competition between local and global mechanisms of two dimensional orientation illusions. *Perception*, 22, 273–286.
- Wolfe, J. (1984). Short test flashes produce large tilt aftereffects. *Vision Research*, 24(12), 1959–1964.
- Zoccolotti, P., Antonucci, G., Daini, R., Martelli, M. L., & Spinelli, D. (1997). Frame-of-reference and hierarchical-organization effects in the rod-and-frame illusion. *Perception*, 26(12), 1485–1494.