

Dynamic tilt illusion induced by continuous contextual orientation alternations

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In the classic tilt illusion, the perceived orientation of a center patch is shifted away from its oriented context. Additionally, a stronger illusion effect is yielded when the center patch is simultaneously rather than asynchronously presented with a constant context for a shorter duration. However, little is known about the temporal characteristic of the tilt illusion in a reverse situation in which a constant center patch is presented throughout while the contexts change. Therefore, we continuously alternated two opposite-oriented contexts and manipulated alternate speeds to examine how the tilt illusion would build up as a function of dynamic contextual alternation. Our results revealed that dynamic alternations between leftward- and rightward-oriented contexts caused a static vertical grating at the center to apparently sway from side to side. More importantly, the apparent sway illusion was modulated by the alternate speed of the oriented contexts (up to 8–10 Hz); the quicker the alternation is, the faster and weaker the apparent sway is. Intriguingly, the temporal characteristic of the “dynamic tilt illusion” suggests that, under a varying environment, the suppressions from temporally adjacent surrounds would be chunked into discrete epochs before affecting our percept.

Introduction

Objects are rarely seen in isolation. The visual perception of an object can be significantly modulated by the context in which it is embedded. Of significant relevance is the direct tilt effect, a well-known illusion with which the presence of an oriented surround stimulus (e.g., 15° tilted from the vertical orientation) biases the perceived orientation of a concurrently presented center patch in the opposite way (Clifford, 2014; Gibson, 1937). Several models have been proposed to explain the tilt illusion (Clifford, 2014; Schwartz, Hsu, & Dayan, 2007). For example, it has been suggested that, due to lateral inhibition, the responses of the orientation-selective neurons whose classical receptive field (CRF) covers the center are more strongly inhibited if their preferred orientation is closer to the surround orientation. In contrast, these orientation-selective neurons are almost unaffected if their preferred orientation is far away from the surround orientation. It manifested as if the hill activity of the neuron population shifted away from the surround orientation.

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The temporal aspect of the tilt illusion has also been investigated for decades to fully elucidate its characteristics. Early psychophysiological studies have shown that a stronger illusion is yielded by shorter exposure of the context and center. Usually, a briefly flashed context and center (10–30 ms) induces the greatest illusionary shift, which gradually decreases to an asymptotic value as the display duration is lengthened to 100–300 ms (Wenderoth & Johnstone, 1988; Wenderoth, Zwan, & Johnstone, 1989; Wolfe, 1984). Moreover, the simultaneous presentation of the oriented context and the center patch at an extremely shorter duration, such that the context is suppressed from awareness, could also result in an observable tilt illusion (Clifford & Harris, 2005; Mareschal & Clifford, 2012).

This strongly manifested and rapidly aroused tilt illusion is supported by data directly recorded from the primary visual cortex of primates and cats. Neuron responses to the CRF stimulus surrounded by an iso-oriented context start to decrease no more than about 20 ms from the onset of the neuron responses to the CRF stimulus only or to the CRF stimulus with a orthogonally oriented context (Bair, Cavanaugh, & Movshon, 2003; Knierim & van Essen, 1992; Müller, Metha, Krauskopf, & Lennie, 2003; Nothdurft, Gallant, & van Essen, 1999; Shimegi et al., 2014, but see Zipser, Lamme, & Schiller, 1996, who reported a slightly longer onset latency at about 80 ms). Consistently, surround suppression, as indicated by the reduction of evoked magnetic responses in the human visual cortex, is also accompanied with a small response delay (Ohtani, Okamura, Yoshida, Toyama, & Ejima, 2002).

The immediate influence on a center patch by its surround, however, does not mean that surround suppression will decay at a comparable speed. Researchers manipulating the temporal separation between the center patch and the oriented context found that, although the tilt illusion decreases as the stimulus onset asynchrony increases, it completely disappears only when the context precedes the center beyond about 300 ms (Corbett, Handy, & Enns, 2009; Durant & Clifford, 2006; Matin, 1974). Further, neurophysiological results support the finding that neurons are suppressed not only during the presentation of the context (Knierim & van Essen, 1992; Lamme, 1995; Zipser et al., 1996), but up to almost 200 ms after its disappearance (Ishikawa, Shimegi, Kida, & Sato, 2010; Shimegi et al., 2014).

The aforementioned temporal properties of the tilt illusion, i.e., immediately evoked but temporally extended, are mainly found when a center patch with a short duration (from tens to hundreds of milliseconds) is accompanied by an unchanged context of the same amount of time. However, in a more natural situation,

the contexts may be flexible to change. This inspires an interesting question about how surround suppression will appear in a situation in which the context changes dynamically but the center remains still for a relatively long duration. Therefore, in the present study, to investigate how dynamic contexts affect a static center, we continuously alternated leftward- and rightward-oriented contexts, and examined whether a vertical grating at the center would be dynamically modulated and would apparently sway back and forth as a pendulum.

Moreover, given that the tilt effect, at any moment, is influenced by a preceding context (Corbett et al., 2009; Durant & Clifford, 2006), it is almost impossible to extract the instantaneous tilt effect at any precise time point when the outside world is changing rapidly. Illusory percept, in this case, probably depends on the surround suppression temporally chunked into distinct epochs as shown in many other research fields. For example, if the alternate speed between successive items exceeds the individual's temporal resolution, temporally adjacent items would be parsed into one epoch and integrated into a unified perception instead of being chunked into separate epochs to trigger flicker perception, apparent motion, etc. (Holcombe, 2009; VanRullen, 2016; VanRullen & Koch, 2003). If the “dynamic tilt illusion” exists, it is expected to be modulated by the alternate speed of the oriented contexts too. Specifically, the illusionary sway would be more apparent when the contexts alternate at a relatively slow speed because the inhibition mechanism would rely on one single context, just like that in the classic tilt illusion. When the alternate speed increases, two or more opposite contextual orientations are more likely to be temporally parsed into a single epoch to modulate the visual perception of the central grating.

General methods

Participants

The study was approved by the institutional review board of the Institute of Psychology, Chinese Academy of Sciences, and it adhered to the tenets of the Declaration of Helsinki. In total, 44 participants with normal or corrected-to-normal vision were recruited and paid for their participation. All provided informed consent before formal experiments. Sixteen participants completed Experiment 1 with half of them assigned to the red/green surround condition (four males; mean age = 22.6, $SD = 1.6$ years) and the other half assigned to the gray surround condition (four males; mean age = 21.6, $SD = 2.2$ years). Both Experiments 2 and 3 included 10 participants (Experiment 2: four males;

mean age = 22.2, $SD = 2.3$ years; Experiment 3: four males; mean age = 23.4, $SD = 2.1$ years). Experiment 4 included eight participants (four males; mean age = 23.3, $SD = 3.4$ years).

Stimuli and apparatus

All experiments were conducted in a dim, sound-attenuated room. Participants sat comfortably at a viewing distance of 57 cm from the monitor. Stimulus gratings were generated by Matlab and presented using Psychtoolbox. The luminance of the red, green, and gray was corrected for the CRT monitor with a resolution of 1280×1024 pixels at a refresh rate of 60 Hz. Both the oriented context and center patch were sinusoidal gratings, which had a spatial frequency of 1 $c/^\circ$, and they were presented on a black background with a luminance of 0.22 cd/m^2 .

In our experiments, the oriented contexts were red, green, or gray, and they were drawn in an annulus with inner and outer diameters of 3° and 15° , respectively (Figure 1a, b, c, and d). The orientation of the contexts was alternated at different frequencies between 15° clockwise and 15° counterclockwise tilts with respect to the vertical orientation. During each presentation, the two opposite-oriented contexts were modulated by continuously varying the maximal RGBs of the sinusoidal gratings to match a sinusoidal luminance change of between 0.37 and 8.59 cd/m^2 (Figure 1e; except for the gray surround in Experiments 1 and 4, the minimum luminance equaled that of the background). For example, the clockwise-oriented context grew bright and dark according to a sinusoidal function of specific frequency while the counterclockwise-oriented context was held constant in a dim lightness (see demo, 1 Hz). The test gratings constantly presented at the center with a maximal luminance of 6.14 cd/m^2 were always gray and vertical.

Each presentation lasted for 10 s to ensure that the opposite-oriented contexts alternated at least 10 times in a usual case. However, for alternations at slow frequency (<1 Hz), presentation duration was correspondingly lengthened to include 10 alternations.

Task and design

In general, the opposite-oriented contexts were alternately presented in each trial, and participants were told to judge whether they saw the central grating apparently and continuously swaying from side to side by pressing the up arrow button and if not by pressing the down arrow button in all experiments. The judgments could be made whenever they were sure about their perception during the presentation, and if

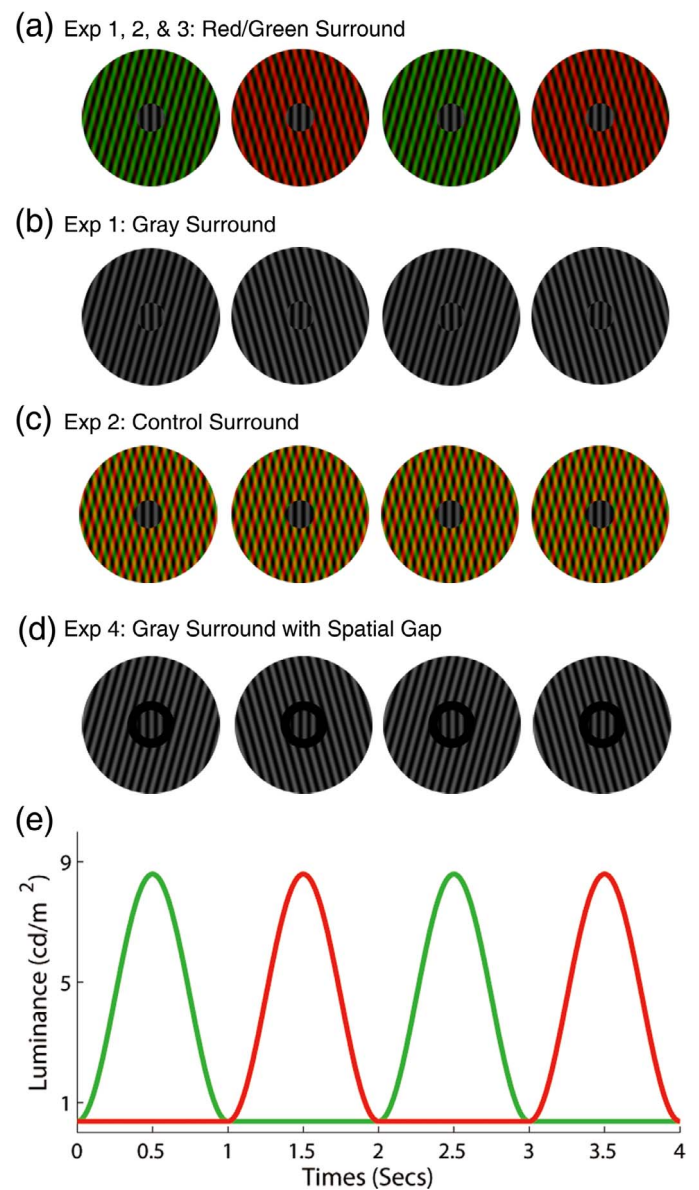


Figure 1. Examples of stimuli and representative luminance changes over time. Panels a through d show the peak luminance of the surround gratings during the alternations for different experiments and conditions, respectively. The spatial gap between the surround and center in panel d was 1° . The temporal function (1 Hz, for example) that controlled the luminance of the surround gratings has been presented in panel e.

no judgments were made until the end of the presentation, we required them to register a quick guess. Participants were reminded to respond according to their real percepts rather than inferences, and they were not informed about how many “sway” percepts would be judged. If participants felt that they saw the apparent sway, they were asked to further compare the relative angles of the apparent sway. In other words, they had to indicate whether the angle of the sway in

the current presentation was relatively small or large on a four-point scale based on all the apparent sways they had seen before (buttons A, S, D, and F, from smallest to largest).

Experiment 1 tested whether the alternation of the opposite-oriented contexts would cause an apparent sway of the central vertical grating and, if so, whether the increase of the alternate speed/frequency would deteriorate the dynamic tilt illusion. Two types of surround and multiple alternate frequencies were used. For the red/green surround (Figure 1a), seven alternate frequencies were used: 0.6, 0.9, 1.5, 2.4, 4.0, 6.0, and 10.0 Hz, and each level was repeated 30 times, mixed trial-by-trial in seven blocks. For the gray surround (Figure 1b), 0.90, 2.4, and 6.0 Hz were adopted with each repeated 30 times in three blocks.

Experiment 2 added a control condition to examine whether the dynamic tilt illusion is a true perceptual illusion rather than a response prompted by the experimenter. For the control condition, the opposite-oriented contexts were both luminance-modulated at the same frequency with identical phases (Figure 1c). That said, in contrast to the experimental condition, the clockwise- and counterclockwise-oriented contexts always grew bright and dark simultaneously in the control condition (see demo, 1 Hz control), such that the surround would be seen as a colorful plaid rather than two individual gratings with opposite orientations, thus no longer favoring either orientation. Each cell of the three (alternate frequency: 1.0, 3.0, and 8.57 Hz) by two (condition: experimental and control) design was repeated 20 times, mixed across four blocks.

Experiment 3 was designed to further confirm and precisely measure this dynamic tilt illusion. In Experiment 3, when participants were sure about the percepts of the apparent sway, they were required to modulate a real sway of a central grating to match the apparent sway they just saw instead of judging its magnitude on a scale. We created a real sway by gradually changing the clockwise and counterclockwise angles of the central grating according to a sinusoidal function so that the speed as well as the clockwise and counterclockwise angles of the real sway can be modulated. Once certain about their current judgment, participants pressed the space bar to continue. They were previously trained to acquaint with this task in case too much time was spent; otherwise, their memory trace of the apparent sway would gradually decay. Four alternate frequencies of 0.8, 1.6, 2.4, and 3.2 Hz were tested because they produced acceptable proportions of the apparent sway reports to measure (see Results). Each manual modulation was repeated 20 times in four blocks.

Experiment 4 tested whether the dynamic tilt illusion is reduced by introducing a spatial gap between the surround and center, consistent with that found in the

tilt illusion. The scenarios and procedures were identical to the gray surrounds of Experiment 1 except that a gap was inserted between the surround and center at 0° , 0.5° , or 1° (e.g., Figure 1d, Demo_1 Hz_GraySpatialGap1degree). The alternate frequency of the oriented surrounds was set to 1 Hz, which was proved very effective in causing the apparent sway (see Results). Each spatial gap was tested 20 times, and the 60 trials were randomly separated into two blocks.

General statistics

In Experiments 1, 2, and 4, we calculated the proportion and magnitude of the apparent sway reported by the participants. The proportion was measured as the probability of pressing the up arrow button. The magnitude at each alternate frequency and condition was measured as follows: first, the press of the down arrow button was thought as an index of no perceived sway and was scored zero; second, if the up arrow button was pressed, the A to F buttons were assigned scores of one to four, respectively, to represent the magnitude (assumed linear); finally, the mean score across trials was computed as the magnitude of the apparent sway.

In Experiment 3, the proportion was calculated as mentioned above. However, the magnitude was computed by dividing the modulated angle of sway by two, the same measurement as the tilt illusion (Clifford & Harris, 2005; Patten & Clifford, 2015). In addition, another index, i.e., the speed of the apparent sway, was calculated. We used the motion of a pendulum (simulated by a sinusoidal function) to simulate the sway of the central grating. The frequency of the pendulum represented the frequency of the apparent sway. Theoretically, it is half of the alternate frequency because the alternation from clockwise- to counterclockwise-oriented contexts induces a complete sway from left to right.

Results

Without particular mention, all the F values from repeated measures ANOVAs were Greenhouse–Geisser corrected, and all the p values from multiple comparisons were Bonferroni corrected to control the family-wise error rate.

Experiment 1

Results have been presented in Figure 2. For the red/green surround, the repeated measures ANOVAs with

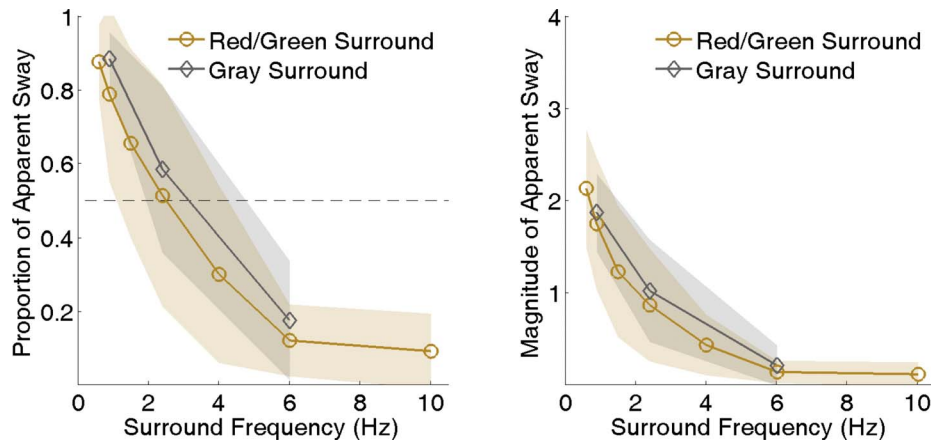


Figure 2. The proportion and magnitude of the apparent sway in Experiment 1. The left and right panels plot the proportion and magnitude of the apparent sway, respectively. The shaded areas indicate the 95% confidence intervals. The dotted line in the left panel represents the proportion of 50% to perceive the apparent sway.

the proportion and magnitude of the apparent sway as dependent variables revealed significant effects of alternate frequency, $F(6, 42) = 27.675, p < 0.001, \eta^2 = 0.798$; $F(6, 42) = 25.767, p < 0.001, \eta^2 = 0.786$, respectively. For the proportion of the perceived dynamic tilt illusion, the post hoc t tests showed that the 0.6-, 0.9-, and 1.5-Hz alternations induced significantly more reports of the apparent sway than at the 6.0- and 10.0-Hz alternations did ($ts > 5, ps < 0.03$), and more apparent sway was perceived at the 0.6-Hz than at the 4.0-Hz alternation, $t(7) = 6.575, p = 0.007$. For the perceptual magnitude of the dynamic tilt illusion, participants judged the swaying angles from left to right as significantly larger at the 0.6-Hz alternation than those at the 2.4-, 4.0-, 6.0-, and 10.0-Hz alternations were ($ts > 5.9, ps < 0.02$) and near significantly larger than that at the 1.5-Hz alternation was, $t(7) = 4.597, p = 0.052$. The angles of the apparent sway at the 0.9-Hz alternation was also significantly larger than those at the 4.0-, 6.0-, and 10.0-Hz alternations were ($ts > 4.7, ps < 0.05$) and near significantly larger than that at the 2.4-Hz alternation was, $t(7) = 4.512, p = 0.058$.

Similar results were obtained for the gray surround. The proportion and magnitude of the apparent sway significantly decreased as the opposite-oriented contexts alternated faster, $F(2, 14) = 23.098, p < 0.001, \eta^2 = 0.767$; $F(2, 14) = 16.049, p < 0.001, \eta^2 = 0.696$. Specifically, the likelihood of the apparent sway measured at the 0.9-, 2.4-, and 6.0-Hz alternations significantly differed from each other ($ts > 3.1, ps < 0.05$), and the magnitude of the apparent sway at the 0.9- and 2.4-Hz alternations was significantly larger as compared with that at the 6.0-Hz alternation ($ts > 3.2, ps < 0.05$).

Furthermore, we tested whether the proportion of the apparent sway at each alternate frequency significantly differed from 50% chance level. Irrespective of

the surround types, significantly more apparent sway was perceived than 50% at the slow frequencies (green/red surround: 0.6 Hz, $t(7) = 8.706, p = 0.0004$; gray surround: 0.9 Hz, $t(7) = 12.689, p < 0.0001$) whereas much less apparent sway was perceived than 50% at the fast frequencies (green/red surround: 6 and 10 Hz, $ts < -9.1, ps < 0.001$; gray surround: 6 Hz, $t(7) = -4.754, p = 0.006$).

As hypothesized, the continuous alternation of opposite-oriented contexts generated a dynamic tilt illusion in which the central grating was perceived as alternately swaying back and forth. Further, this illusion was modulated by the alternate speed of the contexts. Slow speed corresponded to a larger sway magnitude. Moreover, the robust apparent sway was observed in Experiment 1 regardless of the hue of the contexts.

It is necessary, however, to prove that this dynamic illusion was exclusively based on the direct tilt illusion rather than experimenter's expectation given that Experiment 1 provided no quantitative measure about the relationship between the orientation of the apparent sway and the contexts. Fortunately, in the postexperiment inquiry about participants' subjective experience, four out of eight participants in the red/green surround and six of eight in the gray surround noticed that the central grating apparently swayed in an opposite direction against the contextual orientation while the other participants reported that they paid no attention to this relationship. Although the experimental parameters and participant's subjective experience convergently indicate that the dynamic alternation between the clockwise and counterclockwise surrounds caused the apparent sway of the central grating, we carried out Experiment 2, in which a control condition incapable of inducing any tilt illusion (Figure 1c) was brought in to directly compare the apparent sway between the experimental and control conditions.

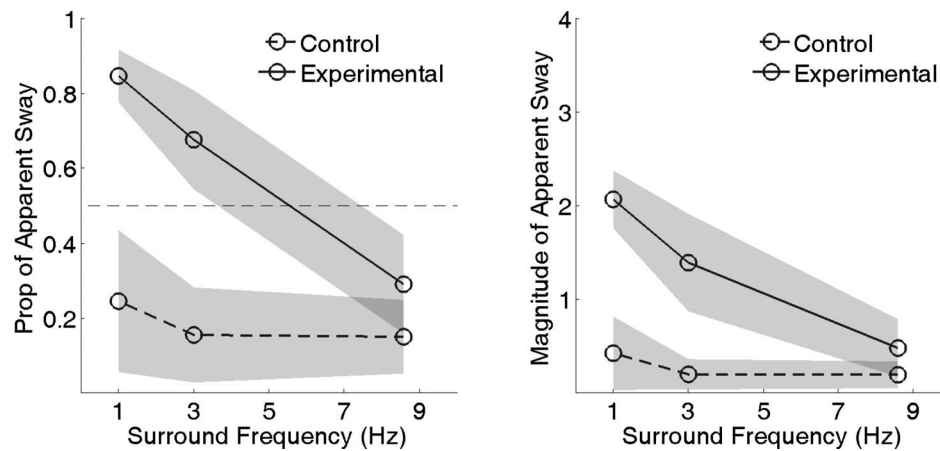


Figure 3. The proportion and magnitude of the apparent sway in Experiment 2. The left and right panels plot the proportion and magnitude of the apparent sway in the control and experimental conditions, respectively. The dotted line in the left panel represents the proportion of 50% to perceive the apparent sway. The shaded areas indicate the 95% confidence intervals.

Experiment 2

The proportion and magnitude of the apparent sway for the experimental and control conditions have been presented in Figure 3. A repeated measures ANOVA with condition (experimental vs. control) and alternate frequency as independent variables and proportion as a dependent variable revealed that the main effects of condition and alternate frequency were both significant, $F(1, 9) = 73.690$, $p < 0.001$, $\eta^2 = 0.891$; $F(2, 18) = 16.383$, $p < 0.001$, $\eta^2 = 0.645$, respectively. More importantly, the interaction was also significant, $F(2, 18) = 16.761$, $p < 0.001$, $\eta^2 = 0.651$. Next, independent ANOVAs were carried out for each condition, and results showed that, only in the experimental condition, the proportion significantly varied as a function of the alternate frequency, $F(2, 18) = 30.144$, $p < 0.001$, $\eta^2 = 0.770$, and this was not true for the control condition, $F(2, 18) = 1.198$, $p = 0.325$, $\eta^2 = 0.117$. Therefore, post hoc t tests were only conducted for the experimental condition. The proportion of the apparent sway was significantly larger at the 1.5- and 3.0-Hz alternations than it was at the 8.57-Hz alternation ($ts > 4$, $ps < 0.01$) with a marginal significance between 1.5 Hz and 3.0 Hz, $t(9) = 2.803$, $p = 0.062$. For the experimental condition, significantly more apparent sway was perceived than 50% at the 1.5- and 3.0-Hz alternations, $ts \geq 3.000$, $p < 0.05$, while much less apparent sway was perceived than 50% at the fast frequency, $t(9) = -3.613$, $p = 0.017$, consistent with the observations in Experiment 1. However, for the control condition, significantly less apparent sway was perceived than 50% at all the alternation frequencies ($ts < -3.0$, $ps < 0.05$).

A similar pattern was found for the magnitude. The two main effects and the interaction were all significant: condition, $F(1, 9) = 67.046$, $p < 0.001$, $\eta^2 = 0.882$;

alternate frequency, $F(2, 18) = 16.252$, $p < 0.001$, $\eta^2 = 0.644$; interaction, $F(2, 18) = 14.356$, $p < 0.001$, $\eta^2 = 0.615$. The significant interaction was also attributed to the significant effect of alternate frequency in the experimental condition, $F(2, 18) = 19.902$, $p < 0.001$, $\eta^2 = 0.689$, but not in the control condition, $F(2, 18) = 1.702$, $p = 0.224$, $\eta^2 = 0.159$. For the experimental condition, the 1.5- and 3.0-Hz alternations generated a greater magnitude of the apparent sway than that at the 8.57-Hz alternation was ($ts > 3$, $ps < 0.05$), and the difference between 1.5 Hz and 3.0 Hz was marginally significant, $t(9) = 2.624$, $p = 0.083$.

The results of Experiment 2 further confirmed that slower alternate frequency instigated and amplified apparent sway, and more importantly, this apparent sway can rarely be perceived when the surround, composed by interweaved clockwise and counter-clockwise orientations, alternates. Therefore, the perceived apparent sway caused by the alternation of opposite-oriented contexts indicates a dynamic illusion on the basis of the direct tilt effect. However, this dynamic tilt illusion was only measured by subjective reports until now. Therefore, we required participants to manually alter a truly swaying grating to match the dynamic tilt illusion in Experiment 3. This design allowed us to precisely measure the perceived angles and alternate speed of the apparent sway concurrently in order to compare with the classic tilt illusion.

Experiment 3

Four alternate frequencies lower than 4 Hz were used in Experiment 3 to ensure there were enough reports of the apparent sway because, only in this case, the participants could be asked to match the truly

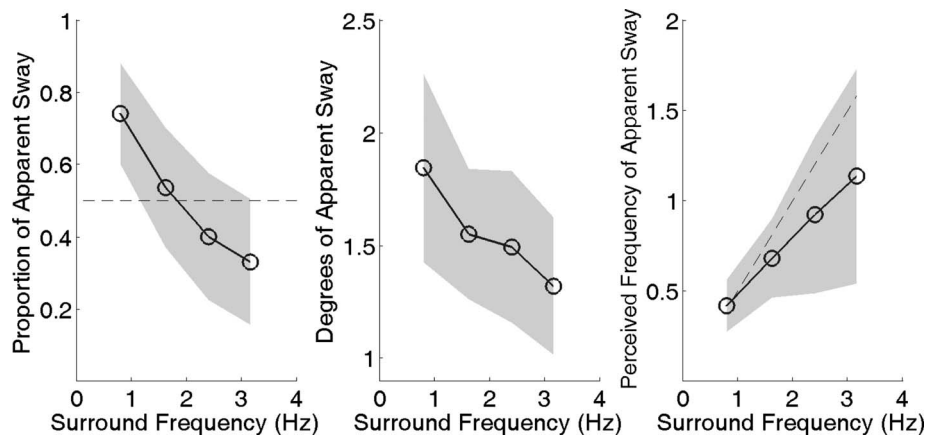


Figure 4. The proportions, modulated angles, and frequencies of the apparent sway in Experiment 3. The dotted lines in the leftmost and rightmost panels represent the proportion of 50% to perceive the apparent sway and the assumed frequency of the apparent sway (half of the alternate frequency), respectively. The shaded areas indicate the 95% confidence intervals.

swaying grating. As illustrated in Figure 4, the influence of the alternate frequency on the reported proportions, modulated angles, and frequencies of the dynamic tilt illusion were all evaluated as significant: for proportion, $F(3, 27) = 10.069$, $p < 0.001$, $\eta^2 = 0.528$; for modulated angles, $F(3, 27) = 3.729$, $p = 0.023$, $\eta^2 = 0.293$; for modulated frequencies, $F(3, 27) = 8.936$, $p = 0.012$, $\eta^2 = 0.498$. The proportions of the apparent sway at the 0.8- and 1.6-Hz alternations were significantly larger than that at the 3.2-Hz alternation was ($ts > 3$, $ps < 0.05$), and the proportion of the apparent sway at the 0.8-Hz alternation was significantly larger than that at the 2.4-Hz alternation was, $t(9) = 3.509$, $p = 0.04$. The swaying angle modulated at the 0.8-Hz alternation was significantly larger than those at the other three alternate frequencies were, $t(9) = 2.27$ – 2.72 , $p = 0.024$ – 0.049 , uncorrected. The swaying frequency modulated at the 0.8-Hz alternation was significantly slower than that at the 1.6-Hz alternation was, $t(9) = -4.171$, $p = 0.014$, and near significantly slower than those at the other two alternate frequencies were ($ts < -3.2$, $ps < 0.06$).

The significance of magnitude here did not pass multiple comparison correction, partially because there were a relatively smaller amount of trials for manual adjustment when the alternation went faster rather than slower due to limited experiment time. Nevertheless, the significant effects obtained from the ANOVAs suggest that our results in Experiment 3 are reliable.

The results of Experiment 3 were quite similar to those of Experiments 1 and 2. Furthermore, the swaying angles modulated (1.32° – 1.84°) resemble those frequently reported about the direct tilt illusion (Clifford, 2014), which supports the finding that the apparent sway is based on the direct tilt illusion. Interestingly, the swaying frequencies modulated did not equal to the assumed frequencies, i.e., half the

alternate frequencies, but were numerically (although not statistically significant) lower than the assumed ones were as the alternate frequency increased (Figure 4 rightmost panel). This finding suggests that the apparent sway may not be a precise reflection of the surround suppression.

Finally, if the dynamic tilt illusion is indeed a temporally extended format of the classic tilt illusion, it ought to be reduced by introducing a spatial gap between the surround and the center, like what is found in the tilt illusion (Durant & Clifford, 2006). Experiment 4 examined this hypothesis.

Experiment 4

As expected, the proportion and magnitude of the apparent sway changed as a function of the spatial gaps between the center and surround (Figure 5). A repeated measures ANOVA with spatial gap (0° , 0.5° , and 1°) as independent variables and proportion as the dependent variable revealed a quite significant effect, $F(2, 14) = 22.107$, $p < 0.001$, $\eta^2 = 0.760$, with post hoc t tests showing that the proportion of the apparent sway was significantly larger when there was no spatial gap than when there were 0.5° and 1° spatial gaps ($ts > 4$, $ps < 0.01$). The same was true for the magnitude, $F(2, 14) = 32.382$, $p < 0.001$, $\eta^2 = 0.822$. The alternation without a spatial gap generated a significantly greater magnitude of the apparent sway as compared with those with spatial gaps ($ts > 5$, $ps < 0.01$) while the alternation with a 0.5° spatial gap showed a marginally significant effect than that with a 1° spatial gap, $t(7) = 2.762$, $p = 0.084$.

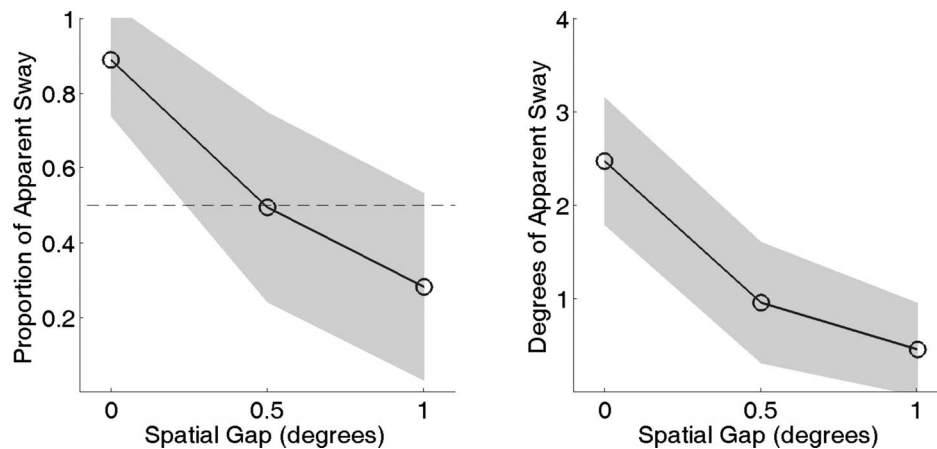


Figure 5. The proportion and magnitude of the apparent sway in Experiment 4. The shaded areas indicate the 95% confidence intervals of judgments. The dotted line in the left panel represents the proportion of 50% to perceive the apparent sway.

Discussion

As hypothesized, Experiments 1–4 consistently revealed that continuous dynamic alternations of two opposite-oriented contexts made the center patch sway apparently. This so-called dynamic tilt illusion based on the classic tilt illusion correlated with the alternate speed of the oriented contexts. It became weaker but faster when the contexts alternated at a higher speed.

Potential mechanistic models have been proposed to explain the tilt illusion (Clifford, 2014; Schwartz et al., 2007). Specifically, the neurons with their preferred orientation closer to the surround orientation are inhibited more than those far away from the surround orientation are (red/green curves in Figure 6). The population responses then have their peak activity shift away from the surround orientation (solid gray curves in Figure 6). To further explain the alternate speed modulation of the dynamic tilt illusion, a discrete temporal parsing mechanism was added to the classical model. The temporal parsing, an extreme form of rhythmic sampling, temporally structures events into discrete epochs within which separate events would be integrated as a unit (Holcombe, 2009; VanRullen, 2016; VanRullen & Koch, 2003).

For the dynamic tilt illusion, it is probable that continuous suppressive responses would be temporally chunked into distinct epochs to bias the preferred orientation of the neuron population (Figure 6). Specifically, when the contexts are slowly alternated, their orientations are more likely to be the same within one epoch. Greater suppressive responses after temporal parsing would therefore bias toward either the clockwise or counterclockwise orientation. Continuous update of the suppressed orientation of the neuron population would phenomenally result in a percept of apparent sway. However, when the contexts are

alternated faster, suppressive responses from the clockwise and counterclockwise surround orientations interweave within one epoch, which may cancel out each other such that the orientation tuning function of the neuron population would shift to neither side.

Although the dynamic tilt illusion examined here may be well explained by temporal parsing of the continuous surround suppressions, one may argue that the tiny illusion at the faster alternate speed simply occurred because the alternate cycle of the contexts was too short (e.g., 100 ms at 10 Hz) to evoke a tilt effect at that moment. However, this argument can be rebutted as previous studies have repetitively shown that a much shorter flashed context (e.g., 30 ms) than that used in the present study can induce a robust tilt effect (Calvert & Harris, 1988; Clifford & Harris, 2005; Mareschal & Clifford, 2012; Wenderoth & Johnstone, 1988; Wenderoth et al., 1989). Another line of evidence comes from neurophysiological studies, as reviewed in the Introduction, which reported that suppressive neuron responses with little latency have been directly recorded from the primary visual cortex (Bair et al., 2003; Knierim & van Essen, 1992; Müller et al., 2003; Nothdurft et al., 1999; Ohtani et al., 2002). Moreover, some individual participants in our experiments indeed perceived sporadic apparent sway at fast alternate frequencies.

Suppose temporal parsing provides the frame to explain the speed modulation of the dynamic tilt illusion; then how long should the chunked epoch be? Although this is still open to answers, some implications can be derived from the present and previous findings. First, as seen from Experiment 1 of the present study, the proportion of apparent sway approached its minimum value at about 6 Hz, suggesting that the dynamic tilt illusion almost disappears when a complete alternation between

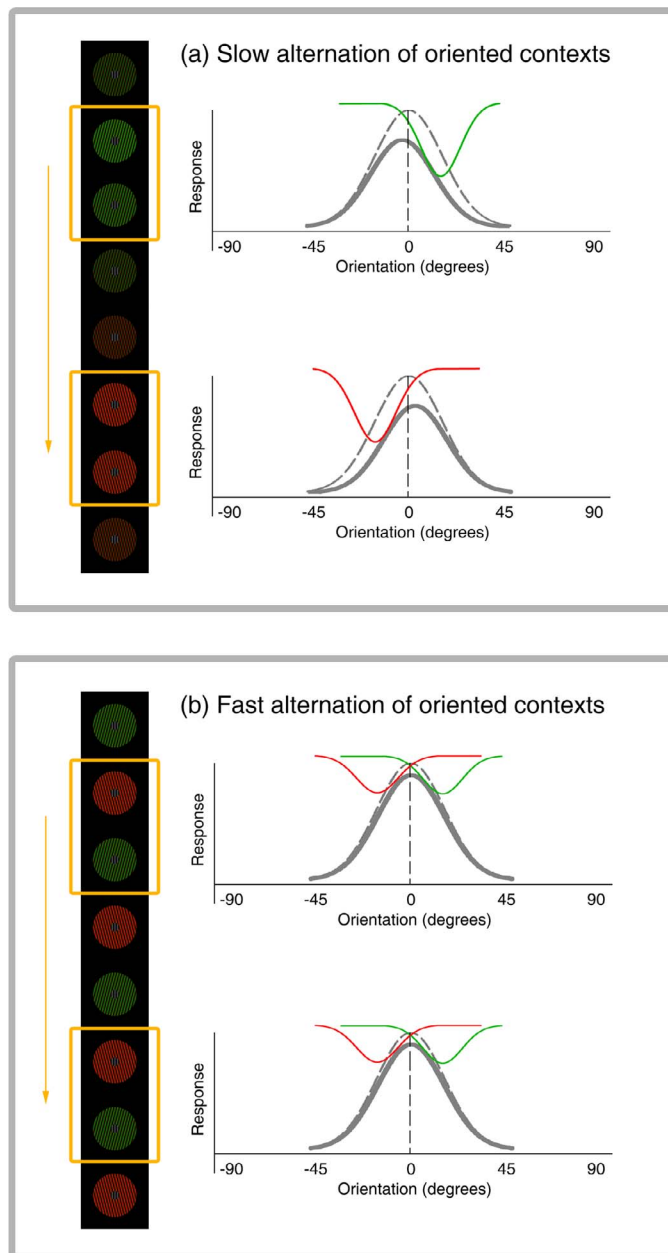


Figure 6. Temporal parsing mechanism of the dynamic tilt illusion. Predictions for the (a) slow and (b) fast alternation of contexts have been illustrated. The time course of oriented context changes is depicted in the leftmost section. The orange frames represent the epochs into which surround suppression was temporally chunked. The right panels are a simplified demonstration of how responses of the neuron population tuning to the center orientation of the vertical are modified by the surround orientation outlined in the orange frame. The green and red curves represent the lateral inhibition tuned to the surround of clockwise and counterclockwise 15° orientation, respectively. The orientation tuning function of the population unaffected by surround has been illustrated by dashed gray curves, and the repulsive shift of the orientation tuning function has been presented in solid gray. Importantly, the suppression is →

opposite-oriented contexts is encapsulated into an epoch of about 300 ms (e.g., Figure 6b). This result is consistent with the temporal properties of brightness and color induction, which showed that the brightness changes induced by a flickering surround occur only at low temporal frequencies (below about 2.5–3 Hz; De Valois, Webster, De Valois, & Lingelbach, 1986). Second, in addition to the magnitude, the experienced speed of the apparent sway was modulated by the alternate speed of contexts, and it was slower than that assumed in Experiment 3. This implies that the temporal parsing mechanism is of a coarse temporal resolution (lower than 4 Hz) because only an alternate speed below such resolution can be decoded. Last, although the tilt illusion declines, it could still persist when the center test is delayed 200–400 ms from the context (Corbett et al., 2009; Durant & Clifford, 2006), which means that nearly all the suppressions from one context occur in an epoch of about 300 ms, marked by their onset. However, it is important to note that the chunked epoch by temporal parsing may be more plastic than a fixed 300 ms to better fit the cognitive requirements under varying environments (VanRullen, 2016).

In summary, the current study demonstrated another version of the direct tilt illusion, called dynamic tilt illusion. That is, under continuous dynamic alternation of two opposite-oriented contexts, a center static patch seems to apparently sway like a pendulum. The magnitude and speed of this apparent sway is modulated by the alternate speed of the oriented contexts. This dynamic tilt illusion probably reflects some temporal parsing of surround suppression at a coarse resolution in our primary visual cortex.

Keywords: tilt illusion, surround suppression, temporal parsing, dynamic alternations

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← determined by all the surrounds chunked into the orange frame. As predicted, the slow alternation of contexts causes the classic tilt illusion as more coherent oriented surrounds might converge within one chunked epoch, and the continuous update of the tilt illusion along successive epochs generates the dynamic tilt illusion.

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