

Texture-surround suppression of contour-shape coding in human vision

Frederick AA. Kingdom^a and Nicolaas Prins^b

Contextual influences on neurons in the primary visual cortex have largely been studied using simple visual stimuli and their functional role is still poorly understood. Using a novel visual after-effect of perceived shape we show psychophysically that the coding of a contour's shape is inhibited by nearby parallel, but not orthogonal texture orientations. This suggests that neurons in the visual cortex that are suppressed by parallel orientations feed their outputs into higher visual areas that are involved in the processing of contour shape and in the recognition of objects. *NeuroReport* 20:5–8 © 2009 Wolters Kluwer Health | Lippincott Williams & Wilkins.

NeuroReport 2009, 20:5–8

Keywords: contour-shape coding, shape after-effect, texture-surround inhibition

^aDepartment of Ophthalmology, McGill University, McGill Vision Research, Quebec, Canada and ^bDepartment of Psychology, University of Mississippi, USA

Correspondence to Dr Frederick Kingdom, PhD, McGill Vision Research, Department of Ophthalmology, McGill University, Quebec, Canada
Tel: +1 514 934 1934; fax: +1 514 843 1691; e-mail: fred.kingdom@mcgill.ca

Received 15 August 2008 accepted 19 August 2008

Introduction

In the primary visual cortex of mammals (area V1) a large proportion of neurons are sensitive to lines of a particular orientation. Of these, a subset are suppressed by oriented lines [1–8], or suppressed or enhanced by naturalistic stimuli [9] placed outside of their classical receptive fields. With oriented lines the suppression is typically maximal when the orientations are the same as the preferred orientation of the neuron, and minimal when orthogonal (at right angles) to it. Neurons with these properties are said to exhibit 'isorientation surround suppression' or IOSS. Computer simulations of the responses of model IOSS neurons to images of natural scenes reveal that they are preferentially sensitive to isolated contours, such as the edges of objects, but relatively unresponsive to lines in dense textures [10,11]. Behavioural support for the idea that IOSS neurons are involved in detecting isolated contours comes from demonstrations of contours becoming 'lost' when surrounded, but not occluded by parallel lines [9].

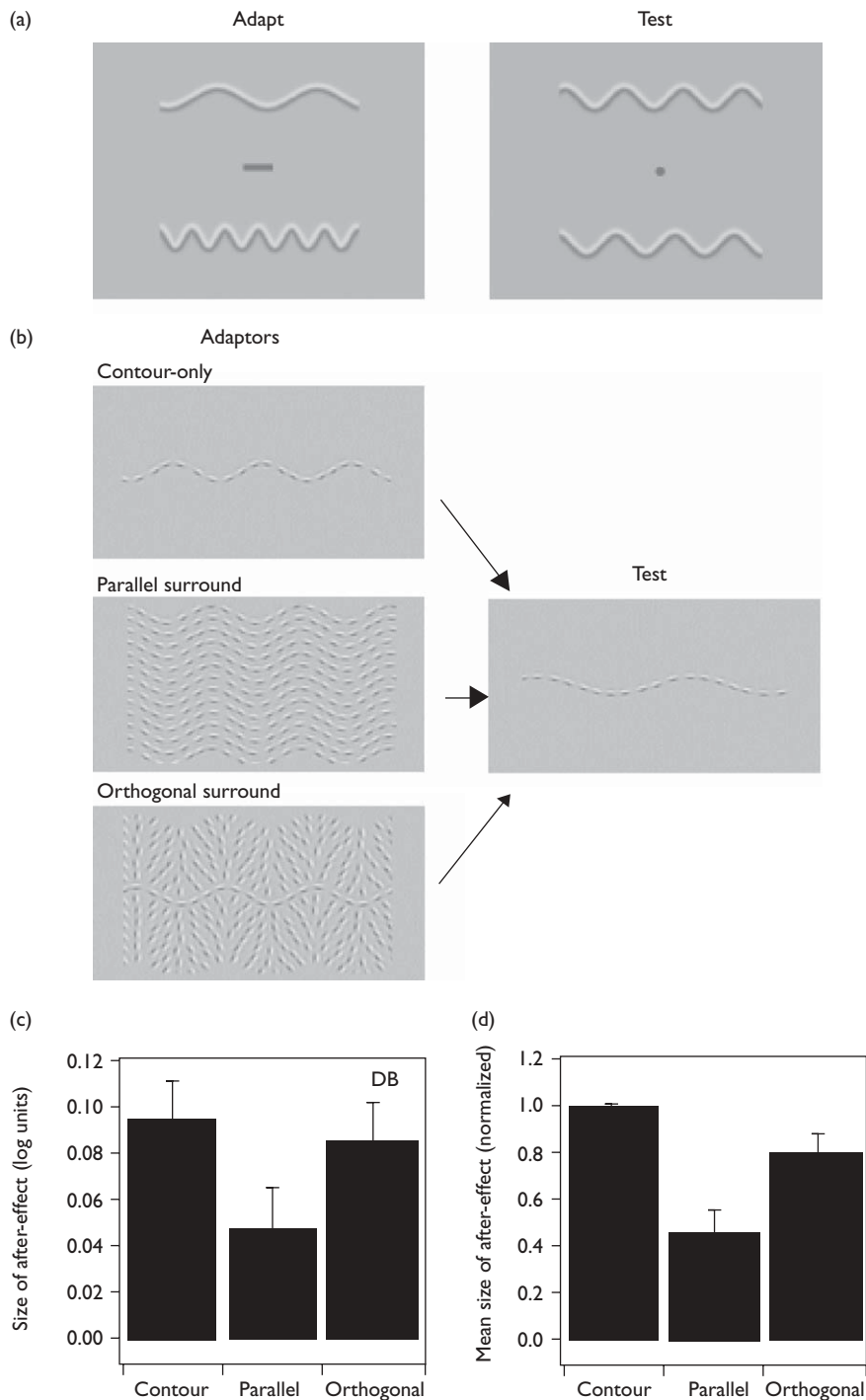
The visual analysis of a contour's shape is crucial for object recognition [12,13], and contour shape processing is believed to be mediated by neurons in visual areas higher than V1, such as V4 [14–18]. It is possible therefore that IOSS neurons feed their responses into contour-shape coding neurons in these higher areas, with the functional role of IOSS being to accentuate isolated contours for the purposes of shape coding.

Here we use a behavioural method to determine whether contour-shape coding is subject to IOSS. The method involves a novel visual after-effect of perceived shape: the 'shape-frequency after-effect' or SFAE [19,20]. The

SFAE is the phenomenon in which adaptation to a sine-wave-shaped contour produces a shift in the apparent shape frequency (the number of cycles of shape modulation per unit visual angle) of a test contour with a slightly different shape frequency from that of the adaptation stimulus. The shift is in a direction away from that of the adapting stimulus [19,20]. Readers can experience the after-effect in Fig. 1a. If one moves one's eyes back and forth along the horizontal marker between the pair of adapting contours on the left for about a minute, and then transfers one's gaze to the spot on the right, the two test contours above and below the fixation dot seem to have a different shape frequency, even though they are physically identical. The after-effect does not result simply from adaptation to local orientation, as with the well-known tilt after-effect, but from adaptation to the curvature in the sinusoidal shape [20]. The nonstatic adaptor version of the SFAE can be viewed on <http://www.mvr.mcgill.ca/Fred/research.htm#contourShapePerception>. The SFAE is useful for probing contour shape processing in human vision as it presumably results from changes in the response distribution of neurons specialized for the coding of contour shape, in a manner similar to that proposed for other spatial after-effects [21,22].

To test whether textured surrounds influence the SFAE we constructed our stimuli from Gabor micropatterns, which are small patches of sinusoidal grating windowed by a smooth Gaussian envelope. Gabors are narrowband in their luminance spatial frequency composition, and their use minimizes the possibility of the texture surround having an impact on the contour's luminance spatial frequency composition. We measured the SFAE using three types of adaptor, shown in Fig. 1b. All three

Fig. 1



(a) The shape-frequency after-effect. To experience the after-effect move one's eyes back and forth along the marker located midway between the pair of adapting contours on the left for about 90 s, and then shift one's gaze to the middle of the test contours on the right. (b) Types of adaptor and test stimulus used in the experiments. Only one of each adaptor pair and only one of the test pair is shown. (c) Shows typical results from one naïve patient. (d) Results normalized to the contour-only condition and averaged across six patients.

adaptors contained a central contour consisting of coaligned Gabor micropatterns. In the 'contour-only' condition there was no surround texture; in the 'parallel-

surround' condition the central adapting contour was flanked by an array of similar contours; in the 'orthogonal-surround' condition the Gabors in the flanking contours

were rotated by 90 deg. The test contours in all three conditions were single contours made from coaligned Gabors, as shown in Fig. 1.

To measure the SFAE we used a conventional psychophysical cancellation method in which test subjects adjusted the relative shape frequencies of two test contours that had been adapted in opposite directions, as in Fig. 1a, until they appeared equal in shape frequency – the point-of-subjective-equality, or PSE (see Methods). The size of the SFAE was then calculated as the logarithm of the ratio of test shape frequencies at the PSE.

Methods

Stimuli

The stimuli were displayed by a VSG2/5 video-graphics card (Cambridge Research Systems, Rochester, Kent, England) with 12-bits contrast resolution, on a calibrated, γ -corrected monitor running at 120 Hz frame rate (resolution of 1024×768 pixels). Stimuli were constructed from Gabors with a centre luminance spatial frequency of 7.0 cycles per degree, contrast of 80%, bandwidth of 1.5 octaves, mean luminance 42 cd/m^2 and odd-symmetric phase. The Gabors were positioned along the sinusoidal shape profile with orientations either tangential or orthogonal to the shape profile. The centre-to-centre spacing between adjacent Gabors was randomly selected from within the range ± 0.1 deg around a mean of 0.3 deg. On average 19 Gabors per string were present. Stimulus width was 5 deg. Viewing distance was 100 cm.

All contours had a shape amplitude of 0.2 deg. The two adaptor contours had shape frequencies of 0.2 and 0.6 c/deg (geometric mean 0.35 c/deg). The relative shape frequencies of the two test contours was varied during the test period (see below) around a geometric mean shape frequency of 0.35 c/deg. The two adaptors/tests were presented in the centre of the monitor 2.5 deg above and below the fixation marker. The shape phases of both adaptors and both tests were randomized on each presentation.

The centre adaptor contour consisted of Gabors oriented tangentially to the profile. Texture surrounds consisted of six contours above and six contours below the central adaptor contour, with Gabors oriented either tangentially ('parallel' condition) or perpendicular to the tangent ('orthogonal' condition) (Fig. 1b).

Procedure

Each session began with an initial adaptation period of 90 s, followed by a test period in which test displays of 0.5 s duration were interspersed with top-up adaptation periods of 2.5 s. Test subjects fixated a marker in between each pair of contours for the entire session. At the start of

the test period the ratio of the two test shape frequencies was set to a random number between 0.71 and 1.4. On each test presentation (signalled by a tone) the subject indicated which of the two test contours had the higher shape frequency. The computer then adjusted the relative shape frequencies of the two test contours in a direction towards the PSE. The session was terminated after 25 trials, and the shape-frequency ratio at the PSE calculated as the geometric mean shape-frequency ratio over the last 20 trials. Nine measurements were made for each condition, three in which the upper adaptor had the higher shape frequency, three in which the lower adaptor had the higher shape frequency, and three without any adaptor. The magnitude of the after-effect was calculated by subtracting the mean log 'without adaptor' PSE ratio from each of the 6 log 'with-adaptor' PSE ratio, then calculating the mean (and standard error) of these results.

Results

Figure 1c shows a typical result from one of the naive test subjects, whereas Fig. 1d shows the average results of six test subjects (only one of whom was an author: F.K.), after normalization of the parallel-surround and orthogonal-surround results to the contour-only condition for each subject. Introducing flanking contours (the parallel-surround condition) reduced the SFAE measured in the contour-only condition by about half. When the micropatterns in the flanking contours were rotated by 90 deg, however, the after-effect was mostly restored. Paired (within-subject) *t*-tests were conducted on the non-normalized data to test for significant differences between each pair of conditions. After Bonferroni correcting the *P* values to allow for multiple comparisons (by increasing the calculated *P* values three-fold), the differences between the contour-only and parallel-surround conditions ($t = 5.9$, d.f. = 5, $P = 0.006$), and between the parallel-surround and orthogonal-surround conditions ($t = 4.253$, d.f. = 5, $P = 0.024$) were both significant using the *P* value of less than 0.05 criterion. The difference between the contour-only and orthogonal-surround conditions was just nonsignificant ($t = 3.216$; d.f. = 5, $P = 0.072$).

Discussion

The parallel-surround adaptors consisted of multiple contours covering most of the regions of visual space containing the test contour, so one might expect their adaptive effect to be greater than that produced from the single-contour adaptors. Yet the opposite was found. Why is this? One might suppose that the 'good continuity' of the individual contours in the parallel surround condition was disrupted by the micropatterns adjacent to it. In a recent brief communication, however, we reported similar results for the parallel-surround versus single-contour adaptors using continuous contours rather than ones

constructed from micropatterns (the study did not use the orthogonal-surround adaptor condition used here) [23]. Thus disruption of contour continuity is not the reason for the reduced after-effect with multiple contour adaptors. It must also be emphasized that the contours in the parallel-surround condition were not in any way occluded by the other contours, so an explanation of the results in terms of overlay masking can also be ruled out.

The central contour in the orthogonal-surround condition seems to 'popout' more than in the parallel-surround condition. The relative effectiveness with which the central contour in the orthogonal-surround adaptor produces shifts in the perceived shape frequency of a single-contour test may therefore be correlated with its degree of popout, though not necessarily so – this is an empirical question. It is worth emphasizing, however, that the degree to which the adaptor contours popped-out was irrelevant to the subject's actual task, which was to compare the relative shape frequencies of two, single test contours. Even more important is that the critical stimulus feature of the adaptor contours – their shape – is as salient in the parallel-surround as in the orthogonal-surround adaptors. Yet the impact of the two adaptors on the perceived shape of the test is so different. Arguably what is most remarkable is that the parallel-surround adaptor is 'packed' with far more relevant-shaped contours than either the orthogonal-surround or the single-contour adaptor, yet produces the smallest after-effect.

The most likely explanation for the selectively weak adaptive effect of the parallel-surround condition is that contour shape mechanisms are inhibited by parallel but not orthogonal orientations. This could be explained by supposing that shape-coding neurons in higher visual areas are directly inhibited by other neurons in the same area sensitive to parallel structure. On the other hand, given that many neurons in V1 exhibit IOSS, the most likely explanation is that these neurons feed their responses directly into shape-coding neurons in higher visual areas, and are therefore intimately involved in the coding of contour shape, and hence object recognition.

Conclusion

Contour shape processing in human vision is inhibited by the presence of nearby parallel contours. This suggests that those orientation-selective neurons in the visual cortex that are inhibited by similar orientations outside

their classical receptive fields are intimately involved in the processing of contour shape.

Acknowledgements

This study was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) grant # OGP01217130 given to F.K.

References

- 1 Blakemore C, Tobin EA. Lateral inhibition between orientation detectors in the cat's visual cortex. *Exp Brain Res* 1972; **15**:439–440.
- 2 Nelson JI, Frost BJ. Orientation-selective inhibition from outside the classic receptive field. *Brain Res* 1978; **139**:359–365.
- 3 Knierim JJ, van Essen DC. Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. *J Neurophysiol* 1992; **67**:961–980.
- 4 Cavanaugh JR, Bair W, Movshon JA. Nature and interaction of signals from the receptive field center and surround in macaque V1 neurons. *J Neurophysiol* 2002; **88**:2530–2546.
- 5 Levitt JB, Lund JS. Contrast dependence of contextual effects in primate visual cortex. *Nature* 1997; **387**:73–76.
- 6 Nothdurft HC, Gallant JL, van Essen DC. Response modulation by texture surround in primate area V1: Correlates of 'popout' under anesthesia. *Vis Neurosci* 1999; **16**:15–34.
- 7 Jones HE, Grieve K, Wang W, Sillito AM. Surround suppression in primate V1. *J Neurophysiol* 2001; **86**:2011–2028.
- 8 Yao H, Li CY. Clustered organization of neurons with similar extra-receptive field properties in the primary visual cortex. *Neuron* 2002; **35**:547–553.
- 9 Vinje WE, Gallant JL. Natural stimulation of the nonclassical receptive field increases information transmission efficiency in V1. *J Neurosci* 2002; **22**:2904–2915.
- 10 Petkov N, Westenberg MA. Suppression of contour perception by band-limited noise and its relation to non-classical receptive field inhibition. *Biol Cybern* 2003; **88**:236–246.
- 11 Grigorescu C, Petkov N, Westenberg MA. Contour and boundary detection improved by surround suppression of texture edges. *Image Vis Comput* 2004; **22**:609–622.
- 12 Marr D. Vision WH. Freeman and Co.; 1982.
- 13 Biederman I. Recognition-by-components: a theory of human image understanding. *Psychol Rev* 1987; **94**:115–147.
- 14 Gallant JL, Braun J, Van Essen DC. Selectivity for polar, hyperbolic and Cartesian gratings in macaque visual cortex. *Science* 1993; **259**:100–103.
- 15 Gallant JL, Connor CE, Rakshit S, Lewis JW, Van Essen DC. Neural responses to polar, hyperbolic, and Cartesian gratings in area V4 of the macaque monkey. *J Neurophysiol* 1996; **76**:2718–2739.
- 16 Pasupathy A, Connor CE. Responses to contour features in macaque area V4. *J Neurophysiol* 1999; **82**:2490–2502.
- 17 Pasupathy A, Connor CE. Shape representation in area V4: position-specific tuning for boundary conformation. *J Neurophysiol* 2001; **86**:2505–2519.
- 18 Pasupathy A, Connor CE. Population coding of shape in area V4. *Nat Neurosci* 2002; **5**:1332–1338.
- 19 Gheorghiu E, Kingdom FAA. Luminance-contrast properties of contour-shape processing revealed through the shape-frequency after-effect. *Vis Res* 2006; **46**:3603–3615.
- 20 Gheorghiu E, Kingdom FAA. The spatial features underlying the shape-frequency and shape-amplitude after-effects. *Vis Res* 2007; **47**:834–844.
- 21 Georgeson M. Visual aftereffects: cortical neurons change their tune. *Curr Biol* 2004; **14**:751–753.
- 22 Clifford CWG. Perceptual adaptation: motion parallels orientation. *Trends Cogn Sci* 2002; **6**:136–143.
- 23 Kingdom FAA, Prins N. Separate aftereffects for the shapes of contours and textures made from contours. *Perception* 2005; **34** (Suppl):44.