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DOI
10.1167/18.11.3

Publication date
2018

Document Version
Final published version

Published in
Journal of Vision

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Link to publication

Citation for published version (APA):
Seymour, K. J., Stein, T., Clifford, C. W. G., & Sterzer, P. (2018). Cortical suppression in human primary visual cortex predicts individual differences in illusory tilt perception. *Journal of Vision*, *18*(11), Article 3. https://doi.org/10.1167/18.11.3

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Cortical suppression in human primary visual cortex predicts individual differences in illusory tilt perception

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Neural responses to visual stimuli are modulated by spatial and temporal context. For example, in primary visual cortex (V1), responses to an oriented target stimulus will be suppressed when embedded within an oriented surround stimulus. This suppression is orientation-specific, with the largest suppression observed when stimuli in the neuron's classical receptive field and surround are of similar orientation. In human psychological experiments, the tilt illusion and tilt aftereffect demonstrate an effect of context on perceived orientation of a target stimulus. Similar to the neurophysiological data, the strength of these effects is modulated by the orientation difference between the target stimulus and context. It has been hypothesized that the neural mechanism underlying both the tilt illusion and tilt aftereffect involves orientation-tuned inhibition in V1. However, to date there is no direct evidence linking human perception of these illusions with measurements of inhibition from human visual cortex. Here, we measured context-induced suppression of neural responses in human visual cortex using functional magnetic resonance imaging (fMRI). In the same participants, we also measured magnitudes of their tilt illusion and tilt aftereffect. Our data revealed a significant relationship between the magnitude of neural suppression in V1 and size of the tilt illusion and tilt aftereffect. That is, participants who showed stronger blood oxygenation level dependent (BOLD) suppression in V1 also perceived stronger shifts in illusory tilt. This agreement between perception and neural responses in human V1 suggests a shared inhibitory mechanism that mediates both spatial and temporal effects of context in human perception.

Citation: Seymour, K. J., Stein, T., Clifford, C. W. G., & Sterzer, P. (2018). Cortical suppression in human primary visual cortex predicts individual differences in illusory tilt perception. *Journal of Vision*, *18*(11):3, 1–10, https://doi.org/10.1167/18.11.3.

https://doi.org/10.1167/18.11.3 Received March 23, 2018; published October 10, 2018 ISSN 1534-7362 Copyright 2018 The Authors

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Introduction

Animal neurophysiology has provided convincing data that neural responses to a visual stimulus are modulated by spatial and temporal context. When a visual stimulus is placed within a neuron's classical receptive field, its response is modulated by stimuli outside its receptive field (Allman, Miezin, & McGuinness, 1985; Blakemore & Tobin, 1972; Maffei & Fiorentini, 1976; Nelson & Frost, 1978). In primary the visual cortex (V1), it has been widely documented that neural responses to an oriented grating are suppressed in the presence of oriented contextual stimuli (DeAngelis, Freeman, & Ohzawa, 1994; Gulyas, Orban, Duysens, & Maes, 1987; Hubel & Wiesel, 1961; Knierim & van Essen, 1992; Levitt & Lund, 1997). This suppressive effect is orientation-tuned, with the most pronounced effect observed when stimuli in the classical receptive field and surround region are of similar orientation (Cavanaugh, Bair, & Movshon, 2002; DeAngelis et al., 1994; Knierim & van Essen, 1992; Sengpiel, Sen, & Blakemore, 1997; Walker, Ohzawa, & Freeman, 1999).

In humans, a number of compelling visual illusions also demonstrate the effect of context on visual perception. For instance, the tilt illusion (Figure 1) reveals that the orientation of a central target grating can be perceived as shifted away from that of its surround (repulsive effect) when the orientation difference between the two gratings is small (e.g., 10°–20°), or shifted toward the orientation of the surround (attractive effect) when this difference is large (e.g., 70°–80°; Gibson & Radner, 1937). The tilt aftereffect, which is a temporal analogue of the tilt illusion, demonstrates a similar effect of context in the temporal domain (for reviews, see Clifford, 2014; Schwartz, Hsu, & Dayan, 2007; Wenderoth & Johnstone, 1987).

Theoretical models of the tilt illusion suggest a neural mechanism (or mechanisms) that involves inhibition in V1 (Blakemore, Carpenter, & Georgeson, 1970; Blakemore, Muncey, & Ridley, 1973; Clifford, Wenderoth, & Spehar, 2000; Gibson & Radner, 1937; Schwartz et al., 2007; Schwartz, Sejnowski, & Dayan, 2009; Series, Lorenceau, & Fregnac, 2003; Solomon & Morgan, 2006). Given the qualitative similarities between the tilt illusion and the tilt aftereffect, it has been proposed that the tilt aftereffect also relies on a similar mechanism (Gibson & Radner, 1937; Mareschal & Clifford, 2012; Wenderoth & Johnstone, 1987). However, to date there is no direct evidence linking human perception of these illusions with measurements of inhibition from human visual cortex.

In the current study, we examined the relationship between contextual effects on visual perception of orientation and contextual suppression of neural responses in V1. We have previously developed a robust fMRI paradigm to measure orientation-tuned contextual suppression of the fMRI signal in human V1 (e.g., McDonald, Mannion, Goddard, & Clifford, 2010; McDonald, Seymour, Schira, Spehar, & Clifford, 2009; Seymour et al., 2013; Zenger-Landolt & Heeger, 2003). We employed the same method here to examine individual differences in suppression of neural responses and their relationship to context-induced differences in orientation perception. Given that the tilt illusion and the tilt aftereffect both show a similar dependence on orientation differences between the target and contextual surround stimulus, we also set out to uncover evidence of a shared neural mechanism in the form of neural inhibition in V1.

Figure 1. Tilt illusion (Gibson & Radner, 1937). In its standard (direct) form, the orientation of a central grating is perceived to be tilted away from the orientation of the surrounding contextual grating that forms its visual context.

Methods and materials

Participants

Ten healthy adults participated in this study. All participants gave written informed consent before participation, which was approved by an accredited Medical Ethics Review Committee.

Measuring contextual suppression in human V1

Stimuli and design

We measured contextual suppression of the blood oxygenation level dependent (BOLD) response associated with viewing a *target grating* embedded within one of two different contextual *inducer gratings*, oriented either parallel or orthogonal to the target grating's orientation (Figure 2). Our stimulus configuration (i.e., the use of an annulus to present the target grating)

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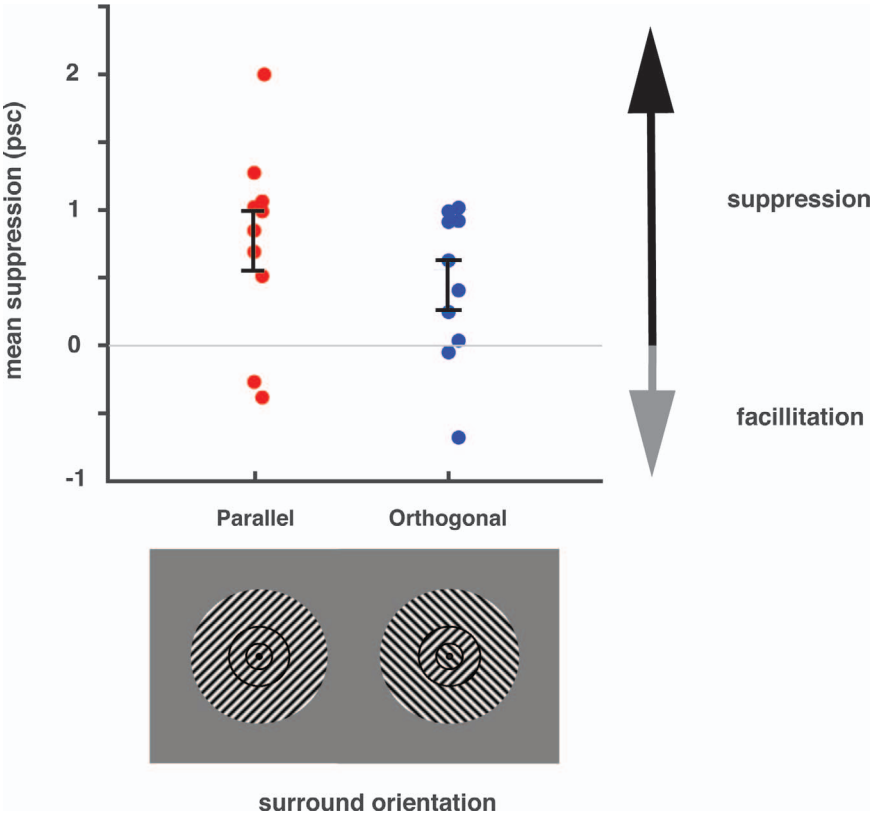

Figure 2. Mean suppression (in units of percent signal change) in primary visual cortex averaged for 10 observers for the two inducer conditions, parallel and orthogonal. Suppression is calculated as the BOLD response to target-alone minus response to target and inducer. Suppression of the BOLD signal by the inducer relative to when the target grating is presented in isolation is indicated by positive values, and facilitation by negative values. Error bars are ±1 *SEM*.

followed earlier fMRI work geared toward measuring suppression of the BOLD signal specifically from human V1 (Seymour et al., 2013; Zenger-Landolt & Heeger, 2003) rather than a region known as the foveal confluence where area V1 cannot be functionally differentiated from other extrastriate regions (Schira, Tyler, Breakspear, & Spehar, 2009). Stimuli were generated using MATLAB (MathWorks, Natick, MA) and Psychtoolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). They were presented at a resolution of 1,280 × 1,024 pixels and a screen refresh rate of 60 Hz from a viewing distance of 75 cm. Stimuli were projected onto a transparent screen at the head of the scanner bore (mean luminance of 50 cd/m^2) and viewed through a tilted mirror fixed to the head coil.

We used an optimized block design in which a sinusoidal grating (1 c/°, reversing in phase at 4 Hz; 100% Michelson contrast) was continuously displayed within the annular target region while a grating in the contextual inducer region appeared and disappeared over a 20-s period (i.e., 10 s "off" and 10 s "on"). The annular target region extended from 1.8° to 4.0° eccentricity and was outlined by a thin black line (0.06°) on the inner and outer edges. This outline served to segment the target from the inducer gratings equally in all conditions. The inducer region, which included the areas both inside and outside of the annulus, extended to 12.0° eccentricity.

We used two contextual inducer conditions. In our *parallel-inducer* condition, gratings of the same orientation and spatial phase were presented to both the target and inducer region. In the *orthogonal-inducer* condition, the target grating and the inducer grating were presented with an angular difference of 90°. We chose these inducer conditions in order to provide a measure of context-dependent BOLD suppression in its strongest and weakest forms (i.e., parallel and orthogonal, respectively).

Each run comprised four off–on cycles for each condition, presented in an alternating sequence over the run. The order of conditions was counterbalanced across runs and subjects. Blank fixation periods (10 s) were also displayed at the beginning, middle, and end of each run. The run duration was 3.167 min. We presented each condition at four different target orientations (0°, 45°, 90°, 135°), such that every discrete target orientation occurred once over the course of each run. Hence, the parallel and orthogonal blocks differed only in the relative orientation of target and inducer and not in the distribution of absolute

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orientations. Blocks were ordered in a balanced design over the entire scan session so that each block type occurred an equal number of times before every other block type. Participants fixated on a fixation point throughout each run and responded to a color change via a button press.

Participants were scanned for a total of 10 fMRI runs. Five runs were devoted to measuring suppression of the BOLD response associated with parallel and orthogonal inducers. Two additional independent localizer runs were employed to isolate the cortical representation of the annular target region from the inducer region. Three retinotopic mapping scans were also conducted to localize V1 (Sereno et al., 1995).

fMRI data acquisition

Functional images were acquired in a 3 Tesla Trio scanner (Siemens, Erlangen, Germany) using a gradient echo planar imaging (EPI) sequence and a 12-channel head coil. We collected 33 slices positioned at an orientation parallel to the calcarine sulcus using a descending sequence with the following parameters: repetition time (TR) 2.5 s; echo time (TE) 30 ms, flip angle: 81°, slice thickness 3 mm, interslice gap 0.3 mm, voxel size $3 \times 3 \times 3$ mm. For each subject, a high-resolution (1 mm isotropic) T1-weighted MPRAGE image was acquired for surface reconstruction and used as an anatomical reference. Functional data were coregistered to the raw anatomical scan and not transformed to any standard coordinate system. We corrected for head motion and made a mean intensity adjustment (global scaling), but no spatial smoothing was applied to the data.

Area V1 was delineated manually on the basis of field sign alternations in Freesurfer (Dale, Fischl, & Sereno, 1999; Fischl, Sereno, & Dale, 1999). We restricted our analysis for examining contextual suppression of the BOLD response to voxels within V1 that responded to the annular test grating (i.e., surviving a threshold of $p < 0.05$, uncorrected, in an SPM contrast between activation associated with a *test-alone condition* and activation associated with an *inducer-alone condition*—collected during separate independent localizer runs). A region of interest (ROI) was created taking the intersection of retinotopically defined V1 with this localizer mask. For each subject, signal time courses for every voxel were estimated using a general linear model (GLM) as implemented in SPM8 (http://www.fil.ion.ucl.ac.uk/spm). We modeled separate regressors for the no-inducer baseline condition, the parallel-inducer condition, and the orthogonal-inducer condition (all convolved with the canonical haemodynamic response function). Using the REX toolbox (http://web.mit.edu/swg/software.html), signal time courses were extracted from each subject's ROI and a voxel-weighted average was computed such that voxels that gave the strongest target-alone response during the independent localizer runs were given the highest weighting (i.e., *t*-values in the SPM contrast between target-alone and inducer-alone conditions were taken as the weights to be used for computing a weighted average across all voxels within the ROI).

Data were then normalized to a percent signal change (psc), which was referenced to the mean signal elicited during fixation periods. A repeated-measures ANOVA examined differences in BOLD amplitude between the no-surround, parallel-inducer, and orthogonal-inducer conditions. BOLD suppression was calculated for the two contextual inducer conditions by subtracting the mean signal measured during the no-surround baseline condition.

Measuring contextual effects on behavioral reports of orientation perception

Stimuli were presented outside the scanner on a 15-in. gamma-corrected CRT monitor (refresh rate of 60 Hz, $1{,}024 \times 768$ pixel resolution, background luminance: 50 cd/m^2) and viewed through a black cylindrical tube from a distance of 57 cm. Stimuli were generated in MATLAB (MathWorks, Natick, MA) and Psychtoolbox (Kleiner et al., 2007; Pelli, 1997; Pelli, Palomares, & Majaj, 2004). Responses were collected via a standard keyboard.

Tilt illusion

We measured the tilt illusion using the standard stimulus (direct effect) configuration (e.g., Clifford, 2014). Stimuli consisted of two concentric sinusoidal gratings presented simultaneously (Figure 1). The central target grating, which extended to an eccentricity of 1.5° of visual angle, was embedded within a contextual inducer grating. The inducer grating extended from 1° to 3° eccentricity. Gratings had a spatial frequency of 1 c/°, a mean luminance 50 cd/m^2, and were presented at 100% Michelson contrast.

Conditions were presented as randomly interleaved staircases split across two blocks. We presented inducer conditions at one of two orientations (i.e., +15° and −15°; positive values refer to clockwise) and included a no-inducer control condition, in which only the target grating was presented. Ten staircases for each condition were presented within each block. On a single trial, a stimulus was presented for 100 ms after which participants were asked to indicate whether they perceived the target grating to be clockwise (CW) or counter-clockwise (CCW) from vertical. Depending on their response, the orientation of the target grating was adjusted (1° in the opposite direction) on the subse-

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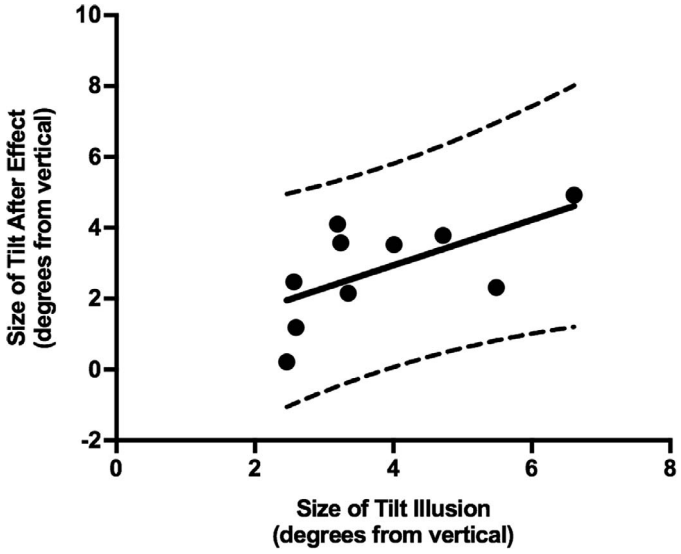

Figure 3. Size of tilt aftereffect correlates with size of tilt illusion ($R = 0.622$, $p = 0.027$, 95% CI: −0.013–0.899). Size of illusions were calculated by averaging the absolute magnitude of the perceived shift in orientation (PSV) under the +15° and −15° inducer conditions. 95% prediction intervals are plotted.

quent trial of that staircase. There was no time restriction and each trial commenced 500 ms after participants gave their previous response. Each staircase had a starting target orientation assigned randomly from ±5° or ±10° (sign dependent on trial type). We obtained an estimate of each participant's point of subjective vertical (PSV), based on an average of the last two reversals for each condition across the 20 trials of each staircase. The magnitude of the illusion was calculated by halving the difference between the magnitude of the perceived shift in orientation (PSV) under the +15° and −15° inducer conditions. A one-sample t test (one tailed) across subjects assessed statistical significance.

Tilt aftereffect (TAE)

We used similar stimulus parameters to those used to estimate participants' tilt illusion magnitudes. In this case, however, the inducer (adapting) grating and target grating were identical in size (i.e., diameter of 3°) and presented in temporal succession. We again included a no-inducer control condition where no adapting grating preceded the target grating.

Trials were presented in a series of staircases, blocked per condition (i.e., five staircases for each condition per block). Each staircase began with a starting target orientation that was assigned randomly from ±5° or ±10° (sign dependent on trial type). At the beginning of each block, participants viewed an inducer grating for 20 s. Following this adaptation period, the first trial began. Participants viewed the adapting (inducer) grating again for a period of a 5 s (top-up adaptation). Then, following an interstimulus interval of 120 ms, a target grating was presented for 100 ms. Participants were then required to indicate whether they perceived the target grating to be CW or CCW to vertical. The orientation of the target grating was then adjusted by 1° in the opposite direction on the subsequent trial of that staircase. There was no time restriction and each trial commenced 800 ms after the previous response.

We obtained an estimate of each participant's point of subjective vertical (PSV), based on an average of the last two reversals for each condition across the 20 trials of each staircase. The magnitude of the tilt aftereffect was calculated by by halving the difference between the magnitude of the perceived shift in orientation (PSV) under the +15° and −15° inducer conditions. A one-sample t test (one tailed) across subjects assessed statistical significance.

Results

Contextual suppression in human V1

The results of a repeated-measures ANOVA indicate that the BOLD response in human V1 was modulated by context, $F(2, 9) = 9.12$ $p = 0.0018$, $\eta^2 = 0.503$. As we have previously shown in human V1, the introduction of a contextual surround resulted in the suppression of BOLD responses for both parallel, $t(9) = 3.503$, $p = 0.003$, $d = 1.108$, and orthogonal surrounds, $t(9) = 2.527$, $p = 0.016$, $d = 0.799$. We also found evidence of stronger suppression when target and inducer gratings were parallel (i.e., mean change from no-inducer baseline: −0.78 psc, SE: 0.22 psc) compared to when they were orthogonal to one another (mean change from no-inducer baseline: −0.45 psc, SE: 0.19 psc. This orientation-specific difference in modulation was found to be significant, $t(9) = -2.362$, $p = 0.021$, $d = 0.747$ (Figure 2).

Contextual modulation of perceived orientation

We measured the effects of context on perceived orientation using the tilt illusion and tilt aftereffect. All 10 participants showed the typical repulsive effects of context on judging the orientation of the target grating.

With regard to tilt illusion magnitudes, the introduction of a surround oriented at 15° resulted in a shift in perceived orientation away from the inducer grating's orientation, mean PSV: 3.822°, SE: 0.438°, $t(9) = 8.718$, $p < 0.001$, $d = 2.757$. Similarly for the tilt aftereffect, adapting to an inducer grating oriented at

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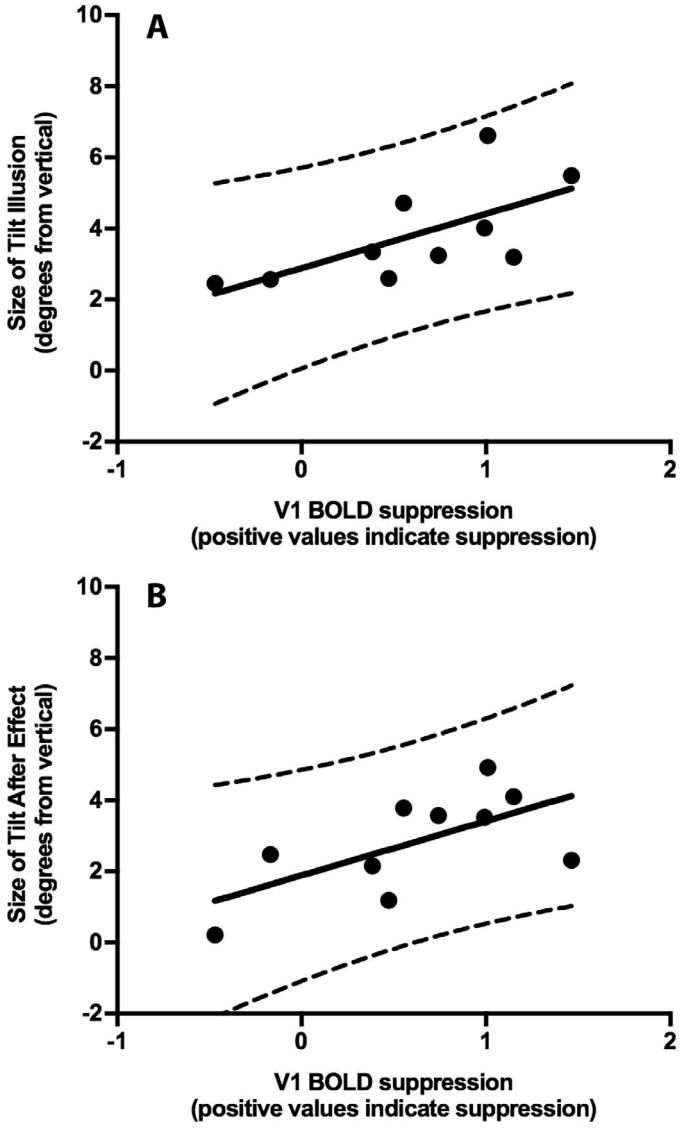

Figure 4. V1 suppression levels correlate with size of perceptual effects. (A) V1 suppression correlates with size of the tilt illusion ($R = 0.655$, $p = 0.019$, 95% CI: 0.044–0.910). (B) V1 suppression correlates with size of the tilt aftereffect ($R = 0.637$, $p = 0.023$, 95% CI: 0.012–0.904). V1 suppression is calculated as mean suppression averaged across parallel and orthogonal conditions. 95% prediction intervals are plotted.

15° elicited a shift in perceived orientation of the target grating away from the inducer orientation, mean PSV: 2.826°, *SE*: 0.452°, $t(9) = 6.254$, $p < 0.001$, $d = 1.978$.

To test for psychophysical evidence of a common underlying mechanism, we correlated the magnitudes of participants' tilt illusion and tilt aftereffects. A common mechanism would predict that a stronger tilt illusion would predict stronger tilt aftereffects. A significant positive correlation was found ($R = 0.622$, $p = 0.027$, 95% CI: −0.013–0.899, post hoc power: 0.52; Figure 3).

Relationship between contextual effects on neural processing and perception

We examined the inhibitory influence of context on BOLD activity in human V1 and the magnitude of two context-induced visual illusions: The tilt illusion and tilt aftereffect (Figure 4). We found evidence for a significant positive relationship between the magnitude of BOLD suppression in V1, averaged across parallel and orthogonal conditions, and the size of the perceived shift in orientation experienced with the tilt illusion (Figure 4A; $R = 0.655$, $p = 0.019$, 95% CI: 0.044–0.910, post hoc power: 0.580) and tilt aftereffect (Figure 4B; $R = 0.637$, $p = 0.023$, 95% CI: 0.012–0.904, post hoc power: 0.546). That is, participants who showed stronger BOLD suppression in V1 also perceived stronger shifts in tilt with these two illusions.

When we examined our data further, we found no significant positive relationship between the *orientation dependence* of BOLD suppression and the strength of the illusions (tilt illusion: $R = 0.277$, $p = 0.438$; tilt aftereffect: $R = 0.144$, $p = 0.691$). In short, the extent to which V1 suppression was modulated by the orientation difference between target and surround did not explain the significant correlation.

Also, to rule out the possibility that these results were due to individual differences in basic cortical function, rather than V1 inhibition per se, we examined the relationship between illusion magnitude and baseline measurements of BOLD activity in V1 (i.e., elicited by the no-surround condition). We found no significant positive correlation between the size of the tilt illusion or tilt aftereffect and baseline BOLD activity (tilt illusion: $R = -0.098$, $p = 0.789$; tilt aftereffect: $R = -0.597$, $p = 0.597$). Moreover, to estimate the amount of bias introduced by our small sample size, we performed a jackknife analysis. The data were resampled n times (n indicates number of subjects), and, in each resampling, one subject was excluded and the correlation was then computed. This analysis estimated the tendency of the sample correlation to overestimate or underestimate the true, unknown correlation. We found that the sample correlations tended to underestimate the true unknown correlations (tilt illusion vs. tilt aftereffect bias = −0.0568; BOLD vs. tilt illusion bias = −0.0171; BOLD vs. tilt aftereffect: = 0.0567), confirming that the significance of the reported correlations was not an artefact of sample size.

Discussion

In this study, we examined the link between neural and perceptual processing of oriented contextual visual

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stimuli and sought evidence for a shared mechanism underlying the tilt illusion and tilt aftereffect. We found direct evidence for a significant relationship between the magnitude of BOLD suppression in participants' V1 and the size of illusory tilt they experienced in both these illusions. Specifically, participants who showed stronger neural suppression in V1 also perceived stronger shifts in perceived orientation. We also showed that a participant's susceptibility to the tilt illusion (i.e., illusion magnitude) was predictive of their susceptibility to the tilt aftereffect. Together, these data suggest a shared mechanism mediating both spatial and temporal effects of context on the perception of orientation that involves the inhibition of cortical responses in V1.

Our findings of a relationship between BOLD suppression in V1 and illusory tilt magnitude is consistent with theoretical models suggesting that V1 inhibition underlies these perceptual effects (Clifford, 2014; Schwartz et al., 2007; Schwartz et al., 2009; Wenderoth & Johnstone, 1988a, 1988b). For instance, Wenderoth & Johnstone (1988a, 1988b) proposed that repulsive effects in both the tilt illusion and the tilt aftereffect arise from a combination of lateral inhibition between neurons tuned to similar orientations (Bosking, Zhang, Schofield, & Fitzpatrick, 1997; Dragoi & Sur, 2000; Stettler, Das, Bennett, & Gilbert, 2002; Weliky, Kandler, Fitzpatrick, & Katz, 1995) as well as an untuned component fed back to V1 from higher visual areas (Hupe et al., 1998; Shushruth et al., 2013; Zipser, Lamme, & Schiller, 1996). While the current study found no evidence for illusion strength being correlated with the orientation tuning of V1 suppression, we did find support for involvement of V1 inhibition. Thus, while *direction* of the tilt illusion and tilt aftereffect might be determined by inhibitory interactions between neurons tuned to similar orientations, our data suggest that untuned inhibition might be of importance to both of these illusions in driving the magnitude of the effects.

In a recent human fMRI study by Song et al. (2013), it was reported that individual differences in the strength of effective connectivity within V1 were significantly correlated with participants' tilt illusion magnitudes (Song et al., 2013). This finding was attributed to differences in the strength of orientation-tuned lateral inhibition in V1, but no evidence of orientation-tuned BOLD suppression was reported to support this claim. Also, because the study did not specifically dissociate V1 responses from other early visual regions (i.e., by avoiding the foveal confluence (Schira et al., 2009), it is possible the reported orientation-tuned modulations were from extrastriate sources. This possibility is consistent with suggestions that the tilt illusion relies on neural contributions outside of V1 (Wenderoth & Johnstone, 1987). Thus, while there is evidence from psychophysics and computational modeling that lateral inhibition plays a critical role in generating the tilt illusion (Blakemore & Tobin, 1972; Carpenter & Blakemore, 1973; Clifford, 2014; Magnussen & Kurtenbach, 1980; Schwartz et al., 2007; Schwartz et al., 2009; Wenderoth & Johnstone, 1987, 1988a, 1988b), the current human fMRI data only provide evidence to support an involvement of context-induced suppression of neural activity in V1. Future studies that employ more sensitive fMRI methods (e.g., Haynes & Rees, 2006; Kamitani & Tong, 2005; Wardle, Ritchie, Seymour, & Carlson, 2016) may provide evidence for orientation-tuned suppression underlying the tilt illusion. Moreover, the data presented here is limited in terms of its sample size and thus, although consistent, the effect size estimates are essentially undetermined and might therefore be misleading. Accordingly, greater statistical power using the current approach might also help to detect a significant relationship between the orientation tuning of BOLD suppression and illusion strength.

The current research provides empirical evidence that the suppression of neural activity in human V1 mediates the effects of context on orientation perception. We build on evidence from human psychophysics and computational neuroscience for a shared mechanism underlying these effects in both the spatial and temporal domain (Chen, Chen, Gao, Yang, & Yan, 2015; Clifford, 2014; Clifford et al., 2000; Gibson & Radner, 1937; Schwartz et al., 2007; Schwartz et al., 2009; Wenderoth & Johnstone, 1987). Inhibition between orientation selective cortical neurons has been suggested to underlie both the tilt illusion and tilt aftereffect, with the inhibition being tonic to account for the tilt aftereffect (Wenderoth & Johnstone, 1988a). Our data provide evidence in support of this. However, it should be noted that the BOLD signal is a proxy for neuronal activity and thus should be interpreted with caution. That is, BOLD suppression in a brain region could result from a number of sources including lateral inhibition, feedback, or a combination of the two. Moreover, it is possible that the tilt illusion and tilt aftereffect rely on distinct neural mechanisms that are indistinguishable with fMRI. Indeed, the tilt illusion might recruit GABA (γ-Aminobutyric acid) mediated lateral inhibition, while the tilt aftereffect might result from synaptic depression or fatigue of excitatory neurons due to changes in ion channel dynamics (e.g., Carandini, Heeger, & Movshon, 1997; Carandini, Movshon, & Ferster, 1998; McLean & Palmer, 1996; Shepherd, 2001; Ursino, Magosso, & Cuppini, 2008). In both cases, suppression of the BOLD response would be observed. Moreover, GABA agonists have been reported to affect the tilt illusion and tilt aftereffect differently (Gelbtuch, Calvert, Harris, & Phillipson, 1986). Thus, future research to examine the

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role of V1 GABA in human V1 will provide important insight into the relationship between neural and perceptual processing of oriented contextual stimuli.

Keywords: contextual modulation, visual perception, fMRI, primary visual cortex, suppression, tilt illusion, tilt aftereffect

Acknowledgments

This research was supported by a grant awarded to K.S. from the Alexander von Humboldt Foundation. We thank Damien Mannion for his helpful comments.

Commercial relationships: none.
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