Awareness is the key to attraction: dissociating the tilt illusions via conscious perception

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Abstract

The tilt illusion is a compelling example of contextual influence exerted by an oriented surround on a target's perceived orientation. A vertical target appears to be tilted away from a 15° oriented surround but appears to be tilted towards a 75° tilted surround.

We tested the claim that these biases result from distinct sensory processes: a low-level repulsive process and a higher-level attractive process. If this claim were correct, then surround visibility would be a requirement for attraction, but it would not necessarily be a requirement for repulsion. Indeed, Motoyoshi and Hayakawa (2010) have already demonstrated that repulsion can survive removal of the surround from phenomenal awareness using adaptation-induced blindness.

Here we sought to test this prediction by measuring the orientation biases in a parafoveally presented Gabor patch surrounded by tilted gratings after 20s adaptation. The adapting stimulus was an annularly windowed plaid composed of a vertical and horizontal jittering gratings. Observers were instructed to maintain

fixation throughout the trial and report whether the Gabor appeared to be tilted clockwise or anticlockwise of vertical. They also had to indicate whether the surround was visible after adaptation. Post-adaptation biases were then compared to those obtained in a control experiment without dynamic adaptation.

We found large repulsive biases induced by 15° oriented surrounds, but no attractive biases were induced by 75° tilted surrounds. This result shows that attractive effects do require visual awareness, and thereby provides robust evidence for the existence of two separate mechanisms mediating the phenomenology of the tilt illusions.

Keywords

Tilt illusion, visual awareness, adaptation, contextual interactions.

Introduction

The Tilt illusion (Figure 1a) is a well-known phenomenon of simultaneous orientation contrast where the orientation of a line is misperceived when presented within a tilted surround. Gibson and Radner (1937) first noticed that a slightly tilted line “appears progressively less tilted during the course of perception” positing a shift of the “visual reference axes” towards the line’s orientation. A similar explanation is possible for the tilt illusion (Gibson, 1933). In this case, the titled surround (the inducer) attracts whichever subjective reference axis (either horizontal or vertical) is closest. This “normalization” will decrease the surround’s apparent tilt, but it may increase the apparent tilt of the target it surrounds. When the surround has a relatively small tilt (e.g. 15°) away from vertical, a vertical target will appear to have a tilt in the opposite direction. This repulsion is known as the direct effect. When the surround has a relatively large tilt (e.g. 75°) away from vertical, a vertical target will appear to have a tilt in the same direction. This attraction is known as the indirect effect. However, without ad hoc modification, Gibson's normalization theory cannot account for the fact that the indirect effect is weaker than its direct counterpart (Figure 1b).

Blakemore, Carpenter, and Georgeson (1970) proposed an alternative explanation of the direct effect based on lateral inhibition between neurons selective for similar orientation. If both this model and Gibson's were correct, then the direct effect should be larger because it reflects the sum of two processes. The indirect effect reflects only normalization.

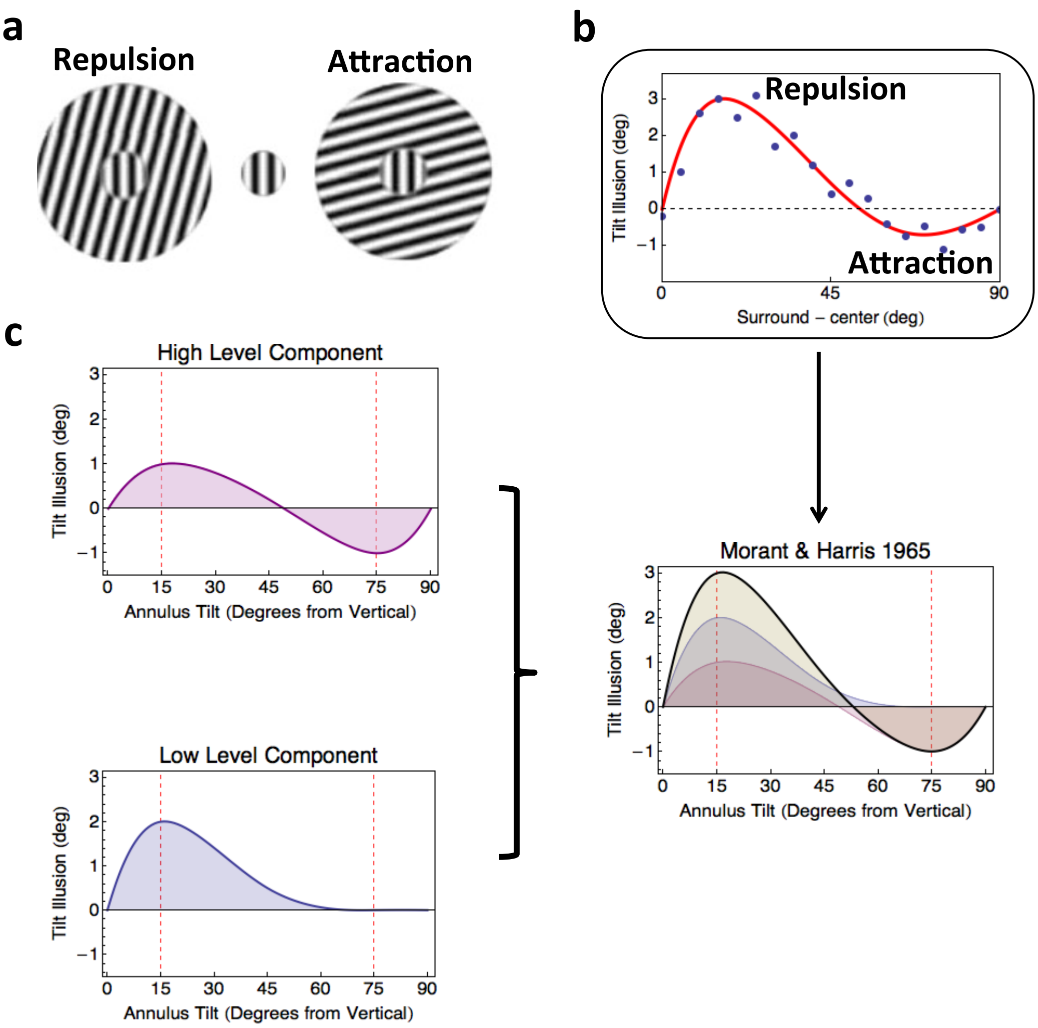


Fig. 1: Tilt illusion and linear summation model.

a) Tilt illusion: Although the three small gratings are all perfectly vertical, their apparent orientations differ. The one on the left is repelled from its 15° surround and the one on the right is attracted to its 75° surround. Without a surround, the orientation of the middle grating is perceived veridically. Figure adapted from Schwartz et al. 2009.

b) Tilt illusion's angular function: The magnitude and sign of the tilt illusion vary as a function of the angle between the surround and the central grating. Repulsive and attractive effects peak at angular differences of ~15° and ~75° respectively.

c) Linear summation model: Morant and Harris (1965) suggested that the tilt after-effect reflected the combination of a local repulsive process and a more global process capable of repulsion and attraction. The tilt illusion may be similar.

Morant and Harris (1965) offered a similar suggestion for the difference in magnitude between direct and indirect versions of the tilt after-effect (Figure 1c). The tilt after-effect and the tilt illusion show many parametric similarities and it has been debated whether they could be accounted for by a common mechanism. Rich empirical evidence seems to favor this hypothesis (Sekuler and Littlejohn, 1974; Tolhurst and Thompson, 1975; Magnussen and Kurtenbach, 1979) suggesting that the tilt illusion should be thought of as the result of some sort of "fast adaptation." In particular, asynchronous presentations of test and inducer increase the illusions (both direct and indirect effects) when the inducer is visible for a proportionally longer time (Sekular & Littlejohn, 1974; Wolfe, 1984; Harris and Calvert, 1989; Wenderoth and van der Zwan, 1989). This is also observed in the tilt after-effect (Wenderoth and Johnstone, 1988) and is consistent with the visual system adapting to the inducing context (Corbett, Handy, Enns 2009). Bearing this in mind, we can safely extend Morant and Harris' idea to the simultaneous domain of tilt illusion.

Evidence consistent with a unique cause of the indirect effect is its relative immunity to contrast manipulations (Wenderoth and Johnstone, 1988). This finding can also be taken as evidence against its mediation by low-level mechanisms, which should be sensitive to contrast.

Another piece of evidence linking the indirect effect to high-level mechanisms is

Wenderoth and Johnstone's report that a square frame surrounding the stimulus abolishes the indirect effect. Since the frame's contours are relatively far away from the central target grating, its effect seems unlikely to be mediated by the relatively short-range lateral connections between neurons in primary visual cortex (Wenderoth and Johnstone, 1987).

The Rod and Frame effect (Asch and Witkin, 1948) offers a suggestive parallel to the functional properties of the tilt illusion. When a vertical rod is presented within a tilted square, its orientation appears distorted systematically in a fashion similar to the tilt illusion (Beh, Wenderoth, Purcell, 1971): it shows both direct and indirect effects for small (about 15˚) and large (about 75˚) rod-frame angular distances, respectively (Beh, Wenderoth, Purcell, 1971). The interesting aspect of this illusion is that, given the shape of the surround and the distance of its borders from the rod, the misperception can't be readily accounted by the interplay of V1 simple cells (Beh, Wenderoth, Purcell, 1971; Wenderoth and Beh, 1977; Wenderoth, van der Zwan, Johnstone, 1989). Hence, the direct effect in the rod and frame illusion is likely to lie on mechanisms dealing with more global features than oriented contours. Even more interestingly, the reported direct and indirect effects have about the same magnitude (about 1.3˚; Beh, Wenderoth, Purcell, 1971) similarly to what posited by Gibson's normalization (Gibson and Radner, 1937). The existence of an indirect effect also for an illusion mediated by global orientation mechanisms provides indirect support to idea that the repulsive effect of the tilt illusion may result from the linear combination of high and low level components.

A growing body of evidence shows that orientation contextual illusions can occur also when the inducing stimulus is suppressed from awareness (He and MacLeod, 2001; Pearson and Clifford, 2005; Clifford and Harris, 2005). In a recent work, Motoyoshi and Hayakawa (2010) demonstrated that after adaptation to a drifting grating, static gratings often become invisible. They named this effect adaptation induced blindness (AIB) and they also reported the direct effect's immunity to a lack of phenomenal awareness. Given the presumed localization of direct and indirect effects at two different levels we reasoned that the manipulation of visual awareness could be a suitable mean to characterize such a dissociation, the assumption being that mechanisms responsible to the indirect effects involve activity in visual areas at least as high as those mediating conscious vision. We would then expect an angular function similar to that predicted by a lateral inhibition model (Figure 1) with only a repulsive component for inducer's orientations close to the vertical. Hence, we measured the tilt illusion after removing the oriented surround stimuli from phenomenal awareness by using the paradigm of adaptation-induced blindness (Figure 2). Post-adaptation biases were then compared to those obtained in a control experiment without dynamic adaptation. Results confirm our expectations, showing that only the indirect effect requires visual awareness, and thereby provide robust evidence for the existence of two separate mechanisms mediating the phenomenology of the tilt illusions.

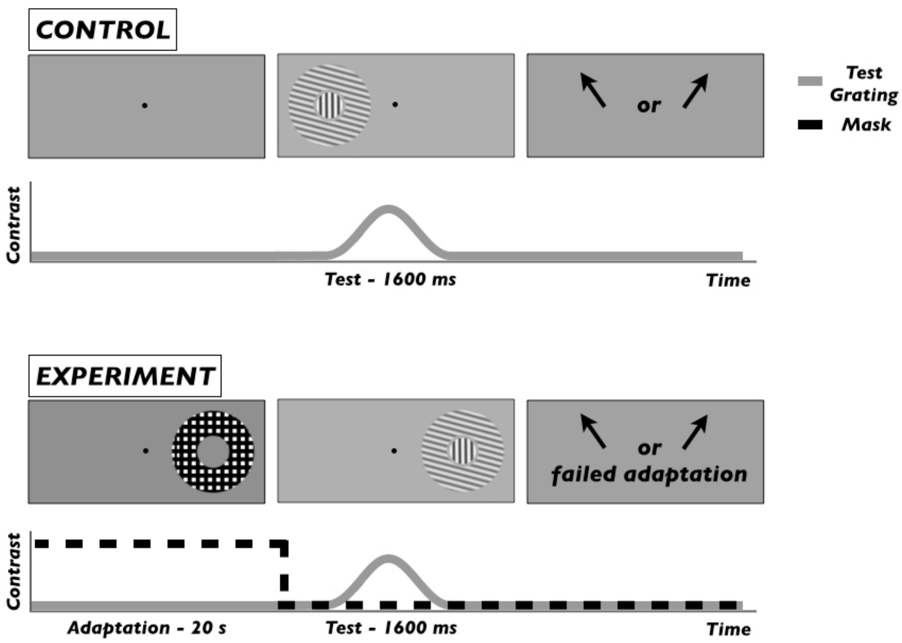


Fig. 2: General experimental procedure.
During the experiment (bottom panel) observers adapted for 20s to an annularly windowed, spatially jittering mask at full contrast, presented either to the left or right of a central fixation mark. The mask was then replaced by an oriented grating having the same annular window. A central target grating appeared within this surround. The contrasts of both center and surround were given the same Gaussian profile in time. Observers had to report the perceived orientation of the central grating by pressing the left or right arrow key. They also had to indicate whether the surround was visible after adaptation. The control experiment (top panel) was identical, except there was no adapting phase.

Methods

Main experiment

Observers

Four naïve observers took part to the experiment (three female and one male) aged between 27 and 38 years old and with corrected-to-normal vision.

Apparatus

Stimuli were presented using Matlab and the Psychtoolbox routines (Brainard 1997; Pelli 1997) on a 20-inch calibrated LCD display controlled by an Apple iMac via an ATI Radeon HD 26000 PRO card (refreshing rate 60Hz) having 8-bit gray-scale resolution. Each pixel subtended approximately 0.02° of visual angle, at the viewing distance of 60 cm. Observations were carried out in a lighted room. Data analysis was conducted using Mathematica and PSYCHOMETRICA (Watson and Solomon, 1997).

Stimuli

At a viewing distance of 60 cm, the inducer and target diameters subtended 10° and 5.2° of visual angle respectively. Inducer and target were separated by a 30-arc-min gap and all contours were smoothed via a raised cosine filter subtending 7.8 arc min. Each of these sinusoidal gratings had a spatial frequency of 1.5 c/deg and a spatial phase ϕ, randomly chosen from the interval $(-\pi, +\pi)$. The Michelson contrasts of target and inducer were 0.99 and 0.59 of their maxima, respectively. These values were chosen in order to obtain a reliable “invisibility” of the inducer as assessed in a pilot experiment. The inducer was always present, and its orientations were drawn from the set {±15°, ±75°}. These specific orientations where chosen as to maximize the magnitude of the direct and indirect effects (O'Toole and Wenderoth, 1977). The adapting mask had the same annular window as the inducer. Within this window we presented the product of two orthogonal square-wave gratings (at ±45° with respect to vertical) at full contrast. Jitter was introduced by randomly selecting the spatial phase of each grating every 0.1 s.

Procedure

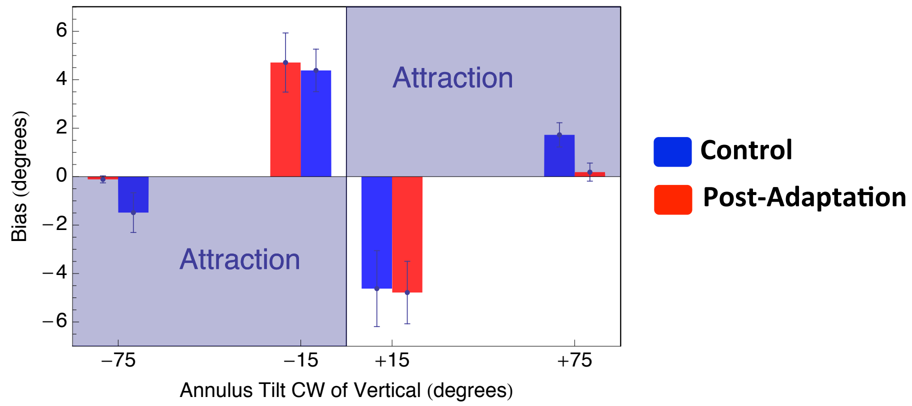
The adapting mask was centered at 3 degrees of eccentricity either on the left or right side of the fixation point. On each trial, following 20 seconds of adaptation, the mask was replaced by the target and inducer at time $t = 0$, which ramped on and off smoothly in a Gaussian temporal window ($\mu = 800$ ms; $\sigma = 200$ms). Observers had to report whether the test grating appeared tilted clockwise or anticlockwise of vertical by pressing the left or right arrow key. They were also instructed to press the bar instead of the arrow keys to report cases in which the surround was visible after adaptation. If such was the case, the trial was discarded and had to be repeated. On each trial, the target's orientation was adjusted by one of eight randomly interleaved staircases (Watson & Pelli, 1983). Two staircases were associated with each inducer's orientation; one designed to converge on P("ACW") = 0.16, the other on P("ACW") = 0.84. Each observer performed one session consisting of about 240 trials.

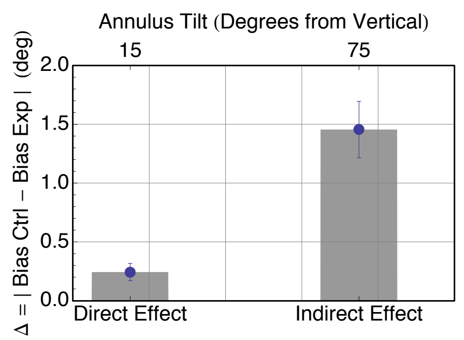
Control experiment

In order to quantify the effect induced by lack of visual awareness, we compared post-adaptation biases with the biases measured in a control experiment, where both the target and the inducer were visible. We therefore designed our control experiment to be identical to the main experiment, apart from the absence of the adapting jittering mask as outlined in Figure 2.

Results

We tested the role of visual awareness in both the direct and indirect effects by rendering the inducer invisible through dynamic adaptation. Observers reported the inducer as visible in only the 6% of trials. This value is comparable to the 8% reported by Motoyoshi and Hayakawa (2010), confirming the efficacy of our methods. Orientation bias was adopted to quantify the tilt illusion. That is, for each inducer's orientation, we estimated how far the central test had to be tilted in order to appear vertical. That corresponds to the point on the psychometric curve where the probability to respond clockwise, given a certain orientation of the test grating, equals chance level (50%).





Aggregate bias (deg)

Inducer Tilt	Adapt: Yes	Adapt: No	
15°	4.74±1.16	4.50±1.18	MEAN±SD
75°	0.14±0.26	1.60±0.64	

Fig. 3: Effect of inducer's visibility on orientation biases.

Upper panel shows biases collapsed across observers and plotted against the inducer's orientation. In the control condition inducers tilted ±15° and ±75° produced ~5° of repulsion and ~2° of attraction, respectively. When the inducer is removed from awareness (Post-adaptation condition) only the indirect effect is abolished while the direct effect appears remarkably unaffected.

Lower plot quantifies net bias between control and post-adaptation conditions confirming that only indirect effect is notably affected by lack of visual awareness.

For all the plots error bars contain 2 standard errors.

Lower table shows mean biases in function of the inducer's orientation and visibility.

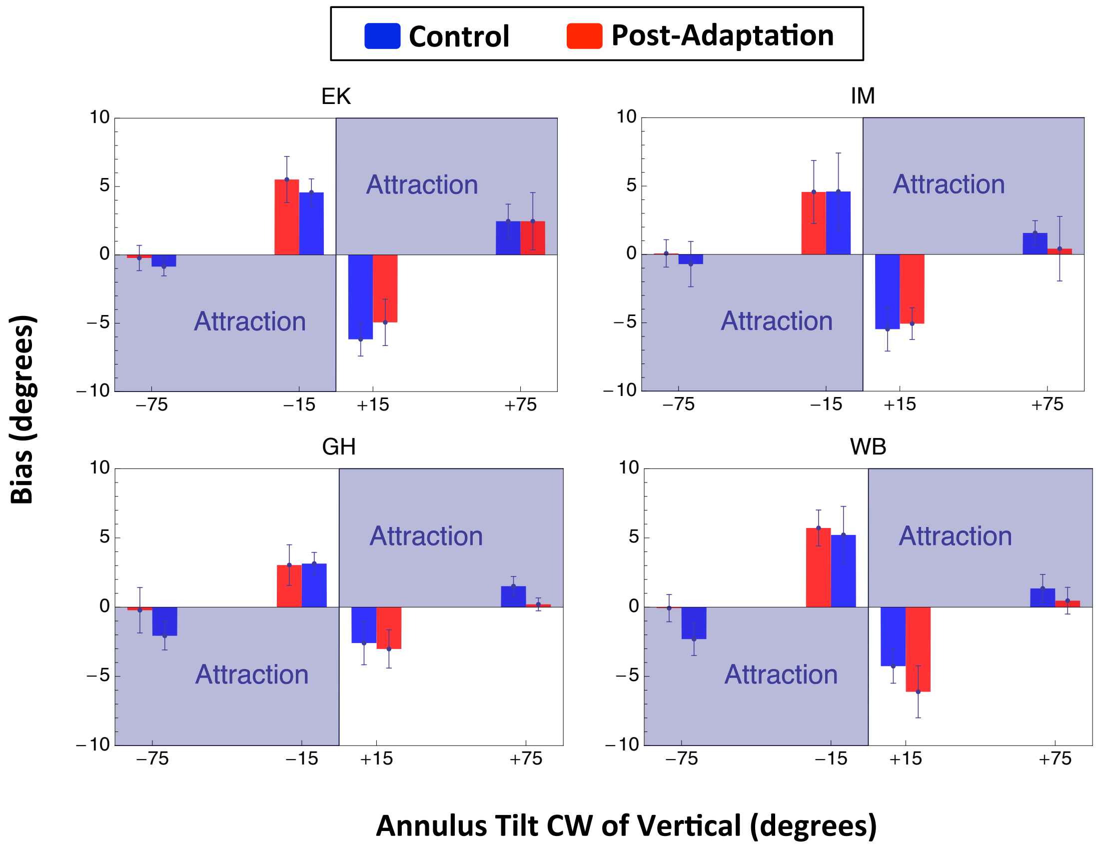


Fig. 4: Effect of inducer's visibility on orientation biases, individual data. Format follows the conventions established in the top panel of Fig. 3.

Each point in Figure 3 (upper panels) shows the average biases of our four observers, segregated on the basis of the visibility of the inducing surround. In the control condition (visible surround), as expected, near-vertical inducers (±15°) produced repulsive biases (direct effect) of 4.5° ± 1.2° (mean ± SD) while near to horizontal inducers caused 1.6° ± 0.6° of attraction (indirect effect; Figure 3 upper panels and Table 1). In the post-adaptation condition (invisible surround), near-vertical inducers again produced significant biases (4.7° ± 1.2°), but the near-horizontal inducers did not (0.1° ± 0.3°). Hence, when the inducer is not perceived there is almost no evidence of attraction, but repulsion is only marginally diminished. The same pattern of results can be observed at the individual level (Figure 4). A paired t-test confirms that the effect of adaptation on the (unsigned) magnitude of the direct effect is larger than its effect on the magnitude of the indirect effect [$t(7) = 2.19$, $p < 0.03$]. Therefore, our data reveal that visual awareness is required only by processes mediating the indirect effect advocating the notion that attraction and repulsion are mediated by distinct mechanisms (Wenderoth and Johnstone, 1988).

Discussion

Here we tested the claim that the tilt illusion's phenomenology might be accounted for by the interplay between two different mechanisms located at different stages of the visual processing stream (Morant and Harris, 1965). To isolate early stages of processing, we used AIB to remove illusion-inducing stimuli from phenomenal awareness. The rationale of using this approach is based on the idea that consciousness emerges only after elaborate perceptual processing unfolding over multiple processing levels (Erdelyi, 1974). If one of these levels is interrupted, the visual information will be unconsciously processed until that stage (Lin and He, 2009). In our specific case, by making the inducing surround unconscious we wanted to see where the mechanisms mediating the indirect and direct effects are located in the visual hierarchy with respect to the stage where phenomenal awareness emerges.

We found that AIB was successful in eliminating the so-called indirect version of the tilt illusion, but not the direct one. Adaptation is likely to decrease low-level neural responses to the surround. Hence, it could be argued that in our experiment the indirect effect is diminished by a decrease in contrast, rather than by the lack of awareness of the surround. However, this criticism is inconsistent with evidence showing the relative immunity of the indirect effect to contrast manipulations (Wenderoth and Johnstone, 1988).

Blakemore et al (1970) explained the direct effect in terms of lateral inhibition between striate neurons with adjacent receptive fields and similar orientation selectivity operating on a local scale. The indirect effect, on the other hand, is believed to reflect mechanisms involved in global orientation analysis occurring, therefore, in extrastriate sites where neurons are tuned to global stimulus properties (Wenderoth and Johnstone, 1987).

The latter conclusion however is not completely clear-cut. In fact, there is evidence that some global processes (such as texture segmentation) are implemented as early as V1 (possibly through feedback from extrastriate areas; Lamme, van Dijk et al. 1993). Therefore, it is not impossible for the direct and indirect effects to be at least partly mediated by a common substrate. If this were the case, then the indirect effect could be understood as a consequence of re-entrant activity from extrastriate areas to striate cortex (Poom, 2000). Our main finding that the indirect effect is abolished by lack of phenomenal awareness is consistent with this idea since it is believed that re-entrant connections from high level areas to V1 could be crucial for conscious perception (Lamme, 2003). Further support comes from the finding that the direct effect saturates after 100ms of stimulus presentation. The indirect effect, on the other hand, does not saturate until after 400 ms (Wenderoth and Johnstone, 1988).[1]

Multiple levels of the visual processing hierarchy might be engaged in determining the repulsive direct effect as well (Wenderoth and Johnstone 1987; Clifford and Harris, 2005). Previous studies (Wade, 1980; Forte and Clifford, 2005) reported an incomplete inter-ocular transfer of the direct effect. That is, the size of the effect is lessened when the inducer is presented to one eye and the test to the other (dichoptical presentation) compared with when inducer and test are presented to the same eye (monocular presentation). The amount of inter-ocular transfer is thought to be related to the amount of monocular and binocular neurons engaged in the processing. Therefore it indicates that monocular neurons, mainly present in V1 (Hubel and Wiesel, 1962), are only partly responsible for the direct effect.

Taken together these observations are consistent with Morant and Harris' hypothesis of high and low level components interacting to generate the angular tuning function that describes the phenomenology of the tilt illusion. Indeed, Morant and Harris' idea can explain the fact that low-level manipulations don't extinguish the direct effect but just reduce it to roughly the same magnitude of its direct counterpart (Wenderoth and Johnstone, 1987). Another prediction implied by a linear combination model is that by suppressing the indirect effect we should expect a commensurate reduction in direct effect's magnitude (Wenderoth, van

[1] These temporal estimates were obtained in the absence of adaptation. Examining the effect of AIB on the dynamics of the tilt illusion is beyond the scope of this paper, but it is conceivable that AIB may have merely slowed the indirect effect to the point that our stimuli disappeared before it could manifest.

der Zwan, Johnstone, 1989).

Our data are at odds with this latter prediction. The fact that repulsive biases are only marginally affected by lack of awareness, however, could suggest that the interaction might be non-linear instead of additive as posited by their original model. For example, the tilt illusion's angular function might result from the implementation of a max rule so that only the maximum output between the two processes contributes to the bias.

An alternative explanation could be related to the proposal of the direct effect resulting from the contribution of multiple levels of the visual hierarchy. A mounting body of psychophysical and neurophysiological evidence suggests that erasing visual stimuli from awareness only weakens but doesn't eradicate the corresponding neural signal (Lehky and Blake, 1991; Sobel, Blake, Raissian, 2004; Blake, Tadin, Sobel, Raissian, Chong, 2006). Furthermore, these weakening effects are first expressed at early levels of processing and become progressively more potent at subsequent stages (Nguyen, Freeman, Wenderoth, 2001; Blake and Logothesis, 2002; Freeman, Nguyen, Alais, 2005). If the repulsive effect is really based on low-level mechanisms, we can speculate that it would be subjected to a relatively small amount of suppression. High-level processes, like those mediating the indirect effect, would instead endure a stronger suppression. Therefore, the smaller weakening observed on the direct effect would be explained in terms of different levels of suppression exerted by removing the visual stimulus from awareness.

It must be noted that our results are at odds with the conclusions of Mareschal and Clifford (2012) who reported the persistence of the indirect effect when the surround's orientation was rendered indiscernible through rapid presentation. The major difference in our study is that our surrounds were perceptually invisible to the observers and phenomenal awareness was assessed on a trial-by-trial basis. However, it is also possible that discrepancies could stem from the techniques employed by the two studies. Indeed, it has been reported that different methods to manipulate visual awareness could yield divergent results when applied to contextual phenomena such as visual crowding (Chakravarthi and Cavanagh, 2009; Wallis and Bex, 2011) and orientation after-effects (Arthorp, Cass, Alais, 2011). Further investigation could clarify a possible role of different techniques in the discrepancy here observed.

Conclusions

Our results demonstrate that the neural counterparts of direct and indirect effects are likely to be found largely in V1 lateral interactions and in global extrastriate processes, respectively. More specifically, here it is shown that only the attractive indirect illusion is based on mechanisms that require visual awareness to operate.

Acknowledgments

This research was supported by a Grant from the Engineering and Physical Sciences Research Council (EP/E064604).

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