Vision Research 104 (2014) 3–11

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

The tilt illusion: Phenomenology and functional implications

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ARTICLE INFO

Article history:
Received 28 March 2014
Received in revised form 18 June 2014
Available online 1 July 2014

Keywords:
Visual perception
Orientation processing
Contextual modulation
Spatial vision
Psychophysics
Gain control

ABSTRACT

The perceived orientation of a line or grating is affected by the orientation structure of the surrounding image: the tilt illusion. Here, I offer a selective review of the literature on the tilt illusion, focusing on functional aspects. The review explores the merits of mechanistic accounts of the tilt illusion based upon sensory gain control in which neuronal responses are normalized by the pooled activity of other units. The role of inhibition between orientation-selective neurons is discussed, and it is argued that their associated disinhibition must also be taken into account in order to model the full angular dependence of the tilt illusion on surround orientation. Parallels are drawn with adaptation as modulation by the temporal rather than spatial context within which an image fragment is processed. The chromatic selectivity of the tilt illusion and the extent of its dependence on the visibility of the surround are used to infer characteristics of the neuronal normalization pools and the loci in the cortical processing hierarchy at which gain control operates. Finally, recent evidence is discussed as to the possible clinical relevance of the tilt illusion as a biomarker for schizophrenia.

1. Introduction: basic phenomenology and early ideas

Here, I provide a selective review on the tilt illusion that aims to complement rather than supersede previous such reviews (e.g. Schwartz, Hsu, & Dayan, 2007; Wenderoth & Johnstone, 1987) of the now extensive literature. The current review focuses on the functional implications of the tilt illusion and on aspects of its phenomenology that speak to the underlying neural mechanisms. From a functional perspective, I explore the merits of mechanistic accounts based upon sensory gain control implemented through lateral interactions between orientation-selective neurons. In terms of phenomenology, I concentrate on relatively recent developments in establishing the chromatic selectivity of the tilt illusion and its persistence even when the orientation of the inducing stimulus is not perceptible. I draw parallels with adaptation as modulation by successive context, and discuss possible clinical relevance of the tilt illusion as a diagnostic tool in the context of schizophrenia. For a fuller treatment of earlier work on the tilt illusion and its temporal analogue, the tilt aftereffect, I direct the reader towards the review by Wenderoth and Johnstone (1987). I strongly recommend also the review by Schwartz, Hsu, and Dayan (2007), particularly for its sophisticated treatment of the modelling literature.

Since the early work of Gibson (1937), a large body of literature has built up on the characteristics and determinants of the tilt illusion. In the tilt illusion, the presence of an oriented surround stimulus biases the perceived orientation of a simultaneously presented test (Fig. 1A). The phenomenon shows a characteristic dependence on the angle between the inducing stimulus and the test, illustrated in Fig. 1B. The usual form of this angular tuning function for a vertical test stimulus (0°) in central vision can be summarized as follows. For inducing stimuli between 0° and 50°, the test appears repelled away from the inducer in orientation, with the strongest effect occurring between 10° and 20° (the *direct* tilt illusion). For larger angles there is a smaller attraction effect, such that the test appears rotated towards the inducer (the *indirect* tilt illusion). The strongest attraction effect occurs between 75° and 80° (e.g. Over, Broerse, & Crassini, 1972; Wenderoth & Johnstone, 1987).

The tilt illusion is evident in foveal (Gibson, 1937) and parafoveal vision (Solomon, Felisberti, & Morgan, 2004), exhibits partial interocular transfer, such that is reduced but not abolished under dichoptic viewing (Virsu & Taskinen, 1975; Walker, 1978), and is selective for spatial frequency such that illusion magnitude is greatest for test and surround similar in spatial frequency (Georgeson, 1973). The influence of the surround declines with distance from the test (Mareschal & Clifford, 2013; Virsu & Taskinen, 1975). Repulsive and attractive effects do not require awareness of the surround orientation (Mareschal & Clifford, 2012) and are observed not only for orientation defined by (first-order)

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http://dx.doi.org/10.1016/j.visres.2014.06.009
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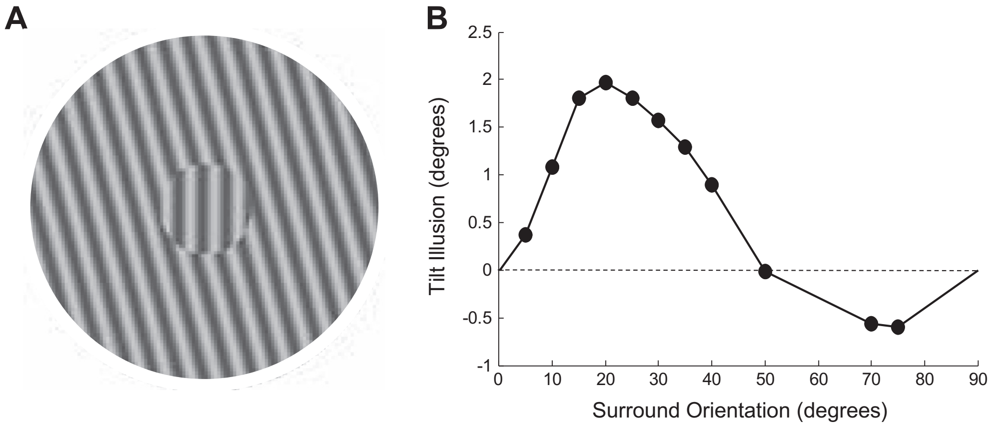

Fig. 1. The tilt illusion and its angular dependence. (A) Example centre–surround configuration used to elicit the repulsive (direct) tilt illusion. The vertical test grating in the centre appears repelled in orientation away from the 15° surrounding grating. (B) Magnitude and direction of the tilt illusion at vertical as a function of the orientation of the surround (data redrawn from Westheimer, 1990, Fig. 1, averaged across subjects). Positive values denote repulsion; negative attraction.

modulations in luminance but also for (second-order) contrast modulations (Smith, Clifford, & Wenderoth, 2001; Wenderoth, Clifford, & Ma Wyatt, 2001) and purely chromatic modulations (Clifford et al., 2003a, 2003b).

The search for a functional explanation of the tilt illusion dates back to the Normalization Theory of Gibson (1937). According to the Normalization Theory, vertical and horizontal are norms of visual space.[1] Perception of an orientation tilted away from one of these norms (15° clockwise from vertical, say) over a large area of the visual field will cause the nearest norm to shift in the direction of the inducing orientation (clockwise). As a result, a test at the orientation of the original norm (vertical) will appear rotated from the shifted norm in the opposite direction (anti-clockwise). Thus, the test will appear repelled in orientation away from that of the inducer (Fig. 2).

If the effect on perceived orientation were a simple rotation then one would expect there to be a corresponding attractive effect of the same magnitude for a horizontal test. Gibson (1937) did indeed observe an attractive effect with a horizontal test. However, it was of a smaller magnitude (1.07 ± 0.25°) than the repulsive effect on vertical (2.01 ± 0.22°). To account for the fact that the magnitude of attraction effects is smaller than that of repulsion effects (Gibson, 1937), Normalization Theory assumes that "the vertical and horizontal norms ... may be said to constitute a single system and yet to operate in partial independence". As Coltheart (1971) points out, this explanation is rather *ad hoc*. Moreover, the similarity of the angular dependence of the tilt illusion for vertical and oblique test stimuli (O'Toole & Wenderoth, 1977) indicates that consideration of relative rather than absolute orientation is key to understanding the tilt illusion.

2. The tilt illusion as a consequence of sensory gain control

Primary visual cortex (V1) is the earliest stage of the primate visual processing hierarchy at which neurons showing significant selectivity for stimulus orientation are routinely observed (Hubel & Wiesel, 1968). Lateral inhibition between neural mechanisms tuned to different orientations was first proposed as an explanation of the repulsive tilt illusion by Blakemore, Carpenter, and Georgeson (1970) and Blakemore, Muncey, and Ridley (1973). However, a purely inhibitory account of the tilt illusion is unable to explain the existence of an attractive tilt illusion when the surround is remote in orientation from the test (Fig. 3). To explain the attractive tilt illusion, O'Toole and Wenderoth (1977) extended the lateral inhibition account proposed by Blakemore and colleagues to incorporate disinhibition. Inhibition between mechanisms tuned to different orientations at the same location, as well as between those tuned to the same orientation at different locations, can together lead to disinhibition of mechanisms remote in both position and orientation (Fig. 4). Such a pattern of interactions can be implemented in the form of a divisive gain control mechanism whereby the responsiveness of orientation-selective mechanisms is normalized by the activity of a pool of other similar units (Goddard, Clifford, & Solomon, 2008; Schwartz, Sejnowski, & Dayan, 2009).

Modelling the contextual interactions underlying the tilt illusion in terms of sensory gain control is appealing on many levels (although see Solomon & Morgan, 2006; for arguments against such an account). Gain control can be considered as a canonical neural computation, evident across many brain regions and sensory modalities (Carandini & Heeger, 2011). Gain control allows a system to be self-calibrating (Andrews, 1964; Clifford, 2005; Ullman & Schechtman, 1982), changing itself in response to changes in the environment (recalibration) and adjusting to perturbations within the system in an unchanging environment (error-correction). Recalibration and error-correction are fundamental properties of our sensory systems. Thus gain control models of the tilt illusion are likely to be readily applicable to the many other visual modalities where analogous contextual effects are evident.

Unique to the modelling approach of Schwartz, Sejnowski, and Dayan (2009) is that the theoretical motivation for the particular elaboration of standard divisive gain control employed is rigorously based on the statistical properties of natural images (see also Coen-Cagli, Dayan, & Schwartz, 2012; Schwartz & Simoncelli, 2001). When information about scene segmentation is incorporated into the model it is able to accommodate the attractive as well as the repulsive tilt illusion. Specifically, when test and surround are likely to correspond to different segments of the visual scene, the model neurons responding to the test stimulus receive less normalization from the surround. This is consistent with psychophysical evidence that segmentation cues reduce the magnitude of the repulsive tilt illusion (Durant & Clifford, 2006; Qiu, Kersten, & Olman, 2013). Indeed, it may also be possible to interpret the chromatic selectivity of the tilt illusion (described in a subsequent section) in terms of the role of chromatic signals in segmenting test and inducer.

[1] It should be noted that the meaning of the term "normalization" in Normalization Theory is quite different from its usage in the context of sensory gain control.