

## SELECTIVE MECHANISMS FOR COMPLEX VISUAL PATTERNS REVEALED BY ADAPTATION

J. W. PEIRCE\* AND L. J. TAYLOR

Visual Neuroscience Group, School of Psychology, University of Nottingham, University Park, Nottingham NG7 2RD, UK

**Abstract**—A great deal is known about the initial steps of visual processing. We know that humans have neural mechanisms selectively tuned to simple patterns of particular spatial frequencies and orientations. We also know that much later in the visual pathway, in inferotemporal cortex, cells respond to extremely complex visual patterns such as images of faces. Very little is known about intermediate levels of visual processing, where early visual signals are presumably combined to represent increasingly complex visual features. Here we show the existence of visual mechanisms in humans, tuned and selective to particular combinations of simple sinusoidal patterns, using a novel method of compound adaptation. © 2006 IBRO. Published by Elsevier Ltd. All rights reserved.

**Key words:** conjunctions, Fourier, compound adaptation, second-order, V4, plaid.

One of the common principles of sensory processing is that at each step along the processing stream the signals from an earlier stage are generally combined in some way to create a new, more complex and sparse, representation of the world. For example, the outputs from the retinal photoreceptors are combined to form the center-surround antagonistic receptive fields of retinal ganglion cells. These respond selectively to the presence of contrast, rather than simply luminance. Similarly, the outputs of retinal ganglion cells are combined by neurons in primary visual cortex (V1) to form elongated receptive fields. These neurons, often characterized as Fourier energy detectors (De Valois and De Valois, 1988), respond selectively to luminance contrast of a particular orientation and spatial frequency.

We investigated the presence and nature of mechanisms that combine the outputs of V1 neurons, looking for a system that might respond selectively to particular combinations of Fourier energy, namely to particular plaids. Plaids have been used in vision research predominantly in the study of visual motion perception (Movshon et al., 1986; Rodman and Albright, 1989; Huk and Heeger, 2002) but also to show interactions between early visual channels (Olzak and Thomas, 1991; Georgeson, 1992; Carandini et al., 1997a; Georgeson and Meese, 1997). None of these studies has demonstrated the existence of mech-

anisms selective to the form of the compound patterns per se.

Using a novel method of compound adaptation we show that such mechanisms do exist in the human visual system. The method bears strong similarities to that used to show the existence of spatial frequency selective mechanisms (Blakemore and Campbell, 1969), in which prolonged exposure to a particular sinusoidal grating reduces sensitivity to the adapter but not to other gratings. The compound adaptation method works by adapting subjects simultaneously to multiple sinusoidal plaid patterns and then testing the apparent contrast of each. The apparent contrast of a pattern in a retinal location where it had been adapted as an intact pattern (compound adaptation) is compared with another location where its components had been used to comprise other plaid patterns (component adaptation). We show that the test plaid has a lower apparent contrast in the compound-adapted field than the component-adapted location, indicative of mechanisms selective to the form of the pattern rather than its components.

### EXPERIMENTAL PROCEDURES

#### Participants

Four healthy volunteers (three experienced observers and one naïve participant), with normal or corrected-to-normal vision, gave their informed consent and participated in the study. All procedures were approved by the School of Psychology Ethics Committee, University of Nottingham, UK.

#### Apparatus

Stimuli were presented on a computer-controlled CRT monitor (Vision Master Pro 514, Iiyama) at a resolution of 1152×864 pixels and at a refresh rate of 85 Hz with a mean luminance of 50.9 cd/m<sup>2</sup>. The monitor was driven by 14-bit DACs (Bits++, Cambridge Research Systems, Cambridge, UK). It was calibrated using a photo-spectrometer (PR650, Photo Research, Chatsworth, CA, USA) and the gamma correction was verified psychophysically using a 2nd-order motion-nulling procedure (Ledgeway and Smith, 1994). Stimuli were presented and data collected using the PsychoPy stimulus generation library (<http://www.psychopy.org>). The observer's head was stabilized in a chin-rest 57 cm from the monitor with the viewable area subtending 40.5 degrees of visual angle horizontally.

#### Stimuli

Plaids were constructed from the linear combination of four luminance-modulated sinusoidal gratings, each with different spatial characteristics; grating A had spatial frequency (SF)=1.5c/° and orientation (ori)=0°; B (SF=1.5c/°, ori=90°); C (SF=2.5c/°, ori=135°); D (SF=2.5c/°, ori=45°). These gratings were com-

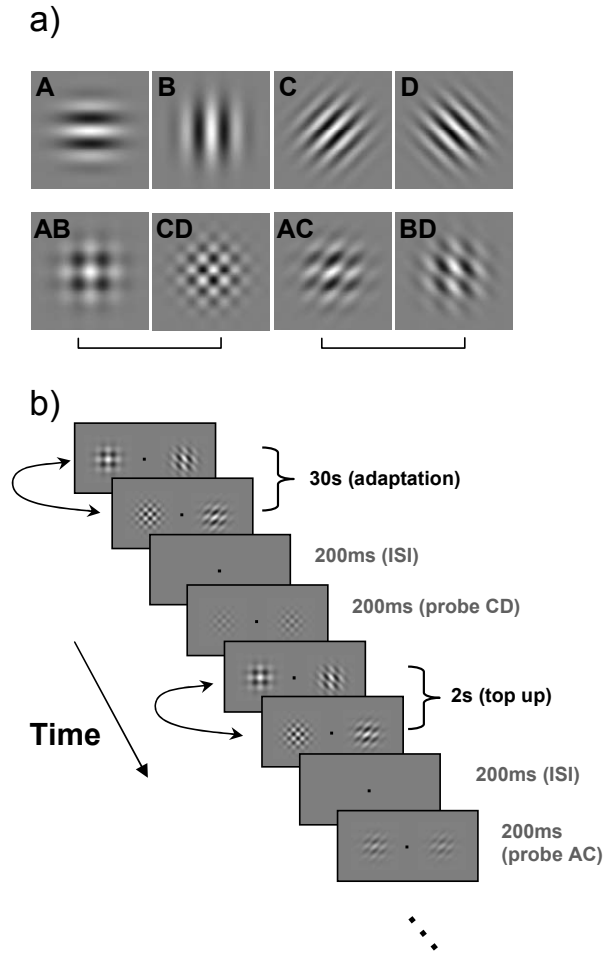
\*Corresponding author. Tel: +44-115-8467176.

E-mail address: jon@peirce.org.uk (J. W. Peirce).

Abbreviations: ISI, inter-stimulus interval; ori, orientation; PSE, point of subjective equality; SF, spatial frequency; V1, primary visual cortex.

0306-4522/06/\$30.00+0.00 © 2006 IBRO. Published by Elsevier Ltd. All rights reserved.

doi:10.1016/j.neuroscience.2006.04.039



**Fig. 1.** (a) Construction of the four plaid stimuli from their component gratings. Note that each pair of plaids contains all four components. (b) Procedure. After an initial adaptation of 30 s, probes were presented for 200 ms, each preceded by a top-up of 2 s.

bined into four different plaid patterns; AB, CD, AC and BD (Fig. 1a). In all stimuli the components contributed equal contrast to the plaid. Note the plaids form complementary pairs where AB and CD together share the same components as AC and BD. All stimuli were presented in a Gaussian envelope with standard deviation of  $0.5^\circ$  (such that the stimulus had a diameter of  $3^\circ$  at the point where it fell below 1% contrast). This size of stimulus corresponds roughly to the size of the excitatory portion of the receptive field for a macaque V1 neuron under low-contrast stimulation (Sceniak et al., 1999; Cavanaugh et al., 2002).

During adaptation a pair of plaids (e.g. AB and CD) was presented at maximum contrast (0.982) in one visual hemi-field, alternating between patterns every second, with the complementary pair alternating equivalently in the other field. The patterns were also counter-phase modulated at 2 Hz. This modulation was rapid enough to prevent the occurrence of luminance afterimages on the retina but is too slow to result in sub-cortical contrast adaptation (Solomon et al., 2004). The Michelson contrast of the probes varied between 0.155–0.245 in steps of 0.015 and each probe pair had an average contrast of 0.2. As a result all stimuli had a low contrast but were comfortably suprathreshold.

### Procedure

The procedure is shown schematically in Fig. 1b. Participants were adapted to pairs of plaids simultaneously at different posi-

tions on the retina (centered at  $3^\circ$  either side of the fovea on the horizontal meridian); plaids AB and CD were presented at high contrast in the one visual hemi-field, alternating between plaids once per second, while AC and BD were adapted at the same time and in the same manner in the other hemi-field. The observers were then probed with one of the patterns (e.g. AB) presented at different contrasts in each location and were required to report the side on which the probe appeared to have higher contrast.

Exposure to the component gratings was identical in both hemi-fields, since the same four components were presented in each and for the same amount of time. If this were the only form of adaptation occurring then the point at which the stimuli appear equal in contrast would be the point at which they were physically identical. If, however, there were a neural mechanism responding (and adapting) selectively to the particular combination of components then the probe patterns would appear equal in contrast when the physical contrast was higher in the compound-adapted hemi-field. This is referred to as a shift in the point of subjective equality (PSE).

Effects of additional non-linearities such as cross-orientation inhibition (e.g. Morrone et al., 1982; Carandini et al., 1997b) might also be observed if these are not uniform across stimuli. For example, if there were greater cross-orientation suppression for plaid AB than for the other plaids then this might activate cortex less strongly and be a less effective adapter. In this case, all four probes will appear higher in contrast on the side of the weaker adapter(s), resulting in a positive PSE shift for the strong-adapting stimuli and a negative shift for the weakly-adapting stimuli. If the strength of these non-linearities is roughly uniform between adapters then they should not impact the PSE since, again, the two hemi-fields would be balanced.

There was an initial adaptation period of 30 s and this was ‘topped up’ with a 2 s period before each trial. There followed a blank inter-stimulus interval (ISI) of 200 ms and the two probes were presented for a further 200 ms. The fixation point, a black circle six arc minutes in diameter, was visible throughout the adaptation period, ISI and probe presentation. During probe presentations the same plaid (randomly chosen each trial) was presented in the two fields with different contrasts in each. The subject then responded by pressing a button on a keypad to indicate whether the right or left stimulus had a higher contrast. The response triggered the next trial to begin, with another top-up period.

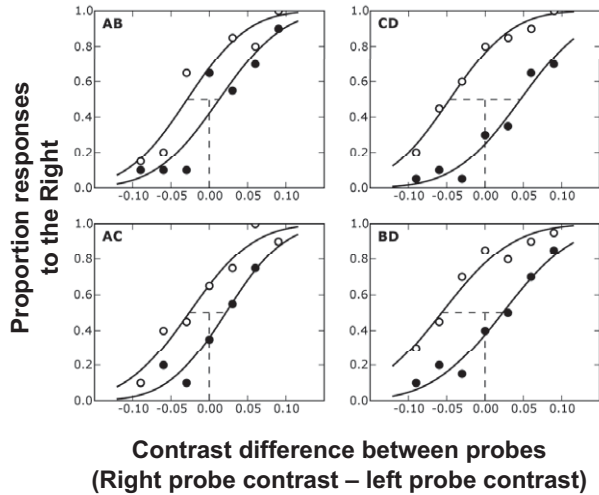
Trials were conducted in blocks of four with all probes and all contrasts randomly interleaved. For each stimulus, and in each adapter configuration (AB and CD adapted in the left hemi-field and then the right), 40 trials were conducted by experienced observers and 20 trials were conducted by the naïve observer. The additional trials run by the experienced observers did little, if anything, to reduce the confidence interval of the fitted curve parameters. On any day of testing subjects were only adapted to one adapter configuration (e.g. AB and CD in the left hemi-field).

### Data analysis

For each of the four plaids, we quantified the effect of compound adaptation as the amount of additional contrast needed in the adapted hemi-field for the probes to appear equal (PSE). Weibull functions were fit to the psychometric data and to 5000 bootstrap resamples of it. From these fits the PSE, its standard error and 95% confidence interval were derived for each subject and each stimulus (Hesterberg et al., 2005).

## RESULTS

The psychometric functions for the naïve observer (V.E.S.) are shown in Fig. 2. When plaid AB was adapted on the left and its components on the right (Fig. 2, upper left panel,



**Fig. 2.** Psychometric functions for one naïve observer (V.E.S.) for trials where each of the four probes had been used as an adapter on the right (filled symbols) or on the left (open symbols). Dashed lines represent the separation between the functions (horizontal) and the point of veridical equality (vertical). The effect of compound adaptation can be quantified as the mean shift of these functions from zero (i.e. half the length of the horizontal dashed line).

open symbols) the psychometric function was shifted to the left, indicating that greater contrast was needed in the left visual hemi-field for the stimuli to appear equal. Conversely, when this plaid was adapted on the right and its components on the left (closed symbols) the psychometric function was shifted to the right. The same pattern can be seen for all four stimuli.

The amplitude of the effect for each plaid and for each observer is shown in Fig. 3. The compound adaptation effect size is the average magnitude of the PSE shift in the predicted direction (compound adaptation =  $(PSE_R + PSE_L)/2$ ). For every observer and for every stimulus the compound adaptation effect was significantly greater than expected by chance (zero PSE shift, predicted by the null hypothesis, falls outside the 95% c.i.). The average magnitude of the effect across all stimuli and subjects was 3% contrast, meaning that the stimuli appeared equal when the probe had a contrast of roughly 21.5% in the compound-adapted field versus 18.5% in the component-adapted field. There was a statistically significant difference between the effect size for different plaids (based on a repeated measures ANOVA,  $F(3,12)=4.917$ ,  $P<0.05$ ). It is not yet clear whether this difference is meaningful or what might have caused such a difference.

The fact that no stimuli showed a negative PSE shift suggests that the data were not caused by a single stimulus being dominant in adaptation (as might arise from differential cross-orientation suppression between adapters).

**DISCUSSION**

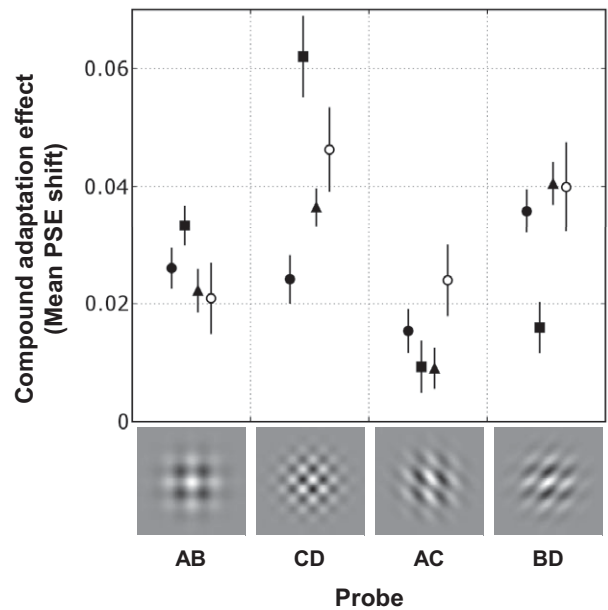
We have shown that the human visual system shows a selective adaptation to particular combinations of sinusoidal gratings after controlling for the effect of adaptation to the component gratings. In the same way that selective

adaptation to specific spatial frequencies and orientations suggests the existence of human visual mechanisms selective and tuned for those parameters, our results are indicative of mechanisms selective and tuned for particular compound patterns.

While there is much evidence that the first stage of visual processing involves the detection of Fourier components in an image, it is clear that visual form perception is based on a great deal more than this. The way in which components are combined has a profound effect on the visual perception of objects. For example, the four plaids in Fig. 1 give rise to very different percepts despite sharing, between them, the same Fourier components. The mechanisms implied here, unlike the spatial frequency channels previously found to be sensitive to particular gratings, are capable of discriminating such patterns.

These plaid-form-selective mechanisms should not be confused with the plaid-motion-selective mechanisms described by others studying cortical regions such as area MT/V5 (e.g. Movshon et al., 1986; Gizzi et al., 1990; Huk and Heeger, 2002). The two systems may or may not be related. For instance, the plaid-motion MT neurons might work by combining the Fourier components of the stimulus and extracting the motion of the combined pattern (in which case the plaid-form mechanisms might be considered a precursor to the MT cell). Alternatively, they may extract the motion information of each component and combine those motion signals (in which case the plaid-form neurons are not needed and presumably form part of a separate system).

Olzak and Thomas (1999) suggest a model for a putative plaid-form-selective mechanism based on the non-



**Fig. 3.** The magnitude of the compound adaptation effect. This is calculated for each probe and subject as the mean PSE shift (half the length of the horizontal dashed lines shown in Fig. 2). The shift was significantly greater than zero ( $P<0.05$ ) for all plaids and for all subjects. [●: J.W.P., ■: L.J.T., ▲: B.S.W., ○: V.E.S. (naïve)]. Error bars represent  $\pm 1$  S.E.M. based on 5000 bootstrap resamples.

linear summation of outputs from quasi-linear filters. The current data support the existence of such a mechanism and our compound adaptation method might also allow further details of that model to be investigated. We would like to know, for instance, how many input channels can be combined by any one conjunction-selective unit and over what spatial extents and contrast ranges the mechanisms operate. We would also like to know where the mechanisms are located anatomically. Area V4, which sits in the ventral visual stream between V1 and temporal cortex, is very well positioned to carry out such processing and neurons in this area are certainly sensitive to moderately complex, arbitrary patterns (Gallant et al., 1996; Pasupathy and Connor, 1999). Combining the compound adaptation method with fMRI, in a similar manner to Huk and Heeger's (2002) study on MT motion-selectivity, might allow us to determine the areas involved in the selective detection of particular plaid forms.

We have shown, using a novel method compound adaptation, the presence of neural mechanisms selective to particular conjunctions of Fourier energies. These bridge a gap between the relatively simple edge-detection of neurons in V1 and the highly complex pattern analyzers in temporal cortex. The study demonstrates the existence of neural mechanisms for which the whole visual percept is greater than the sum of its Fourier parts, and provides a method with which to study their properties further.

*Acknowledgments*—Many thanks to Prof. David Heeger and Dr. Ben Webb for their useful comments. The work was supported by grants from the Royal Society (2003/R2) and the BBSRC (BB/C50289X/1) to J.W.P. and by a Wellcome Trust Vacation Scholarship (VS/04/NOT/AA23) to L.J.T.

## REFERENCES

- Blakemore C, Campbell FW (1969) On the existence of neurons in the human visual system selectively sensitive to the orientation and size of retinal images. *J of Physiology* 203:237–260.
- Carandini M, Barlow HB, O'Keefe LP, Poirson AB, Movshon JA (1997a) Adaptation to contingencies in macaque primary visual cortex. *Philos Trans R Soc Lond B Biol Sci* 352:1149–1154.
- Carandini M, Heeger DJ, Movshon JA (1997b) Linearity and normalization in simple cells of the macaque primary visual cortex. *J Neurosci* 17:8621–8644.
- Cavanaugh JR, Bair W, Movshon JA (2002) Selectivity and spatial distribution of signals from the receptive field surround in macaque V1 neurons. *J Neurophysiol* 88:2547–2556.
- De Valois RL, De Valois KK (1988) *Spatial vision*. Oxford: Oxford University Press.
- Gallant JL, Connor CE, Rakshit S, Lewis JW, Van Essen DC (1996) Neural responses to polar, hyperbolic, and Cartesian gratings in area V4 of the macaque monkey. *J Neurophysiol* 76:2718–2739.
- Georgeson MA (1992) Human vision combines oriented filters to compute edges. *Proc R Soc Lond B Biol Sci* 249:235–245.
- Georgeson MA, Meese TS (1997) Perception of stationary plaids: the role of spatial filters in edge analysis. *Vision Res* 37:3255–3271.
- Gizzi MS, Katz E, Schumer RA, Movshon JA (1990) Selectivity for orientation and direction of motion of single neurons in cat striate and extrastriate visual cortex. *J Neurophysiol* 63:1529–1543.
- Hesterberg T, Moore DS, Monaghan S, Clipson A, Epstein R (2005) Bootstrap methods and permutation tests. In: *Introduction to the practice of statistics* (Moore DS, McCabe GP, eds). New York: WH Freeman.
- Huk AC, Heeger DJ (2002) Pattern-motion responses in human visual cortex. *Nat Neurosci* 5:72–75.
- Ledgeway T, Smith AT (1994) Evidence for separate motion-detecting mechanisms for first- and second-order motion in human vision. *Vision Res* 34:2727–2740.
- Morrone MC, Burr DC, Maffei L (1982) Functional implications of cross-orientation inhibition of cortical visual cells. I. Neurophysiological evidence. *Proc R Soc Lond B Biol Sci* 216:335–354.
- Movshon JA, Adelson EH, Gizzi MS, Newsome WT (1986) The analysis of moving visual patterns. *Exp Brain Res* 11:117–152.
- Olzak LA, Thomas JP (1991) When orthogonal orientations are not processed independently. *Vision Res* 31:51–57.
- Olzak LA, Thomas JP (1999) Neural recoding in human pattern vision: model and mechanisms. *Vision Res* 39:231–256.
- Pasupathy A, Connor CE (1999) Responses to contour features in macaque area V4. *J Neurophysiol* 82:2490–2502.
- Rodman HR, Albright TD (1989) Single-unit analysis of pattern-motion selective properties in the middle temporal visual area (MT). *Exp Brain Res* 75:53–64.
- Sceniak MP, Ringach DL, Hawken MJ, Shapley R (1999) Contrast's effect on spatial summation by macaque V1 neurons. *Nat Neurosci* 2:733–739.
- Solomon SG, Peirce JW, Dhruv NT, Lennie P (2004) Profound contrast adaptation early in the visual pathway. *Neuron* 42:155–162.

(Accepted 14 April 2006)  
(Available online 6 June 2006)