

Available online at www.sciencedirect.com

SCIENCE @ DIRECT®

Vision Research 46 (2006) 1530–1539

Vision
Researchwww.elsevier.com/locate/visres

Effects of global shape on angle discrimination

Graeme J. Kennedy, Harry S. Orbach, Gunter Loffler *

Department of Vision Sciences, Glasgow Caledonian University, Cowcaddens Road, Glasgow G4 0BA, Scotland, UK

Received 15 April 2005; received in revised form 3 June 2005

Abstract

Previous studies have been inconclusive as to whether angle discrimination performance can be predicted by the sensitivity of orientation discrimination mechanisms or by that of mechanisms specialised for angle coding. However, these studies have assumed that angle discrimination is independent of the shape of the object of which the angle is a part. This assumption was tested by measuring angle discrimination using angles that were parts of different triangular shapes. Angle discrimination thresholds were lowest when angles were presented in isosceles triangles (sides forming the angle were of identical length). Performance was significantly poorer when angles were presented in scalene triangles (sides of different lengths) and as much as three times worse when the sides forming the angle varied randomly in length between presentations. Comparing orientation discrimination for single lines with angle discrimination for different stimulus conditions (isosceles, scalene and random triangles) leads to conflicting conclusions as to the mechanisms underlying angle perception: line orientation sensitivity correctly predicts angle discrimination for random triangles, but underestimates angle acuity for isosceles triangles. The fact that performance in angle discrimination tasks is strongly dependant on the overall stimulus geometry implies that geometric angles are computed by mechanisms that are sensitive to global aspects of the stimulus.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: Angle discrimination; Shape perception; Image geometry; Form vision; Global processing

1. Introduction

The computation of object shape is a fundamental task for the visual system. As such, much attention has been directed towards understanding how an accurate percept of object shape is constructed, using psychophysical (for a review see Regan, 2000), neurophysiological (Desimone, Albright, Gross, & Bruce, 1984; Gallant, Braun, & Van Essen, 1993; Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996; Gross, Rocha-Miranda, & Bender, 1972; Kobatake & Tanaka, 1994; Missal, Vogels, Li, & Orban, 1999; Pasupathy & Connor, 1999; Rolls, Baylis, & Hasselmo, 1987) and computational (Biederman, 1987; Marr, 1982; Pitts &

McCulloch, 1947; Riesenhuber & Poggio, 1999; Tarr & Bulthoff, 1998; Ullman, 1989) approaches.

Form vision is processed at several hierarchical levels, spanning from the first cortical stage (primary visual cortex, V1; Hubel & Wiesel, 1968) via intermediate area V4 (Gallant et al., 1996) to the inferior temporal region (IT; Ungerleider & Mishkin, 1982; Van Essen & Gallant, 1994). This anatomical hierarchy correlates with the increasing complexity of shapes to which neurons respond. Filters in the early stages are selective for stimulus attributes such as local orientation, spatial frequency, and temporal frequency (DeValois & DeValois, 1990; Hubel & Wiesel, 1968), while cells in IT are selective for highly complex objects such as faces and hands (Desimone et al., 1984; Gross et al., 1972; Perrett, Rolls, & Caan, 1982).

The spatial frequency and orientation tuning characteristics of early filters or “channels” have been studied

* Corresponding author. Tel.: +44 0141 331 3386.
E-mail address: gloe@gcal.ac.uk (G. Loffler).

widely (Campbell & Robson, 1968; Graham & Nachmias, 1971; Wilson, 1991). Experiments using adaptation (Blakemore & Campbell, 1969; Georgeson & Harris, 1984), subthreshold summation (Kulikowski & King-Smith, 1973; Robson & Graham, 1981; Wilson, 1978) and masking (Legge & Foley, 1980; Wilson, McFarlane, & Phillips, 1983) techniques have provided evidence that these channels are band-pass for spatial frequency and orientation. Furthermore, measurements of the accuracy of line orientation discrimination at different absolute orientations have shown these mechanisms to be anisotropic (Appelle, 1972; Heeley & Timney, 1988). Observers can discriminate the orientation of lines oriented vertically and horizontally more accurately than lines oriented obliquely: “the oblique effect” (Appelle, 1972).

After line orientation discrimination, a logical next stage in increasing task complexity, and a useful way of studying shape perception at a relatively low level, is the study of geometric angles in the fronto-parallel plane, which are completely defined by *two* orientations. Several studies have investigated the ability of human observers to judge such angles (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996; Regan, Gray, & Hamstra, 1996; Snippe & Koenderink, 1994). These investigations focused on two alternative hypotheses for angle processing. One hypothesis is that angles are computed by determining the difference in orientation of two lines (Snippe & Koenderink, 1994). If this were the case, angle discrimination performance could be predicted from the sensitivity of two mechanisms for orientation discrimination. The second hypothesis is that angle discrimination is not limited by the accuracy of orientation discrimination but is, instead, based on specialised detectors (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996; Regan et al., 1996). According to this view, if angle discrimination performance is *more* accurate than that predicted (using, for example, a simple variance summation model of two independent orientation mechanisms) by the accuracy of encoding the orientations of the angle components, then this would imply the existence of specialised mechanisms for computing angles. Evidence has been presented to support both hypotheses (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996; Regan et al., 1996; Snippe & Koenderink, 1994), with conflicts due possibly to the design of the experiments, leaving the question open as to whether or not the visual system contains special mechanisms for encoding angles.

In all previous studies of angle discrimination, an assumption appears to have been made that performance is independent of the overall shape or geometry of the stimulus that defines the angle. Given that an angle is entirely defined at the point of intersection of two lines, this seems a reasonable assumption. However, recent studies have provided evidence for the use of global

strategies in a variety of very basic shape perception tasks, including the judgement of circularity (Hess, Wang, & Dakin, 1999; Levi & Klein, 2000; Loffler, Wilson, & Wilkinson, 2003), detecting structure embedded in fields of random dots (Wilson & Wilkinson, 1998; Wilson, Wilkinson, & Asaad, 1997) and detecting deviations from symmetry of circles and squares (Regan & Hamstra, 1992).

The aim of this study was to investigate the effect of global shape on angle discrimination by presenting angles as parts of different triangular shapes. The rationale behind these experiments is that if angles are computed locally, either as a difference of two line orientations or by specialised mechanisms, changing the overall stimulus shape should have no effect on angle discrimination performance. If, however, angles are computed by global mechanisms, then altering the overall stimulus configuration may affect performance. This is, in fact, shown to be the case.

2. Methods

2.1. Stimuli

We term the angle to be judged the “apex angle.” This angle in all experiments was part of a triangle that was either outlined (Fig. 1, left) or defined by a “dot” at each corner (Fig. 1, right). In the case of an outline triangle, the contrast cross-section profile of each line was given by the following exponential function:

$$f(x,y) = C \cdot \exp \left\{ -\left(\frac{x}{\sigma_x}\right)^{N_x} \right\} \cdot \exp \left\{ -\left(\frac{y}{\sigma_y}\right)^{N_y} \right\} \quad (1)$$

This was done to avoid pixelation artefacts (anti-aliasing) for orientations other than horizontal and vertical

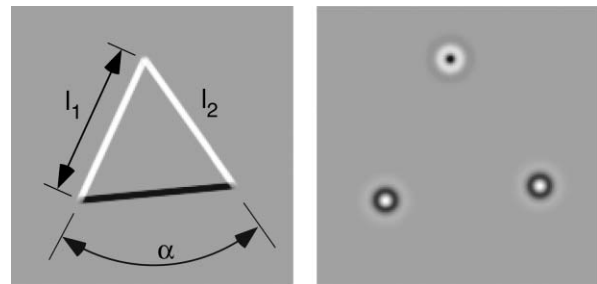


Fig. 1. Stimuli. The angles to be compared were parts of triangles, which were either outlined (left) or defined by a “dot” at each corner (right). Different contrasts of the lines or dots were used to mark the location of the apex angle to be judged. This was either the angle enclosed by the white lines (‘ α ’) or the angle at the location of the white dot with a dark centre (the top angle in these panels). ‘ l_1 ’ and ‘ l_2 ’ are the lengths of those sides of the triangle which enclose the angle to be tested.

(Loffler & Orbach, 2001). Note that Eq. (1) is for a vertical line; other orientations were produced by simple coordinate rotations. The space constants, σ_x and σ_y , were chosen to give lines a width of 0.08° and a desired length (see below). The exponents (N_x , N_y) were assigned values of 6 and 30 to give line edges and tips an equally smooth appearance. The contrast (denoted by C) of the two lines forming the apex angle (the angle to be judged) was set to $+98\%$ and the contrast of the opposite line to -98% , to make it obvious which of the three angles of the triangle had to be judged.

In the case of triangles defined by their corner points, the contrast cross-section profile of each dot was given by a circularly symmetric fourth derivative of a Gaussian (D4):

$$D4(r) = C \cdot \left(1 - 4\left(\frac{r}{\sigma}\right)^2 + \frac{4}{3}\left(\frac{r}{\sigma}\right)^4 \right) \cdot \exp\left\{-\left(\frac{r}{\sigma}\right)^2\right\} \quad (2)$$

In this equation, r is the radius in a polar coordinate system ($r = \sqrt{x^2 + y^2}$), with respect to the centre of the dot, σ determines its peak spatial frequency, and C denotes contrast. The full spatial frequency bandwidth for such a D4 profile is 1.24 octaves at half amplitude; its peak spatial frequency was set to 8 cpd. The contrast of the apex dot at the location of the angle to be judged was set to -98% and the remaining two dots to $+98\%$.

It has been shown that angle discrimination is superior when the angle to be judged is a right angle (Chen & Levi, 1996; Gray & Regan, 1996; Heeley & Buchanan-Smith, 1996). It has also been reported that angle discrimination thresholds depend on the magnitude of the angle (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996), following approximately a Weber's law relationship, i.e., the larger the angle to be judged, the higher the discrimination threshold. This dependence has, however, been controversial (Regan et al., 1996). To carry out a general investigation as to whether or not triangle shape influences angle discrimination, we therefore tested performance around several reference angles (30° , 60° , 90° , and 120°).

An important factor in the stimulus design was to eliminate any cue to the task other than the angle to be judged (for an extensive discussion see Regan et al., 1996). First, to prevent observers basing their judgement on an absolute measurement (e.g., corner position or line orientation), the initial orientation of the two triangles for each trial was chosen randomly (within 0° to 360° ; Fig. 2). Here, and elsewhere, triangle orientation was defined as the orientation of the triangle's apex angle bisector. This randomisation guaranteed that all angle measurements were the average performance for angles of different orientations.

The orientation of the two triangles within each trial was not randomised within 0° to 360° to avoid the de-

mand required to mentally rotate the two stimuli before comparing them, a computation which is presumed to take place in tasks where subjects decide whether or not two objects are the same (Shepard & Metzler, 1971). However, to avoid a change in orientation of one of the two triangle sides as a cue to the task, the two triangles within each trial did not share identical orientation, but differed randomly by up to $\pm 10^\circ$.

Finally, to prevent subjects using the length of the side of the triangle opposite the apex angle as a cue, the length of the two sides defining the apex angle was varied randomly within and across trials (by up to $\pm 70\%$ of the mean length). All randomisations were made using uniform distributions.

Three different blocks of experiments were carried out to determine the effect of triangle shape on angle discrimination performance. In the first condition, all triangles were isosceles (Fig. 2, first column), hence the two sides defining the apex angle (l_1 and l_2) were always of the same length, although this length was randomised:

$$\begin{aligned} l_1 &= l_{\text{mean}} \pm (\text{rand} \cdot 0.7 \cdot l_{\text{mean}}) \\ l_2 &= l_1 \end{aligned} \quad (3a)$$

Here, and elsewhere, l_{mean} is the average length of the two sides defining the angle, which was 1.75° for all triangles, and 'rand' is a random number from a uniform distribution (0 to 1).

In the second condition all triangles were scalene (Fig. 2, second column), that is, the two sides defining the apex angle were always of different lengths. The side lengths always differed by the same absolute amount:

$$\begin{aligned} l_1 &= l_{\text{mean}} + (\text{rand} \cdot 0.7 \cdot l_{\text{mean}}) \\ l_2 &= l_1 - 0.7 \cdot l_{\text{mean}} \end{aligned} \quad (3b)$$

Hence, for each triangle, the length of the first side of the angle was chosen randomly and the second side was shorter by 70% of the mean side length.

In the third condition the shape of each triangle was chosen randomly for each presentation (Fig. 2, third column), that is, the length of each side defining the apex angle was chosen independently of the other:

$$\begin{aligned} l_1 &= l_{\text{mean}} \pm (\text{rand} \cdot 0.7 \cdot l_{\text{mean}}) \\ l_2 &= l_{\text{mean}} \pm (\text{rand} \cdot 0.7 \cdot l_{\text{mean}}) \end{aligned} \quad (3c)$$

In the isosceles condition, any two triangles with the same apex angle were similar triangles, i.e., they differed in scale but not in shape. Due to our design, any two triangles with the same apex angle in the scalene condition were *not* necessarily similar. An additional experiment was carried out to determine whether or not this lack of similarity between triangles has an effect on performance, using scalene triangles where the lengths of the sides defining the angle always differed by the same ratio rather than by the same absolute amount (Fig. 2, fourth column):

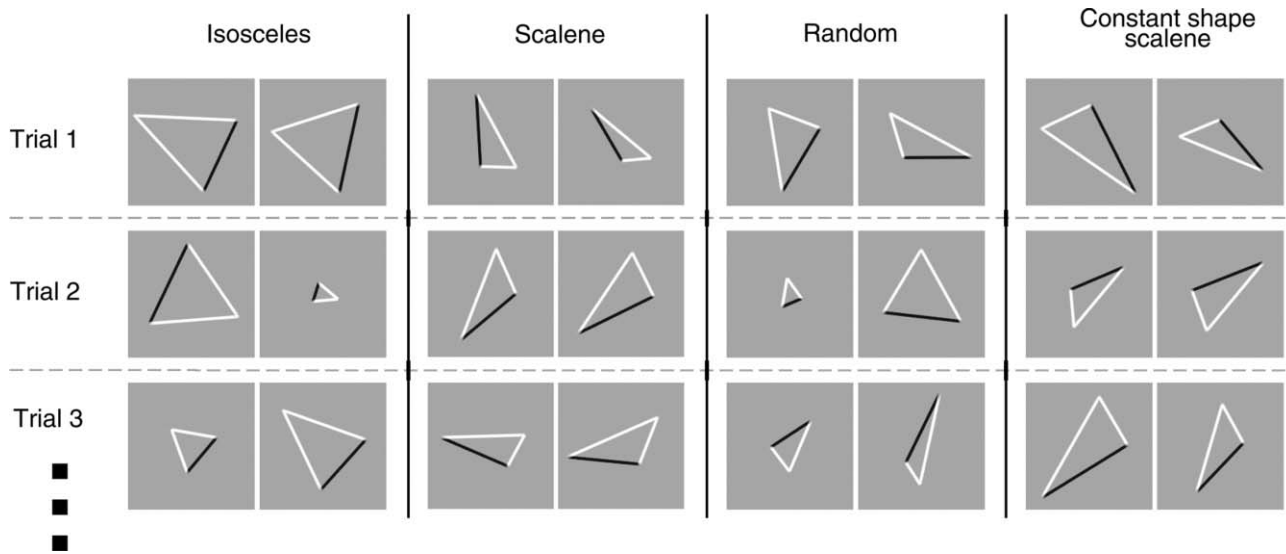


Fig. 2. Different triangle geometries used to test the effect of stimulus shape on angle discrimination. Four different triangle geometries were tested (columns) and the rows show examples of three trials for each. For each trial, the overall orientation of the two triangles (apex bisector) was chosen randomly. Within trials, the orientation of each triangle was varied randomly by up to $\pm 10^\circ$. The length of the two triangle sides enclosing the relevant angle was altered randomly within $\pm 70\%$ of the mean side length. In the first condition (first column) all triangles were isosceles, i.e., the two sides defining the angle were of the same length. In the second condition (second column) all triangles were scalene, i.e., the two sides defining the angle differed in length, and always differed by a fixed amount. In the third condition (third column) the length of each side defining the angle was chosen randomly and independently of the other for each presentation. In an additional experimental condition the design of the scalene triangles was altered so that the length of the two sides defining the angle always differed by the same constant ratio (fourth column) rather than by a fixed amount (second column).

$$l_1 = l_{\text{mean}} + (\text{rand} \cdot 0.7 \cdot l_{\text{mean}})$$

$$l_2 = l_1 \cdot \left(\frac{l_{\text{mean}} - \frac{1}{2} \cdot 0.7 \cdot l_{\text{mean}}}{l_{\text{mean}} + \frac{1}{2} \cdot 0.7 \cdot l_{\text{mean}}} \right) \quad (3d)$$

2.2. Procedure

The screen background was initially set to mid-grey. A fixation mark, consisting of a small dark circle, appeared on the screen prior to each trial and subjects were encouraged to maintain fixation. The method of constant stimuli was employed in a temporal two-alternative forced choice paradigm. Each trial was initiated by pressing a key on the keyboard. This was followed by two, temporally separated, stimuli. The time between pressing a key and the onset of the first stimulus was 300 ms. Each stimulus was presented for 400 ms. The centre of the triangular patterns (centre of gravity) was presented at the centre of the screen. To minimise neural persistence, all stimuli were followed immediately by a mask for 500 ms. The mask consisted either of randomly positioned and oriented white lines (average length = 1.75°) or randomly positioned D4 dots depending on the type of triangle (outline or dots). This experimental design is illustrated in Fig. 3.

Angle discrimination performance was measured for 6 different angular increments (3 positive and 3 negative), distributed symmetrically around the reference angle. The absolute values of these increments were chosen

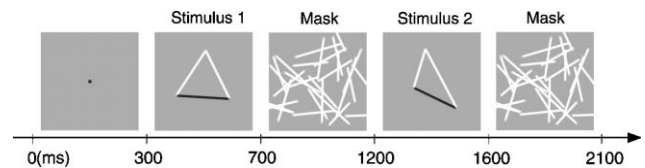


Fig. 3. Experimental procedure. Each trial was initiated by pressing a key on the keyboard, followed by two, temporally separated, stimuli (in this case, triangles defined by an outline). The presentation time for each stimulus was 400 ms. After each stimulus presentation, a mask appeared immediately for 500 ms. After the second stimulus interval, the subject pressed one of two keys to indicate which interval had shown the triangle with the more obtuse apex angle.

to allow an accurate estimation of the psychometric function and varied depending on task difficulty and subject sensitivity (ranging from $[\pm 1^\circ, \pm 2^\circ, \pm 5^\circ]$ to $[\pm 10^\circ, \pm 15^\circ, \pm 20^\circ]$). One of the stimulus intervals always contained the reference angle and the other contained one of these six increments. Subjects indicated which interval had the more obtuse angle by pressing one of two keys. Different increments were presented randomly in different trials and the order of presentation within trials (i.e., reference angle in the first or second interval) was also random. Each of the increments was presented 30 times, giving a total of 180 trials per experiment. The resulting data were fitted by a Quick function (Quick, 1974), using a maximum likelihood procedure. Angle discrimination thresholds were defined as half the distance between the 25% and 75% correct points on the psychometric function. For each condition, each observer carried out at least two experimental runs on

different days, and separate threshold estimates were averaged.

2.3. Observers

Six observers (four of whom were experienced in psychophysical tasks) participated in these experiments, four of whom were naïve as to the purpose of the study. All observers had normal or corrected-to-normal vision (visual acuity of 6/6 or better). Viewing was binocular. No feedback was given to the observers as to their performance.

2.4. Apparatus

Stimuli were presented on a LaCie “electron22blue” high-resolution monitor controlled by an Apple PowerMac G4 computer. The frame refresh rate of the monitor was set to 85 Hz and the spatial resolution to 1024×768 pixels. The software lookup table was defined to maximise contrast linearity using 151 equally spaced grey levels. Pattern luminance was modulated about a mean of 61.4 cd/m^2 . Subjects viewed the stimuli under dim room illumination and a chin and forehead rest was used to maintain a constant viewing distance of 120 cm. At this distance each pixel subtended 0.0177° . To avoid reference cues, the monitor frame was covered with a white cardboard mask with a circular aperture subtending 12° in diameter. Individual patterns were calculated in MATLAB prior to the experiments. The patterns were displayed using custom-written Pascal code within the CodeWarrior environment, including routines from Pelli’s VideoToolbox (Pelli, 1997).

3. Results

The aim of these experiments was to test the influence of shape on angle discrimination using three different types of triangular shape: isosceles triangles, scalene triangles, and triangles where the two sides were chosen randomly, and independently of one another.

Angle discrimination thresholds for both outline triangles and triangles defined by three dots, for a reference angle of 60° , are shown in Fig. 4. Thresholds shown for each condition are the mean of five observers. Error bars here and elsewhere show standard errors of the mean.

Observers are able to make remarkably accurate judgements of angles presented in outlined isosceles triangles: thresholds are as low as 2° (Fig. 4, left). This is comparable with previous studies, which report discrimination thresholds of between 1° and 3° for a 60° stimulus comprising two lines intersecting at a point (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996; Regan et al., 1996). Surprisingly, when the same angles are presented in scalene triangles, performance drops by a factor of 2.2. Furthermore, when the length of each side defining the angle is chosen randomly for each presentation, performance is even poorer. Compared with isosceles triangles, observers are 3.2 times poorer at discriminating angles in this random condition.

It is clear that the results for different triangle shapes defined by D4 profile dots (Fig. 4, right) follow the same pattern as those for outline triangles, with performance best for isosceles triangles compared to scalene, and worst for random triangles. The absolute thresholds for each condition are, however, higher than for outline triangles. This reduced sensitivity to angles defined by

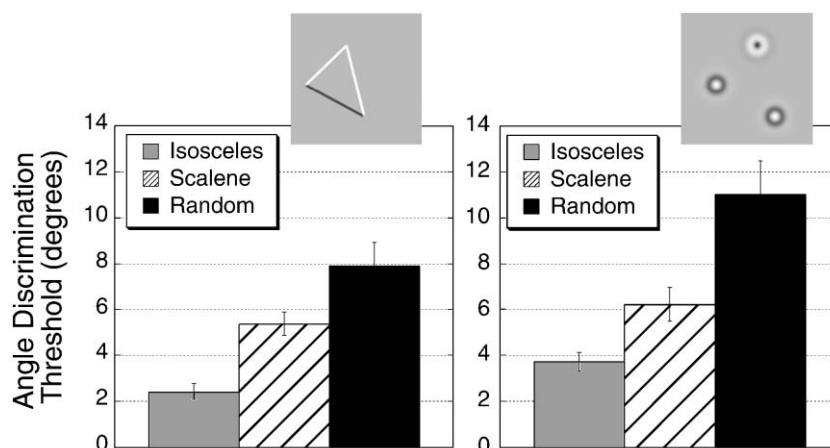


Fig. 4. Mean angle discrimination thresholds for angles presented in different triangular shapes (isosceles, scalene, and random) averaged across five observers. Data on the left show performance for outlined triangles, those on the right are for triangles defined by their corner dots. Angle discrimination performance was measured around a reference angle of 60° . Error bars are SEM. Observers are able to make very accurate judgements (thresholds are as low as 2°) when angles are presented in outlined isosceles triangles. Performance reduces by about a factor of two when angles are presented within scalene triangles, and about a factor of three when the lengths of the lines bounding the angle are chosen randomly for each triangle. Both cases (outline triangles and dot triangles) give the same pattern of results, but angle discrimination thresholds are higher for dot triangles than for outline triangles.

dots compared to lines is in agreement with previous studies (Heeley & Buchanan-Smith, 1996; Snippe & Koenderink, 1994).

A repeated-measures, two-way ANOVA (triangular shape type \times dots/lines) was carried out and shows a significant effect ($F_{2,54} = 53.47$, $p < 0.0001$). Post hoc tests (Fisher's PLSD, at 1% significance level) were carried out, and these show two significant results. Firstly, angle discrimination thresholds for the three types of triangular shape are significantly different. Secondly, angle discrimination thresholds are higher for dot triangles compared to outline triangles.

Our results show that performance in angle discrimination tasks is dependent on the stimulus shape. This is striking since, for outline triangles, the entire information about the angle is available locally, around the point where two lines intersect. Nevertheless, angle discrimination is affected by the global geometry of the shape of which the angle is a part, and we are significantly more precise in judging angles that are enclosed by equal sides.

Earlier investigations have found that angle discrimination performance can depend on the magnitude of the angle to be judged (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996). Are our results for a reference angle of 60° representative of performance for an arbitrary angle? To investigate whether or not the effect of stimulus shape seen in Fig. 4 holds for other angles, a second experiment was carried out using triangles with reference angles of 30° , 90° and 120° . Experiments for each reference angle were carried out using outline triangles in the isosceles and random conditions, the two conditions that exhibited the maximum difference in performance for a reference angle of 60° .

Mean angle discrimination thresholds for three observers are plotted in Fig. 5. These observers' thresholds for a reference angle of 60° are also shown for comparison. The data exhibit the same pattern as seen in Fig. 4. For all reference angles, thresholds are lower for isosceles triangles compared to triangles with a randomly chosen shape. Thresholds in the random conditions are 1.3, 3.2, 1.4, and 1.7 times higher than in the isosceles conditions for reference angles of 30° , 60° , 90° and 120° , respectively. To assess these differences statistically, a repeated-measures, two-way ANOVA (triangular shape type \times reference angle) was performed and shows a significant effect ($F_{1,8} = 17.75$, $p < 0.005$) for angle shape but not for reference angle ($p = 0.178$). Thus, over a range of reference angles, observers can discriminate angles more accurately when the two sides defining the angle are of the same length. Regardless of whether the angle to be judged is acute, obtuse, or a right angle, angle discrimination is influenced by the overall geometry of the shape of which the angle is a part.

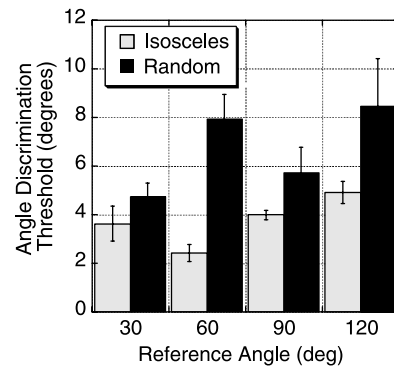


Fig. 5. Angle discrimination thresholds for outline triangles with reference angles of 30° , 60° , 90° , and 120° in the isosceles and random conditions. The data (averaged across three observers) show the same pattern of results as seen in Fig. 4, namely that performance is superior in the isosceles condition compared to the random condition. Over a range of reference angles, observers can discriminate angles more accurately when the two sides defining the angle are of the same length.

In the isosceles condition in our initial experiments (Fig. 4), any two triangles with the same apex angle were similar triangles, i.e., they differed only in scale. However, in the scalene condition, where one of the side lengths defining the apex angle was chosen randomly and the two side lengths always differed by the same absolute amount, triangles were usually *not* similar. This lack of similarity between triangles in the scalene condition (and, indeed, the random condition) could be a key to the poorer performance in these blocks of trials when compared to the isosceles condition.

To investigate this possibility, a third experiment was carried out using a different scalene triangle design. Here, rather than the two sides defining the apex angle always differing in length by the same absolute value, the two sides always differed by the same ratio (see Fig. 2). Thus, any two triangles with the same apex angle *were*, in this case, similar triangles. Trials were carried out using both outline and dot triangles for a reference angle of 60° .

Mean angle discrimination thresholds for two observers for scalene triangles that differed in size but not shape (Scalene Constant Ratio) are shown in Fig. 6. These observers' thresholds for the isosceles and original scalene (Scalene Constant Difference) conditions are also shown. It is clear that thresholds for scalene triangles with a constant side length ratio are indistinguishable from those for scalene triangles with a constant difference between side lengths. In neither condition does performance reach the level seen for isosceles triangles. Thus, it would appear that even when angles are presented in similar scalene triangles, they still cannot be discriminated as accurately as when they are presented in isosceles triangles. The superiority seen for isosceles triangles cannot, therefore, be explained on the basis that observers are simply better at discriminating differences between shapes that are similar.

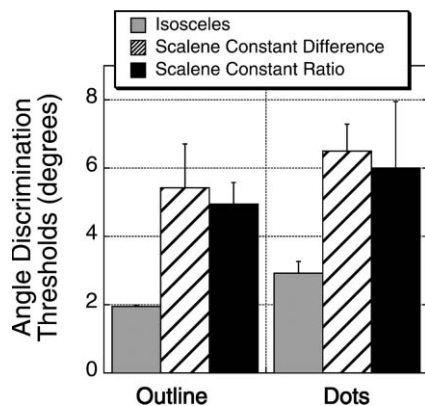


Fig. 6. Angle discrimination thresholds for two types of scalene triangles: the lengths of the two sides defining the angle either differed by the same absolute value (Constant Difference) or by the same ratio (Constant Ratio). When scalene triangles have the same ratio of side lengths, two triangles with the same apex angle are similar triangles. Thresholds (mean for two observers) for both types of scalene triangles (for both outline and dot triangles) are similar and are higher than for isosceles triangles, indicating that our main result of superior angle discrimination performance for isosceles triangles is not due to the fact that triangles within an experiment are similar.

4. Discussion

4.1. The isosceles superiority effect

Earlier studies have been inconclusive as to whether angles are encoded as a difference of two line orientations (Snippe & Koenderink, 1994) or by special “angle detectors” (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996; Regan et al., 1996). In these studies, an implicit assumption has been made that discrimination performance is not influenced by the overall geometry of the shape of which the angle forms a part. Our experiments show that this assumption is not valid. Angle discrimination is most precise when the angles to be judged form part of an isosceles triangle, and these discrimination thresholds confirm the high degree of accuracy found in previous studies. However, performance drops significantly when angles are presented within scalene triangles, and is poorer by as much as a factor of three when the triangle shape is chosen randomly, even though the information defining the angle is identical in all these conditions. This is particularly striking in the case where the angle can be determined locally as a difference of two line orientations (outline triangle).

Let us consider possible explanations for these results. In our initial experiments (Fig. 4), angle discrimination was measured around a reference angle of 60° . All of the reference stimuli in the isosceles condition, therefore, were equilateral triangles (all three sides of equal length). It may be that such a shape is encoded in a special way by the visual system, and that our ability to detect deviations from “equilaterality” is therefore superior to that for other triangle shapes. This may be a reason for the

significantly superior performance for isosceles over scalene triangles when the reference angle is 60° . Our results, however, do not confirm this suggestion. When the reference angle is 30° , 90° , or 120° , performance is still superior in the isosceles condition even though the triangles for these conditions are not equilateral (Fig. 5). Thus, superiority in performance for equilateral triangles cannot explain our general result that angles presented within isosceles triangles are easier to discriminate than those presented within other triangle shapes.

Another suggestion is that detecting differences between features of any two objects is easier when the two objects are the same shape (similar) than when they are not. For example, in any of the isosceles conditions, any two triangles with a given apex angle were similar triangles, i.e., they differed only in scale. In the scalene and random conditions two triangles with the same apex angle were *not* necessarily similar. It is possible, therefore, that the superior performance in the isosceles conditions is due to observers being able to discriminate differences more easily between these similar shapes. This notion is not, however, confirmed by our experimental results. In a further experiment (Fig. 6) we changed the design of the scalene triangles so that any two triangles with the same apex angle would now be similar and differ only in scale. The results from this experiment show that performance is still superior for isosceles triangles, thus ruling out the possibility that the difference between isosceles and scalene shapes is due to observers being able to make more accurate judgements between two shapes that are similar.

4.2. Relation to previous studies

Snippe and Koenderink (1994) reported that angle discrimination was dependent on the reference angle of their stimulus and argued that their results could be explained by the “oblique effect” for orientation discrimination (Appelle, 1972). They proposed that angles are encoded simply by computing the difference of the two orientations that define the angle. In this model, vertical and horizontal orientations are represented more accurately than oblique orientations, resulting in performance that is dependent on the orientations of the angle’s bounding lines.

Our results are inconsistent with such a two-orientation model in its simplest form. Such a model should predict performance to be unaffected by the manipulations of stimulus shape that we employed in our experiments. This is because the *same* orientation information is available regardless of the triangle shape.

Several studies have investigated the influence of line length on line orientation discrimination (Heeley & Buchanan-Smith, 1998; Orban, Vandebussche, & Vogels, 1984; Scobey, 1982). It has been found that line orientation acuity increases as the line length is increased

up to a critical length over which there is no further improvement in performance. Given these findings, could the ‘two-orientation’ model proposed by Snippe and Koenderink (1994) be used to explain our results if it is modified to take into account the length of the two components defining the angle?

There are two arguments against this suggestion. Firstly, the shortest side length we employed in any experimental condition was 0.525° , and the longest was 2.975° . Previous studies of the influence of line length on orientation discrimination (Heeley & Buchanan-Smith, 1998; Orban et al., 1984; Scobey, 1982) show performance to be relatively independent across this range of lengths, with variations too small to account for the three-fold difference in thresholds we see in our experimental conditions. Secondly, in all our experimental conditions (isosceles, scalene or random), the absolute range of values from which side lengths were chosen was always the same, i.e., the shortest possible side length was 0.525° and the longest was 2.975° . Thus, if there is any cost to performance for using very short lines, this should affect performance in all conditions to a similar extent.

Snippe and Koenderink (1994) used a stimulus consisting of dots positioned at the ends of imaginary lines, which forces the observer to use a global, or what they term “multilocal,” strategy to extract the geometric angle. They proposed that results might show a different pattern if whole line segments were shown instead, allowing observers to use a “local” strategy. Heeley and Buchanan-Smith (1996) confirmed this proposal by measuring angle discrimination using both a “V” stimulus comprised of two line segments connected at a point, and a “three blob” stimulus where the lines were imaginary. They found discrimination thresholds to be generally lower for the “V” condition than for the “three blob” condition, which is also what we found in our experiments. Moreover, in the “three blob” case their results resembled closely those of Snippe and Koenderink (1994), in that performance was better when the two orientations defining the angle were close to horizontal or vertical, than when the two orientations were oblique, a result that could be explained by the sensitivity to the two orientations comprising the angle. However, performance for the “V” stimulus showed no dependence on the orientation of the lines defining the angle, implying a specialised detector for angles, which is not limited by orientation discrimination mechanisms.

Given this difference in performance for the two stimuli, Heeley and Buchanan-Smith (1996) proposed that there are two functionally distinct mechanisms that the visual system can employ for the extraction of geometric angle. The first, a “multi-local” strategy, operates when (illusory) lines have to be interpolated between two points, i.e., in the case of their “three blob” stimulus. This computation is presumed to be based on a spatial

comparison of symbolic descriptions of the retinal image (Heeley & Buchanan-Smith, 1996). The second, or as it was proposed, “purely local,” strategy is based on the output of localised angle detectors that are stimulated only by extended line segments and within which computations occur between representations of the image in an abstract angle space (Heeley & Buchanan-Smith, 1996).

The use of two mechanisms such as theirs could, therefore, account for our finding that angle discrimination is significantly better for outlined triangles than for triangles defined only by dots. However, neither of the mechanisms proposed by Heeley and Buchanan-Smith (1996) is influenced by the overall geometry of the stimulus and hence neither can explain the dependence of performance on stimulus shape that we find in our experiments.

The conclusion of Heeley and Buchanan-Smith (1996), that angle discrimination thresholds cannot be predicted from orientation discrimination performance for the components defining the angle, is one that has been reached independently by others (Chen & Levi, 1996; Regan et al., 1996). Chen and Levi (1996) found that performance depended primarily on the magnitude of the angle tested, i.e., discrimination was generally poorer for larger angles, following a Weber’s law relationship between angular magnitude and thresholds, with the exception of right angles (90°). Chen and Levi (1996) concluded that an angle is encoded as an irreducible local feature whose properties do not depend on the properties of its component parts (i.e., line orientation). Our results do not confirm this notion in its simplest form. If an angle is encoded as a local feature, then changing the overall shape of a triangle of which the angle is a part should not affect the discriminability of the angle.

A fundamental goal for all investigations into angle perception has been to investigate the underlying computations. Are angles encoded hierarchically, where orientation information is processed initially and used by a second stage, which calculates an angle as a difference of two line orientations? In such a model, any noise arising at the first stage propagates to the second stage and performance for angles can be predicted by simple variance summation from the orientation performance (Heeley & Buchanan-Smith, 1996). Alternatively, are angles encoded by specialised detectors, in which case angle discrimination performance can be better than that predicted by orientation mechanisms? Previous studies have been inconclusive as to these questions, finding evidence for (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996; Regan et al., 1996) and against (Snippe & Koenderink, 1994) specialised mechanisms.

We also measured line orientation discrimination to allow quantitative predictions to be made for angle discrimination. Instead of triangles, the stimuli consisted of single

lines and observers judged which of two successively presented lines was oriented more clock-wise. All other stimulus parameters were identical to the experiments on outline triangles (e.g., randomisation of absolute orientation across trials, line length variation within and across trials). This allows a direct comparison between line orientation discrimination and angle performance.

Fig. 7 shows the results for two observers. Line orientation discrimination performance averages 5° (note that this is the average performance across all absolute orientations) and falls between angle discrimination for isosceles and random triangles (for a reference angle of 60°). The horizontal line shows the prediction for angle thresholds based on simple variance summation of two line orientations. It is clear that this prediction accounts well for the performance when angles are presented within random triangles. It is also obvious that this prediction dramatically over-estimates angle thresholds for isosceles triangles. Hence, depending on the shape of the triangle used when determining angle thresholds, orientation mechanisms either predict angle performance or not, leading to conflicting conclusions regarding the existence of specialised mechanisms for angle detection.

It is of note that those studies that reported angle discrimination to be highly superior to orientation discrimination used angles bounded by equal sides (Chen & Levi, 1996; Heeley & Buchanan-Smith, 1996), while those that did not used lines of different lengths (Regan et al., 1996; Snippe & Koenderink, 1994). In any case, our data show that angle acuity is much finer than ori-

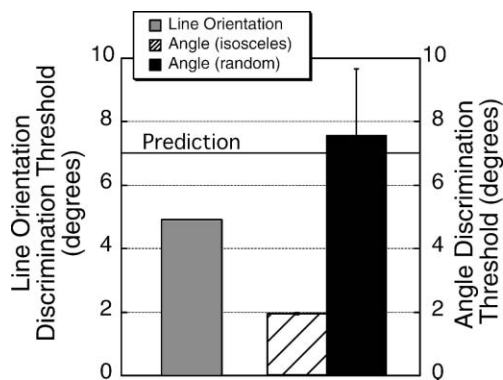


Fig. 7. Comparison between line orientation thresholds and angle discrimination thresholds (for a reference angle of 60°). Orientation discrimination thresholds (left ordinate) for two observers were determined with single lines but all other experimental parameters were identical to those used for angle measurements (right ordinate). Orientation thresholds fall between angle performance for isosceles and random shapes. The horizontal line ('Prediction') marks the prediction for angle thresholds from simple variance summation of orientation thresholds of the two bounding lines. While this prediction can account for angle performance in random triangles, it underestimates performance in isosceles conditions. Error bars are SEM and are too small where they are not visible.

entation acuity when angles are defined by lines of equal length.

Our data are consistent with two different computational strategies underlying angle perception. The first is a single mechanism, which would respond to angles whether part of an isosceles or scalene triangle. Our data constrain such a mechanism to yield a more accurate representation for isosceles shapes. Alternatively, different mechanisms could operate for different shapes. Under the assumption that specialised mechanisms exist if performance for angles is better than that for line orientation, angles within isosceles triangles would be encoded by specialised angle detectors. When angles are part of non-isosceles triangles, angle discrimination would be achieved by comparing the orientation of the bounding lines. While not impossible, having an angle mechanism restricted to isosceles triangles seems improbable. Importantly, regardless of the strategy, our results show that the computations for angle discrimination depend on the overall geometry of the shape that contains the angle.

5. Conclusions

The main finding from our experiments is that angle discrimination is more precise when the two sides of the shape that define the angle are of equal length than when they are different. The difference in performance for angles embedded in different triangular geometries can explain why some studies found evidence for specialised mechanisms underlying angle perception while others did not. Our results cannot be explained by any of the mechanisms proposed in previous studies of angle discrimination, which all assumed computations to be independent of the overall geometry of the stimulus. Our data imply that the mechanisms responsible for angle computation are influenced by the global geometry of the shape containing the angle. This necessitates a reconsideration of mechanisms for angle computation and implies that even a stimulus as simple as an angle is processed in a complex manner incorporating information about the entire pattern geometry.

Acknowledgments

The authors would like to acknowledge the help of Sohail Kiani and Wakas Mohammed in the collection of some of this data. We are also grateful to Gael Gordon and Hugh Wilson for sharing their thoughts. G.J.K. is supported by a Glasgow Caledonian University Studentship grant awarded to G.L. Part of this work was supported by EPSRC Grant # GR/S59239/01 to G.L.

References

- Appelle, S. (1972). Perception and discrimination as a function of stimulus orientation: The “oblique effect” in man and animals. *Psychological Bulletin*, *78*, 266–278.
- Biederman, I. (1987). Recognition-by-components: A theory of human image understanding. *Psychological Review*, *94*, 115–147.
- Blakemore, C., & Campbell, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology (London)*, *203*, 237–260.
- Campbell, F. W., & Robson, J. G. (1968). Application of Fourier analysis to the visibility of gratings. *The Journal of Physiology (London)*, *197*, 551–566.
- Chen, S., & Levi, D. M. (1996). Angle judgment: Is the whole the sum of its parts? *Vision Research*, *36*, 1721–1735.
- Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience*, *4*, 2051–2062.
- DeValois, R. L., & DeValois, K. K. (1990). *Spatial vision*. New York: Oxford University Press.
- Gallant, J. L., Braun, J., & Van Essen, D. C. (1993). Selectivity for polar, hyperbolic, and Cartesian gratings in macaque visual cortex. *Science*, *259*, 100–103.
- Gallant, J. L., Connor, C. E., Rakshit, S., Lewis, J. W., & Van Essen, D. C. (1996). Neural responses to polar, hyperbolic, and Cartesian gratings in area V4 of the macaque monkey. *Journal of Neurophysiology*, *76*, 2718–2739.
- Georgeson, M. A., & Harris, M. G. (1984). Spatial selectivity of contrast adaptation: Models and data. *Vision Research*, *24*, 729–741.
- Graham, N., & Nachmias, J. (1971). Detection of grating patterns containing two spatial frequencies: A comparison of single-channel and multiple-channels models. *Vision Research*, *11*, 251–259.
- Gray, R., & Regan, D. (1996). Accuracy of reproducing angles: Is a right angle special? *Perception*, *25*, 531–542.
- Gross, C. G., Rocha-Miranda, C. E., & Bender, D. B. (1972). Visual properties of neurons in inferotemporal cortex of the macaque. *Journal of Neurophysiology*, *35*, 96–111.
- Heeley, D. W., & Buchanan-Smith, H. M. (1996). Mechanisms specialized for the perception of image geometry. *Vision Research*, *36*, 3607–3627.
- Heeley, D. W., & Buchanan-Smith, H. M. (1998). The influence of stimulus shape on orientation acuity. *Experimental Brain Research*, *120*, 217–222.
- Heeley, D. W., & Timney, B. (1988). Meridional anisotropies of orientation discrimination for sine wave gratings. *Vision Research*, *28*, 337–344.
- Hess, R. F., Wang, Y.-Z., & Dakin, S. C. (1999). Are judgements of circularity local or global? *Vision Research*, *39*, 4354–4360.
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology (London)*, *195*, 215–243.
- Kobatake, E., & Tanaka, K. (1994). Neuronal selectivities to complex object features in the ventral visual pathway of the macaque cerebral cortex. *Journal of Neurophysiology*, *71*, 856–867.
- Kulikowski, J. J., & King-Smith, P. E. (1973). Spatial arrangement of line, edge and grating detectors revealed by subthreshold summation. *Vision Research*, *13*, 1455–1478.
- Legge, G. E., & Foley, J. M. (1980). Contrast masking in human vision. *Journal of the Optical Society of America*, *70*, 1458–1471.
- Levi, D. M., & Klein, S. A. (2000). Seeing circles: What limits shape perception? *Vision Research*, *40*, 2329–2339.
- Loffler, G., & Orbach, H. S. (2001). Anisotropy in judging the absolute direction of motion. *Vision Research*, *41*, 3677–3692.
- Loffler, G., Wilson, H. R., & Wilkinson, F. (2003). Local and global contributions to shape discrimination. *Vision Research*, *43*, 519–530.
- Marr, D. (1982). *Vision*. New York: W.H. Freeman.
- Missal, M., Vogels, R., Li, C.-Y., & Orban, G. A. (1999). Shape interactions in macaque inferior temporal neurons. *Journal of Neurophysiology*, *82*, 131–142.
- Orban, G. A., Vandenbussche, E., & Vogels, R. (1984). Human orientation discrimination tested with long stimuli. *Vision Research*, *24*, 121–128.
- Pasupathy, A., & Connor, C. E. (1999). Responses to contour features in macaque area V4. *Journal of Neurophysiology*, *82*, 2490–2502.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.
- Perrett, D. I., Rolls, E. T., & Caan, W. (1982). Visual neurones responsive to faces in the monkey temporal cortex. *Experimental Brain Research*, *47*, 329–342.
- Pitts, W., & McCulloch, W. S. (1947). How we know universals: The perception of auditory and visual forms. *Bulletin of Mathematical Biophysics*, *9*, 127–147.
- Quick, R. F. (1974). A vector-magnitude model of contrast detection. *Kybernetik*, *16*, 65–67.
- Regan, D. (2000). *Human perception of objects*. Sunderland, MA: Sinauer Associates.
- Regan, D., Gray, R., & Hamstra, S. J. (1996). Evidence for a neural mechanism that encodes angles. *Vision Research*, *36*, 323–330.
- Regan, D., & Hamstra, S. J. (1992). Shape discrimination and the judgement of perfect symmetry: Dissociation of shape from size. *Vision Research*, *32*, 1845–1864.
- Riesenhuber, M., & Poggio, T. (1999). Hierarchical models of object recognition in cortex. *Nature Neuroscience*, *2*, 1019–1025.
- Robson, J. G., & Graham, N. (1981). Probability summation and regional variation in contrast sensitivity across the visual field. *Vision Research*, *21*, 409–418.
- Rolls, E. T., Baylis, G. C., & Hasselmo, M. E. (1987). The responses of neurons in the cortex in the superior temporal sulcus of the monkey to band-pass spatial frequency filtered faces. *Vision Research*, *27*, 311–326.
- Scobey, R. P. (1982). Human visual orientation discrimination. *Journal of Neurophysiology*, *48*, 18–26.
- Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, *171*, 701–703.
- Snippe, H. P., & Koenderink, J. J. (1994). Discrimination of geometric angle in the fronto-parallel plane. *Spatial Vision*, *8*, 309–328.
- Tarr, M. J., & Bulthoff, H. H. (1998). Image-based object recognition in man, monkey and machine. *Cognition*, *67*, 1–20.
- Ullman, S. (1989). Aligning pictorial descriptions: An approach to object recognition. *Cognition*, *32*, 193–254.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In R. J. W. Mansfield (Ed.), *Analysis of Visual Behaviour* (pp. 549–586). Cambridge, MA: MIT Press.
- Van Essen, D. C., & Gallant, J. L. (1994). Neural mechanisms of form and motion processing in the primate visual system. *Neuron*, *13*, 1–10.
- Wilson, H. R. (1978). Quantitative characterization of two types of line-spread function near the fovea. *Vision Research*, *18*, 971–981.
- Wilson, H. R. (1991). Psychophysical models of spatial vision and hyperacuity. In: D. Regan (Ed.), *Spatial vision*, pp. 64–86 (Vol. 10 of *Vision and Visual Dysfunction*). New York: MacMillan.
- Wilson, H. R., McFarlane, D. K., & Phillips, G. C. (1983). Spatial frequency tuning of orientation selective units estimated by oblique masking. *Vision Research*, *23*, 873–882.
- Wilson, H. R., & Wilkinson, F. (1998). Detection of global structure in Glass patterns: Implications for form vision. *Vision Research*, *38*, 2933–2947.
- Wilson, H. R., Wilkinson, F., & Asaad, W. (1997). Concentric orientation summation in human form vision. *Vision Research*, *37*, 2325–2330.