

Evidence that both area V1 and extrastriate visual cortex contribute to symmetry perception

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Bilateral symmetry is common in nature and most animals seem able to perceive it. Many species use judgements of symmetry in various behaviours, including mate selection [1–3]. Originally, however, symmetry perception may have developed as a tool for generating object-centered, rather than viewer-centered, descriptions of objects, facilitating recognition irrespective of position or orientation [4]. There is evidence that the visual system treats the orientation of axes-of-symmetry in the same way it treats the orientation of luminance-defined contours [5], suggesting that axes-of-symmetry act as ‘processing tokens’ [6]. We have investigated the characteristics of neural mechanisms giving rise to the perceived orientation of axes-of-symmetry. We induced tilt aftereffects with symmetrical dot patterns, eliciting perceived angle expansion and contraction effects like those usually observed with luminance-defined contours [7,8]. Induction of aftereffects during binocular rivalry resulted in a reduction of the magnitude of these effects, consistent with the aftereffects being mediated in extrastriate visual cortex, probably between visual areas V2 and MT [9]. In a second experiment in which the aftereffects were induced monocularly, their magnitudes were measured in the unadapted eye. Contraction effects transferred completely, suggesting that they are mediated by binocular cells. Expansion effects did not transfer completely, consistent with their having a monocular component. These data suggest that information about the orientation of axes-of-symmetry may be available as early as area V1, but that processing continues in extrastriate cortex.

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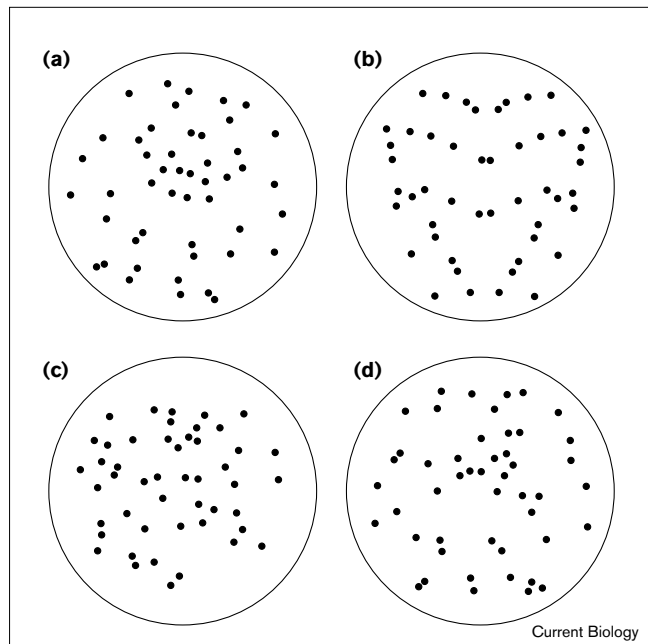
Results and discussion

Prolonged inspection of an inducing contour or grating tilted off vertical makes a subsequently presented,

vertically oriented test contour or grating look tilted. The direction and magnitude of this tilt aftereffect (TAE) depends on how far from vertical the inducing stimulus was originally. If the inducing and test stimuli are separated by between 5° and about 55°, an angle expansion effect is observed such that the angle looks larger than it is. This effect is maximal at separations of about 15° and seems to be mediated by lateral inhibition between orientation-tuned neurons [10]. If the separation between the inducing and test stimuli is small (< 5°) or large (55°–90°), an angle contraction effect, in which the separation appears smaller than it really is, occurs. Typically, contraction effects are maximal for separations of 75°, but even at their largest they remain about half the size of the expansion effects [6,11].

Experiment 1 was designed to investigate whether TAEs could be elicited using axes-of-symmetry and then to measure the impact of binocular rivalry on the magnitude of these effects. Subjects monocularly inspected bilaterally symmetrical dot patterns (Figure 1) for 90 seconds. These patterns had their axes-of-symmetry oriented either 15° or 75° from vertical. Subjects then judged the orientation of a subsequently presented symmetrical dot pattern as being tilted either left or right of vertical. Test patterns were oriented close to ($\pm 3^\circ$), but not at, vertical and the orientation was altered depending on the subject's judgements in order to determine the subject's point of subjective vertical [12]. Test fields were presented for 4 seconds, during which time the subjects made their response. Following each test, subjects were presented again with the inspection grating for a 10 second ‘top-up’ before again judging the test grating. All subjects generated TAEs consistent with the expansion and contraction effects previously observed with luminance contours. As Figure 2a illustrates, the mean expansion effect was $1.69^\circ \pm 0.36$ (95% confidence interval), and the mean contraction effect was $-0.82^\circ \pm 0.50$. Individual student *t*-tests showed that these effects were significantly different from zero (expansion effect: $t_{14} = 10.10$, $p < 0.05$; contraction effect: $t_{14} = 3.53$, $p < 0.05$). In other words, axes-of-symmetry can elicit orientation aftereffects similar to those observed with luminance contours, supporting claims that mechanisms processing the orientation of axes-of-symmetry are like those processing luminance contours [5,6,13].

On the basis of previous findings [9,12], it was hypothesised that if symmetry TAEs arose in extrastriate cortex they would be reduced by periods of rivalrous suppression during their induction. If, however, the aftereffects were

Figure 1

Representations of the different **(a)** inducing and **(b)** test patterns. The vertical axis-of-symmetry in **(b)** looks tilted after prolonged inspection of the tilted pattern in **(a)**. **(c)** Asymmetrical control patterns were composed of the same number of dots, distributed randomly. Experiment 3 tested for aftereffects using stimuli constructed from modified symmetrical patterns: the new patterns preserved low spatial frequency cues, but eliminated axes-of-symmetry. This was achieved by randomly shifting each dot-pair in the patterns along the line of their orientation **(d)**. The orientation of the axis-of-symmetry was vertical in this pattern.

not diminished by rivalrous suppression, it would be evidence that they were arising earlier, probably in area V1. Figure 2a shows that binocular rivalry reduced expansion and contraction effects to $1.37^\circ \pm 0.30$ and $-0.09^\circ \pm 0.12$, respectively. Individual *t*-tests revealed this expansion effect to be still significant ($t_{14} = 9.73$, $p < 0.05$), but the contraction effect was now not different from zero ($t_{14} = 1.51$, $p > 0.05$). A one-way analysis of variance (ANOVA) for repeated measures showed that this 90% reduction of the contraction effect was significant ($F_{1,14} = 8.551$, $p < 0.05$). Similarly, the 20% reduction of the expansion effect was also significant ($F_{1,14} = 11.382$, $p < 0.05$). While a reduction in both effects is consistent with their being mediated at least partly in extrastriate cortex, this does not explain why the proportional reduction of the expansion effect was so much smaller than the contraction effect.

There is evidence that rivalry affects only binocular processing [14], and the large reduction in contraction effects is consistent with their being mediated only by binocular cells. In comparison, the smaller impact of rivalry on

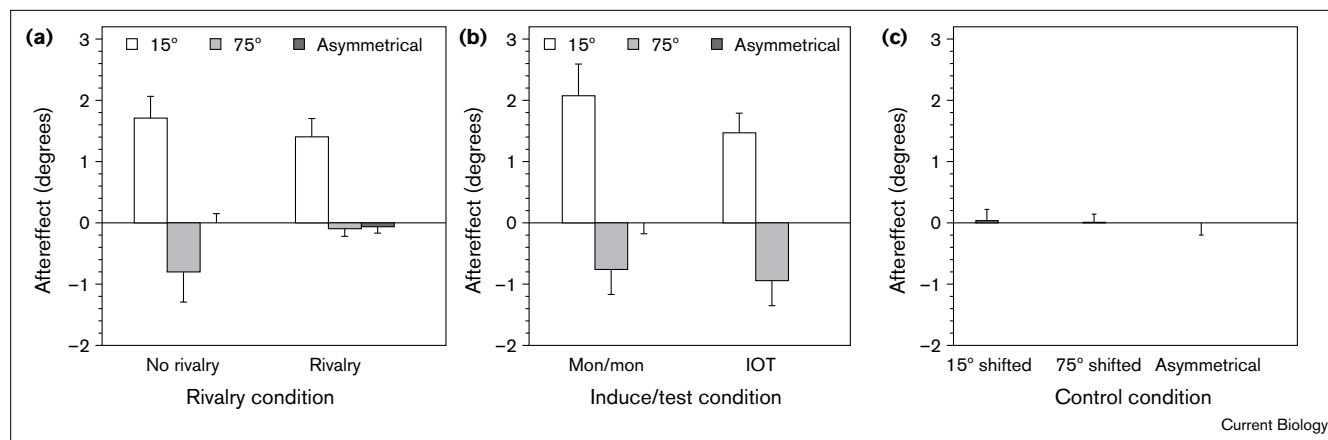
expansion effects may indicate that expansion effects are mediated by both binocular and monocular cells. In this case, the monocular component of the expansion effect may be resistant to rivalrous suppression during its induction. Visual area V1 contains significant numbers of monocular neurons and it is known that orientation processes requiring summation of information over large areas of the visual field occur in this area [15]. Similarly, area V1 contains cells tuned for the medial axis of objects [16]. There is reason to believe, therefore, that some component of the expansion effects observed here could be arising through lateral inhibitory interactions between orientation-tuned monocular cells in area V1.

The degree to which an aftereffect induced in one eye transfers to the other eye is assumed to reflect the relative binocularity of the cells mediating perception of that aftereffect: complete transfer indicates exclusive binocular mediation, whereas a decrement in effect size after transfer indicates some monocular contribution [17]. Experiment 2 was designed to investigate the binocularity of axis-of-symmetry TAEs by measuring the magnitude of the effects after interocular transfer (IOT). Little or no decrement after IOT would be evidence that the effects were mediated by binocular cells, and it was predicted that contraction effects would transfer completely. A reduction in effect size with IOT would indicate some monocular contribution to the effect, and it was predicted that expansion effects would be smaller when measured interocularly if area V1 were involved.

Figure 2b illustrates the results: when measured in the adapted eye, expansion effects were $2.04^\circ \pm 0.52$. Measured interocularly, these effects were reduced to $1.43^\circ \pm 0.33$, but *t*-tests comparing each effect to zero showed that both remained significant ($t_{14} = 8.41$, $p < 0.05$ and $t_{14} = 9.22$, $p < 0.05$, respectively). In comparison, contraction effects were $-0.77^\circ \pm 0.42$ when measured in the adapting eye, and $-0.98^\circ \pm 0.41$ when measured interocularly. The *t*-tests comparing each of these effects to zero revealed both to be significant ($t_{14} = 3.82$, $p < 0.05$ and $t_{14} = 5.12$, $p < 0.05$, respectively). A one-way ANOVA for repeated measures (planned contrasts) showed that the reduction of the expansion effect was significant ($F_{1,14} = 12.595$, $p < 0.05$). However, the ANOVA revealed that the change between contraction effects was not significant ($F_{1,14} = 3.288$, $p > 0.05$). These data support the notion that axis-of-symmetry contraction effects are mediated by binocular cells, probably located in extrastriate cortex. Importantly, these data indicate that area V1 may contribute to the expansion effects, suggesting that information about the orientation of axes-of-symmetry is available very early in cortical processing.

One alternative explanation for the results described here is that they were the product of adaptation to low spatial

Figure 2



(a) Means and 95% confidence intervals for Experiment 1. Dot patterns with one axis-of-symmetry are sufficient to elicit significant expansion and contraction TAEs, and the magnitudes of these effects were reduced by rivalrous suppression during their induction (see text). By convention, angle expansions are represented as positive values and angle contraction effects as negative values. All subjects completed all conditions, in a repeated measures design. For each subject, a point of subjective vertical was determined prior to and again after exposure to each condition and effects were calculated as the difference between these measures [12]. Adaptation to an asymmetrical pattern did not produce significant effects. The mean effects elicited by the asymmetrical patterns were compared to zero using student *t*-tests. Neither asymmetrical effect was found to be significantly different from zero (no rivalry: $t_{14} = 0.02$, $p > 0.05$; with rivalry: $t_{14} = 1.11$, $p > 0.05$). **(b)** Means and 95% confidence intervals for Experiment 2. The reduction of the expansion effect by IOT, when compared with monocular only (mon) measurements, is consistent

with the notion that the orientation of axes-of-symmetry are encoded by some monocular cells. The magnitude of the contraction effect was not affected by IOT, consistent with a binocular and, probably, extrastriate locus for these effects. All stimuli elicited significant effects except the asymmetrical control. A single sample *t*-test revealed this effect not to be significantly different from zero ($t_{14} = 0.01$, $p > 0.05$). **(c)** Means and 95% confidence intervals for Experiment 3. Using the same procedures as the previous experiments, subjects were tested for aftereffects elicited by possible low-spatial frequency components within the stimuli. Preserving dot-pair position relationships while eliminating the axis-of-symmetry from patterns was not sufficient to elicit the TAEs observed in the earlier experiments. Student *t*-tests comparing each mean to zero revealed that none was significantly different from zero (15° asymmetrical pattern: $t_{14} = 0.51$, $p > 0.05$; 75° pattern: $t_{14} = 0.38$, $p > 0.05$; random asymmetrical pattern: $t_{14} = 0.01$, $p > 0.05$).

frequency lines formed by the dot-pairs in the adapting patterns. Cells tuned for the orientation of lines and edges may be stimulated by pairs of dots at the appropriate orientations [18] and, in the stimuli used here, symmetrical dot-pairs have always been orthogonal to the axis-of-symmetry. It could be that these effects were generated not by the axes-of-symmetry of the patterns, but by the dot-pairs orthogonal to them [19]. Experiment 3 was designed to test whether the TAEs observed in Experiments 1 and 2 were really the product of the axes-of-symmetry of the dot patterns or the result of interactions between the oriented dot-pairs.

The stimuli used in Experiment 3 were modified versions of the patterns used in the earlier experiments, but with the axes-of-symmetry removed. This was done by adjusting the lateral position of each dot-pair within the inducing patterns, such that each dot maintained its position relative to its partner, but not relative to all the other dots (Figure 1d). The results (Figure 2c) show that none of the new patterns induced a significant aftereffect, consistent with the TAEs observed in the earlier experiments arising from mechanisms tuned for the orientation of the axes-of-symmetry.

It has been suggested that the process of symmetry perception comprises two stages [20–22]: an immediate process defining a potential axis-of-symmetry, and a second mechanism utilizing the information available for subsequent processing. These data indicate two possible stages in processing the orientation of axes-of-symmetry: binocular rivalry affects processing occurring between areas V2 and MT [9,23], and the reduction of symmetry TAEs by rivalry suggests that those areas are also involved in the encoding of symmetry information. The data indicate, however, that expansion effects have a monocular component. This suggests that area V1 contributes, at least partially, to these effects. What these data do not allow us to determine is whether the encoding of symmetry in striate cortex is done by initial feed-forward processing or by feedback mechanisms [24]. Similarly, it is not clear whether the striate and extrastriate components of the effects reported here represent two different stages in symmetry perception per se, or just two different steps in orientation processing.

What does seem to be the case, however, is that axes-of-symmetry, once encoded, are treated by orientation processing mechanisms in the visual system in the same way

as edges and contours defined by other attributes. It has been argued that there is a contour-invariant neural mechanism for processing orientation [25], and the finding that axes-of-symmetry can induce TAEs like those induced by luminance contours supports that conjecture. Intuitively it makes sense that, if symmetry is used by the visual system as a processing token [6], information about the axis should be available early in order to maximise its usefulness. The picture emerging of the role of area V1 in visual processing is that it contains a series of convergent pathways mediating the integration of information over relatively large areas of visual space [26]. One consequence of this is that some cells encode luminance-defined and also 'second-order' features (for example edges defined just by texture, or motion, or disparity). Symmetry may be another example of a second-order feature, providing cue-invariant information about objects in the visual field.

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