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Studies Of The Visual Detection Of Bilateral Symmetry

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Studies of the visual detection of bilateral symmetry.

by

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Abstract

Ernst Mach (1897) first observed that bilateral symmetry was most easily observed when the axis of symmetry was vertical, and proposed this occurred because of symmetric connections across the vertical midline of the visual system. This neuroanatomical account has been reasserted by Julesz (1971) and Braitenberg (1984, 1990). Braitenberg suggested that the corpus callosum could serve as a conduit for connections between cells representing symmetric areas in space around the vertical midline. If vertical symmetry in the visual system mediates the vertical advantage there are a number of predictions that follow. One would expect that the tuning of symmetry detection around vertical should be narrow, eccentric presentation of patterns should reduce the vertical advantage, and the vertical advantage should be absent at fixation in individuals without a corpus callosum. Five experiments were conducted to test these predictions. Subjects were tested using a signal detection paradigm. Symmetric and random patterns composed of 72 dots placed within a circular field were presented for brief durations. Vertical symmetry was found to be more detectable at fixation than symmetry at other orientations (from 5° to 90° off vertical, Experiments 1 & 3). No systematic differences were observed for the detection of non-vertical symmetry when patterns were presented at different positions along the horizontal midline (up to 4.8° from fixation to the left or right, Experiments 2, 3, & 4), and the vertical midline (Experiment 4). Vertical symmetry was best detected when presented at fixation (Experiments 2, 3, & 4), and detectability dropped off when stimuli were presented as little as 0.6° off fixation (Experiment 3). Two individuals born without a corpus callosum did not detect vertical symmetry best at fixation, whereas their age, intelligence, and gender matched controls demonstrated a vertical symmetry preference (Experiment 5). These results are in general agreement with the neuroanatomical proposal, and are interpreted in relation to other proposals for how bilateral symmetry may be detected. It is unclear how non-vertical or non-fixated bilateral symmetry is detected, although arguments for a spatial-frequency decomposition of images are discussed.

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Chapter 1 - Introduction

Bilateral symmetry, or mirror symmetry, is a type of structure evident in many living things, manufactured objects, and in visual art. For example, all vertebrates have a pronounced axis of bilateral symmetry, so that the long axis of the body can be divided into a left and right side, which are mirror images of each other at a global level. Visible symmetric structure has been shown to influence the behaviour of different animals. Some birds and insects have been shown to recognize symmetry, preferring to select potential mates having bilaterally symmetric features or markings (for example, Ridley, 1992; Swaddle & Cuthill, 1994). Research on pigeons has shown they can discriminate symmetric from asymmetric forms, and demonstrate stimulus generalization for bilateral symmetry (Delius & Nowak, 1982). In humans, the salience of bilateral symmetry in patterns has long been recognized, and the detection of bilateral symmetry has been suggested to play a rôle in object recognition and representation (eg., Marr, 1982; Leyton, 1987). Furthermore, the detection of bilateral symmetry in patterns has been shown to guide active visual exploration of a form or complex image (Locher & Nodine, 1973, 1987), and the identification of potentially interesting areas within a scene may be assisted by detecting regions that are bilaterally symmetric (Yeshurun, Reisfeld, & Wolfson, 1992).

One of the earliest observations made concerning human perception of symmetry was that bilateral symmetry can be recognized most easily when the axis of symmetry is vertical. This observation has been replicated in most studies of symmetry detection, suggesting that bilateral symmetry around a vertical axis must be special in some way. The findings described in this dissertation stem from a detailed examination of a possible mechanism for the detection of bilateral symmetry originally proposed by Ernst Mach (1897) that was based on the observed salience of vertical symmetry. Mach suggested that the vertical symmetry of the optical apparatus and ocular musculature provided the substrate for the recognition of vertical symmetry (Mach, 1897). Braitenberg (1984, 1990) and Julesz (1971) proposed that Mach was correct in assuming that the structure of the visual system subsumes the vertical advantage, but updated the hypothesis to take into account more recent knowledge of psychophysics and the structure of the visual system. They proposed a cortical locus for the vertical symmetry advantage. Braitenberg suggested that the corpus callosum was the conduit for matching across the vertical axis because there are direct connections between cortical loci representing homotopic regions across the vertical midline. Other researchers have presented descriptions of how bilateral symmetry is recognized in general (Jenkins, 1982, 1983; Locher & Wagemans, 1993; Palmer & Hemenway, 1978; Royer, 1981; Wagemans, Van Gool, & d'Ydewalle, 1991, 1992; Wagemans, Van Gool, Swinnen, & Van Horebeek, 1993; Zimmer, 1984), but the "neuroanatomical" proposal has not been refuted by the results of these studies, or the theoretical accounts that have been presented. The purpose of the experiments reported below was to test several predictions that follow from this neuroanatomical hypothesis. First, findings describing human symmetry detection will be reviewed, followed by discussion of other proposals for how bilateral symmetry is detected, a description of the neuroanatomical hypothesis, and an outline of the predictions stemming from this proposal. The introduction concludes with arguments supporting the choice of the stimuli and task used in the present experiments.

Bilateral symmetry detection

Research on the detection of bilateral symmetry has focussed on three main issues. First, differences in the detectability of symmetry depending on the orientation of the axis of symmetry have been examined. Table 1 lists some aspects of studies of symmetry detection using adult subjects. It also includes studies that have examined what may be termed symmetry perception, not just detection. These studies have had an impact on proposals for how symmetry is detected, and are included for that reason. The order of symmetry preference found in the studies is given in Table 1, and this information is reviewed in more detail as follows.

Most researchers have found an advantage for the perception of vertical symmetry over symmetry at other orientations (Barlow & Reeves, 1979; Corballis & Roldan, 1975; Herbert, Humphrey & Jolicoeur, 1989, 1994; Locher & Wagemans, 1993; Masame, 1983; Palmer & Hemenway, 1978; Pashler, 1990; Royer, 1981; Wagemans et al., 1991; Zimmer, 1984), although in a few cases horizontal symmetry has been reported to be perceived most readily (Jenkins, 1983; Pashler, 1990, Experiment 4), or symmetry at all orientations is detected with equal facility (Wagemans et al., 1992). Thus, with a few exceptions, bilateral symmetry detection shows a reliable orientation anisotropy with an advantage for vertical symmetry. The pattern of results for detecting symmetry at non-vertical orientations is more variable, and most experiments have tested symmetry detection for horizontal and 45° oblique (diagonal) symmetry axis orientations. Some researchers have found that horizontal symmetry is detected more readily than diagonal symmetry

Table 1. Comparison of stimulus parameters and results from a variety of symmetry perception experiments.

Study	Number of Elements	Element Size	Display Size	Orientation Effects (from most to least salient)	Exposure Duration	Dependent Measure(s)
Barlow & Reeves (1979)	100	1 pixel (?)	2° - 4.2° circ. or squ.	V, H, ±45°, ±30° = ±60°	100 ms	d'
Bruce & Morgan (1975)	≤30	≥0.2°	≈6° rectangle	tested V only	UL	RT, accuracy
Carmody et al. (1977)	1	polygons	4° to 10°	V = H	25 ms	d', accuracy
Corballis & Roldan (1975)	12	large	10° square	V, ±45°, H	2000 ms	RT, % correct
Fisher & Bornstein (1982)	16*	small	3° circle	V = H, ±45°	1000 ms	RT, % correct
Herbert et al. (1989)	48	1 pixel	≈3° square	V best, 23° = 45° = 67° = H	UL	RT, % correct
Herbert et al. (1994)	48	1 pixel	≈3° square	V, ±45°	UL	RT, % correct
Jenkins (1982)	26/deg^2	1 pixel (?)	3°, 5° & 7° square	tested V only	1000 ms	% correct
Jenkins (1983)	26/deg^2	1 pixel (?)	5° square	H, V	1000 ms	% correct
Locher & Wagemans (1993)	36	.29° to .36°	3.75° square	V, H , ±45° (Ex. 1), & no differences (Ex 2.)	10, 75, & 125 ms**	RT, % correct
Masame (1983)	800	1 pixel (?)	3.2° square	V, H, 30° = 45° = 60°	127 ms	d'
Masame (1984)	18	large	3.5° square	V, H, 45°	2000 ms	RT, % correct
Masame (1985)	72	small	5.3° x 5° rectangle	tested V only	2000 ms	RT, % correct
Palmer & Hemenway (1978)	1	polygons	≈4°	V, H, ±45°	UL	RT, % correct

Table 1. (continued).

Study	Number of Elements	Element Size	Display Size	Orientation Effects (from most to least salient)	Exposure Duration	Dependent Measure(s)
Pashler (1990)	30	1x0.5 mm	≈6°	V, ±45°, H (Ex. 1); V, ±45° = H (Ex. 3); H, V, ±45° (Ex. 4)	150 ms	RT, % correct
Royer (1981)	12-80	varied	1.13°	V, H, ±45°	UL	RT, % correct
Saarinen (1988)	30	2 mm***	1.3° squ., 2° x 2.3° rec.	tested H only	140 ms	% correct
Wagemans et al. (1991)	24	5.7'	5°	V,H,±45	100 ms	d'
Wagemans et al. (1992)	24	5.7'	5°	orientation varied in 15° steps V,H,45°=15°=30°=60°=75°	UL	RT, % correct
Zimmer (1984)	1	polygons	no size given	orientation varied in 5° steps V, ±45°, H, other obliques intermediate to these	UL	RT

Abbreviations: V - vertical symmetry; H - horizontal symmetry (other orientations are given in degrees of angular rotation from vertical); UL - stimulus presentation lasted until a response was made; and, RT - reaction time measured.

* Eight of these dots formed the outer border of the stimuli, and were arrayed as the vertices of an octagon, the other 8 were arranged within that area randomly or symmetrically depending on trial type.

** In this study one of the authors was tested at a 10 ms exposure duration, one at 75 ms, and the remainder of the subjects at the 125 ms exposure duration. This was done to equate the hit rate at 75% across subjects.

***The dot size was large, but the stimuli were viewed from 458 cm away.

(Barlow & Reeves, 1979; Masame, 1983; Palmer & Hemenway, 1978; Royer, 1981; Zimmer, 1984), whereas others have found that diagonal is perceived more rapidly than horizontal symmetry, suggesting a process like mental rotation is involved in detecting off-vertical symmetry (Corballis & Roldan, 1975; Pashler, 1990, Experiment 1). Finally, some researchers have found no difference in the detection of symmetry for non-vertical axis orientations (Herbert et al., 1989; Locher & Wagemans, 1993; Pashler, 1990, Experiment 3; Wagemans et al., 1992, 1993). Thus, different patterns of results have been reported for the detection of symmetry as a function of orientation. Unfortunately, the experiments differ in too many ways to delineate precisely the source(s) of the different results. Some of those differences are highlighted in the other columns of Table 1. Nevertheless, most researchers have found that vertical symmetry is more easily detected than symmetry at other orientations, consistent with Mach's observation.

The second major issue that has been examined is whether perturbations to perfect mirror symmetry can be detected (Barlow & Reeves, 1979; Bruce & Morgan, 1975; Jenkins, 1982; Julesz, 1971; Tapiovaara, 1990; Zimmer, 1984). The general finding has been that the region immediately adjacent to the symmetry axis contributes the most to the detection of symmetry, although the symmetric placement of dots at the outer edge of the patterns also affects detectability (Barlow & Reeves, 1979). Observers take longer to find violations to perfect symmetry the farther they are from the symmetry axis (Bruce & Morgan, 1975), and they may not notice non-symmetrically arranged dots at all when these are relatively far away from the symmetry axis (more than 0.6° from the axis, Jenkins, 1982). Zimmer (1984) showed that global violations to the symmetric structure of forms were more detectable than local violations. Thus, the mechanism detecting symmetry acts over some distance in the stimulus to make symmetric matches, but the region around the axis of symmetry is weighted more heavily than more distant regions. The matching process that occurs to detect bilateral symmetry must be able to operate over some distance in a pattern, because a purely local process would be insufficient to account for the observation that bilateral symmetry can be detected without symmetrically paired elements at midline (Barlow & Reeves, 1979; Jenkins, 1982). In addition, this conclusion is supported by the evidence that deviations from perfect symmetry are detected when they are a large distance from the axis of symmetry, although this takes longer than for perturbations close to the symmetry axis (Bruce & Morgan, 1975). The fact that bilateral symmetry is also detectable in line drawings also supports the conclusion that the mechanism can operate over some distance across a pattern.

The third major issue has been to determine whether the detectability of symmetry changes when the shape or grey-level of elements making up patterns is manipulated (Locher & Wagemans, 1993; Masame, 1985; Royer, 1981). In these studies, the orientations of elements on each side of the symmetric axis were varied with no measurable effect on symmetry detection. There was also little change in the detectability of symmetry in patterns composed of items of different shapes. So symmetric elements need not have the same shape or grey-level for the structure to be detected, symmetrically paired elements do not have to have the same appearance for symmetry to be detectable, and differences in the detectability of patterns composed of different elements are minimal. The results of these studies suggest that the only information that may be encoded when detecting symmetry is the position of elements in a pattern. In contrast, a recent study by Zhang and Gerbino (1992) suggests that the contrast of the elements to be paired across a symmetry axis may affect the detectability of symmetry. They found that black/black and white/white dot pairs resulted in greater detectability than different contrast pairs (there was always a grey background). A full report of this work has not been published yet, nonetheless, it suggests that coding the position of elements alone may not suffice for detecting symmetry.

Table 1 lists the number of elements making up symmetric stimuli used in various experiments, as well as the size of the elements and the size and shape of the symmetric patterns. It is immediately apparent that there has been little consistency along those dimensions in the stimuli used in those studies, although they have generally consisted of "clouds" of dots or irregular polygons. The dot patterns consist of position information and little else, and bilateral symmetry is readily detected in such patterns. The number of dots does not appear to matter, symmetry is detectable in patterns composed of a few dots or thousands of dots. To date, there has not been an examination of the effect of dot number or density on symmetry detection. Despite the inconsistencies in stimulus parameters, bilateral symmetry appears to be detected easily, and the vertical advantage has been found across all types of patterns (Table 1).

In Locher and Wagemans' (1993) study, symmetric stimuli were composed of line segments oriented vertically, horizontally, diagonally, or a mixture of orientations. They also presented dot patterns as a control. Although the figures appeared to have a pronounced structure, and informal examination of these patterns suggests that some line segment orientations produced a better impression of symmetry than others, Locher and Wagemans found little effect of element type on the time required to detect bilateral symmetry. They did find that grouping elements across the symmetry axis, so that several line segments formed symmetric clusters around the axis, affected the detectability of symmetry. Thus, they found that the local micropattern structure was less important than larger scale structure in bilaterally symmetric patterns. One potential problem with Locher and Wagemans' study is that they used 30 patterns and repeatedly presented them to subjects (there were 1800 symmetric trials across their two experiments, so each pattern would have been seen 60 times). It is possible that the large number of repetitions of the same patterns would have resulted in subjects recognizing certain patterns, or clusters in the patterns, and this may have reduced the chances of finding any differences as a function of element type. The potential effects of repeatedly presenting the same patterns have not been systematically examined, so one can only speculate about potential problems with such a design. It seems likely that certain arrangements of elements would become recognizable after a number of repetitions, so patterns may be recognized, and "pure" symmetry detection would not occur.

There are several characteristics of our ability to detect bilateral symmetry that suggest it is a relatively low-level process in vision. Symmetry can be detected in patterns presented very briefly. Symmetric patterns only need to be presented for 10 ms for observers to discriminate vertically symmetric patterns from random patterns (Carmody, Nodine &, Locher 1977; Locher & Wagemans, 1993). The mechanism seems to be relatively hard-wired, because practice has no measurable effect c detection (Cohen, Tabor & Sejnowski, 1986; Royer, 1981), and young human infants respond to bilateral symmetry in a manner analogous to adults (Bornstein, Ferdinandsen, and Gross, 1981; Bornstein & Krinsky, 1985; Humphrey & Humphrey, 1988). Furthermore, as mentioned above, the shape of elements has no effect on detectability, so the position of elements making up a pattern may be all that is coded in judging if a pattern is symmetric (although the contrast of symmetrically paired elements may matter, Zhang & Gerbino, 1992). Nonetheless, bilateral symmetry is a form of structure that only exists for the whole pattern. Bisecting a symmetric figure along its axis of symmetry produces a random pattern, neither half having any indication of the structure that is perceived when the two are juxtaposed. Also, Zimmer (1984) demonstrated that global violations to the perfect symmetry of patterns having both local and global symmetric structure were more easily detected than local asymmetries. So symmetry detection must work across some distance in the target pattern, and may ignore local information at early stages (Palmer & Hemenway, 1978; Zimmer, 1984). In examining symmetry detection we must ask how the information from one half of the pattern is matched with the information on the other side to produce a symmetric percept? To determine that a pattern is symmetric, the position of features or elements on one side must be compared to the position of features or elements on the other side across some putative symmetry axis — a type of correspondence problem. This possible symmetry axis must also be selected before symmetric matches are determined.

There have been numerous studies of symmetry as a Gestalt phenomenon, of how it is related to judgements of the complexity and pleasingness of patterns, its contribution to the perception of art, its possible rôle in models for shape and object recognition, the Goldmeier Effect, and other topics in pattern perception. Although these studies are related to the perception of symmetry in general, they pertain to bilateral symmetry as one of many possible structures in patterns, and are not directly concerned with how bilateral symmetry is detected by observers. For that reason these studies will not be described further.

Proposed mechanisms of symmetry detection

The findings outlined above have led researchers to propose a variety of hypotheses for how symmetry is detected, but thus far none is sufficient to account for all symmetry detection results. Many of these proposals share some general features, primarily that the process requires a number of steps (Mach, 1897; Palmer & Hemenway, 1978; Royer, 1981; Wagemans et al., 1992, 1993; Zimmer, 1984). First, a rapid assessment of the pattern is proposed to occur, where a coarse symmetry judgement is made and a putative symmetry axis is selected. This is followed by a slower, more detailed inspection of the stimulus to confirm this judgement, and to search for symmetry (or violations to it) that is more difficult to detect. According to Mach, the initial assessment allows for the rapid detection of vertical symmetry, and symmetry about other orientations is only detected after more detailed examination of the patterns (see also Julesz, 1971). Mach's proposal, and the modifications made to it by subsequent researchers will be described after a brief description of the other proposed symmetry detection mechanisms.

Palmer and Hemenway (1978) presented the first alternative to the symmetry detection proposal of Mach (and its modification into the neuroanatomical hypothesis advanced by Julesz, 1971). This is one of a family of proposals that have been presented to account for the salience of vertical symmetry, and the order of axis preferences expressed. As shown in Table 1, Palmer and Hemenway found symmetry in patterns was detected in a vertical, then horizontal, then diagonal order for patterns with one symmetry axis. They also examined the detection of symmetry in patterns with multiple symmetry axes, and they found that as the number of axes increased so did the speed of symmetry detection (see also Royer, 1981, who obtained the same result). Palmer and Hemenway suggested that symmetry is detected in a two-stage process, the first involves selecting a symmetry axis, and the second is where symmetry itself is tested for. They attempted to describe the first stage, but not the second. The vertical, horizontal, then diagonal order was observed, according to Palmer and Hemenway, because the potential axis of symmetry around which to test for symmetry is selected probabilistically. The probability of selecting a particular orientation is based on the prominence of those orientations in our representation of space. The order of the orientation preference for symmetry is determined by the normal vertical frame of reference that appears to operate, and the superiority of horizontal symmetry over diagonal symmetry may be related to the oblique effect (e.g., Appelle, 1972). The probabilistic quality of their proposal was included to account for the more rapid detection of symmetry in patterns having multiple symmetry axes. Palmer and Hemenway do not state how symmetry is detected, but they suggest why it is detected in a particular order.

Royer (1981) concurred with Palmer and Hemenway (1978) in the order of orientation preferences, but he suggested that the selection of a putative symmetry axis was relatively inflexible. He suggested a strict hierarchy, with vertical symmetry tested for first, then horizontal, then diagonal. The major drawback with both the Hierarchical and the Probabilistic proposals is that they lack generality. If one adds more symmetry orientations what happens? One possible interpretation of the two proposals is that they describe three special orientations of bilateral symmetry. If this is true, one must ask what occurs in detecting symmetry at intermediate orientations? Is there a gradual change in the detectability of symmetry with the three canonical orientations defining singularities? Zimmer's (1984) results are in agreement with this because there was a gradual decrease in the detectability of symmetry away from vertical, with horizontal and 45° oblique symmetries detected faster than other off-vertical orientations. Experiments 1 and 3 of the thesis examined the detectability of symmetry at non-canonical orientations to explore these questions. A failing of these two models is that they leave out a major part of the story. How is symmetry tested? We know that there must be a comparison of something across the midline, and it appears that what is compared are the positions of items symmetrically arranged across the symmetry axis, as mentioned earlier. The Hierarchical and Probabilistic proposals contribute minimally to that mystery, and in many ways they stand as descriptions of the results obtained in the respective studies, contributing little to our understanding of the mechanism underlying the detection of symmetry itself.

Corballis and Roldan (1975) also described how a prospective symmetry axis may be selected, but they worked from the starting point of the neuroanatomical proposal. Corballis and Roldan suggested that mental rotation was involved in selecting a symmetry axis because they obtained a vertical, diagonal, then horizontal order. They suggested that a prospective orientation is selected, then the pattern is rotated to vertical to match the symmetry in the visual system for a point-by-point comparison of elements in the pattern to detect the symmetry. Fisher and Bornstein (1982), and Pashler (1990, Experiment 1) obtained roughly the same pattern of results as Corballis and Roldan. Pashler found mixed results across five experiments, and suggested that mental rotation occurred in conjunction with reference frame effects. Again, these experiments assumed that testing for symmetry occurred through some undefined operation.

Barlow (1980; Barlow & Reeves, 1979) proposed and tested a mechanism to detect symmetry itself, ignoring the orientation dependence of symmetry detection in an attempt to learn something about how the mapping of symmetric pairs is made across the symmetry axis. Barlow and Reeves (1979) found that the detectability of symmetry varied with orientation and eccentricity, similar to other researchers. They also observed that smearing the exact placement of symmetrically paired dots by up to 24′ of arc did not disrupt the detectability of vertical symmetry (the only orientation tested in that experiment). Further, the detectability of bilateral symmetry was affected by the positioning of symmetric dots within a random pattern. Symmetry was detectable when a pattern was random except for dots symmetrically paired along the outer edge of the pattern, or adjacent to the symmetry axis. If symmetric dots were placed within each half of a pattern symmetry was not easily detected. Again, vertical was the only orientation tested. Troscianko (1987) demonstrated that symmetry was detectable in isoluminant stimuli, and suggested that whatever mechanism detects symmetry does not require precise information about the position of elements that are symmetrically paired. The apparent insensitivity demonstrated to the precise positioning of dot pairs that are symmetric seems paradoxical given the aforementioned results suggesting that the position of elements in a display is all that may be encoded in symmetry detection. This paradox has not been resolved empirically thus far, although results reported by Barlow (1980) are provocative.

The mechanism for symmetry detection tested by Barlow (1980) stemmed from the observation that one could not detect symmetry by counting all the symmetrically paired dots in the kinds of patterns used by Barlow and Reeves, which consisted of briefly presented patterns of 100 dots (Table 1). Barlow suggested that symmetry might be detected by a mechanism that counts dots falling in symmetrically arranged regions of a pattern and compares them across the putative symmetry axis. For example, a stimulus 2° square might be divided into sixteen 1/2° by 1/2° squares, and the number of dots in symmetrically placed squares could be compared. This could be conceived of as a comparison of the density of dots in the different regions. In symmetric patterns the number of dots in symmetric regions in space would be equal, whereas the numbers would differ for random patterns. Despite early successes, the simulations of this mechanism did not match human performance. The biggest problem with this segment->count->compare model is that it requires a relatively high-resolution system, but experiments by Barlow, and Julesz and Chang (1979), showed that bilateral symmetry can be detected using low-resolution information alone. Barlow (1980) blurred symmetric patterns by presenting them behind diffusing filters, and found that the detectability of symmetry *improved* with moderate amounts of blur (less than 1/4° to 1/2°) before deteriorating when the amount of blur was increased further. This result suggests comparison of the numbers of dots in different regions was not occurring, and that whatever mechanism detects symmetry can operate using low-resolution information in symmetric stimuli. Tapiovaara (1990) tested a similar density comparison mechanism for symmetry detection, and found it did not match human performance.

Locher and Wagemans (1993) examined the effect of element type and grouping on bilateral symmetry detection. Like Barlow, they worked from the position that some sort of density comparison is made in detecting bilateral symmetry rather than an intensive point-to-point matching of elements across a putative axis. They found that element structure had no effect on symmetry detection, but symmetry was detected more rapidly in patterns composed of grouped elements. As discussed earlier, the repeated presentation of the same patterns in their experiments raises difficulties in the interpretation of their results, but they interpreted their results as evidence that bilateral symmetry is detected early in visual processing. They suggest that elements in close proximity are grouped, and treated as a unit, so that there is a reduced work load for the matching process that occurs across the symmetry axis. The means by which the visual system would do this was based on the work of Marr (1982) and Watt (1987). Both Marr and Watt suggested that a pattern is decomposed into a series of spatially filtered images early in visual processing, and that low-frequency information is available before high-frequency information. The information at lower spatial frequencies can be used to guide the processing that occurs at higher spatial frequencies. According to Locher and Wagemans, the spatial grouping of elements is somehow perceived across images at different spatial frequencies, and the symmetry percept is derived from the coincidence of features across the different band-pass filtered images. This proposal predicts that bilateral symmetry should be rapidly and accurately detected, which has often been demonstrated, but it does not predict the orientation anisotropy evident for bilateral symmetry detection. Their proposal is incomplete as yet, and it differs greatly from what Wagemans and others have suggested elsewhere.

Wagemans and co-workers have presented another mechanism for how symmetry is detected across an axis. This proposal is both the most explicitly stated thus far, and has the greatest scope, since it accounts for the recognition of many regularities in patterns, not just bilateral symmetry (Wagemans, 1993; Wagemans et al., 1993). Repetition symmetry, skewed symmetry, and other rigid transformations of patterns are purported to be detected by recognizing higher-order structure in patterns. The starting point for Wagemans' ideas were observations made by Jenkins (1982, 1983). Jenkins made note of the fact that bilateral symmetry could be described in different ways. The most common way it is described is as the structure present in a pattern when elements on one side of an axis are mirror images of those on the other side of that axis. Jenkins noted that pairs of dots in random dot displays can be joined by a line, so they can be seen as the endpoints of a line. The lines that can be drawn between symmetric pairs of dots in a bilaterally symmetric pattern are all at the same orientation, and the midpoints of these lines lie along the symmetry axis. In repetition symmetry the virtual lines (between the symmetric points) are uniformly oriented, and of constant length. Jenkins suggested that bilateral symmetry in dot patterns could be detected by recognizing the homogeneity of the orientation of the virtual lines and/or the collinearity of their midpoints. Wagemans has taken this idea further, noting that the array of virtual lines in bilaterally symmetric patterns form a pattern of "correlation quadrangles" (Wagemans et al., 1991, 1992). Wagemans suggests that this pattern of second order regularities is what is recognized in detecting bilateral symmetry. The array of correlation quadrangles that can be generated from patterns with multiple axes of symmetry is more regular than those in single axis symmetric patterns, and this increased regularity is what gives the advantage to multiple axes of symmetry according to the model. Wagemans and co-workers have also examined the effect of skewing bilateral symmetry, finding it more difficult to detect than bilateral symmetry, but its detectability generally followed the predictions of the model.

There are two problems with the model for regularity detection proposed by Wagemans and co-workers. First, research has indicated that bilateral symmetry is special, and it is usually more easily recognized than repetition (Corballis & Roldan, 1975; Zimmer, 1984). Although the notion that one mechanism underlies the detection of different kinds of structure in patterns is appealing, it cannot be reconciled with the results of many studies. Whereas Wagemans and co-workers (Locher & Wagemans, 1993; Wagemans et al., 1991, 1992) report variability in the detectability of bilateral symmetry with changes in the axis orientation, all other studies of symmetry detection have found some systematic orientation anisotropy (Table 1). One of the reasons that Wagemans and co-workers may have concluded that there is little systematic difference in the detectability of bilateral symmetry as a function of axis orientation is that observers were provided with unlimited viewing (Wagemans et al., 1992), so they may have been responding at ceiling. Wagemans and co-workers (1991) only report *d′* values that are very high (greater than 3) in their other study, which is also consistent with a possible ceiling effect. Any differences in the salience of symmetry as a function of orientation may be unmeasurable when performance is at ceiling.

The second problem with the correlation quadrangle model is that it seems to have been formulated to account for the detection of bilateral symmetry (and other regularities) for dot patterns only. The pattern of results obtained with stimuli composed of polygons and dot patterns has been similar, and many of the assumptions of the model make it difficult to see how it would function for detecting regularity in polygons. A line drawing would create a situation where there would be infinite possible virtual lines, and correlation quadrangles, or there must be some segmentation of the outer border into parts from which virtual lines would extend (from the vertices or curvature extrema of such closed figures, for example). At the first stages of pattern decomposition virtual lines could connect each dot to all neighboring dots. The location of the correct matches between symmetric pairs, and the subsequent recognition of correlation quadrangles appears to be a time consuming, intensive process. The positions and spatial relations of all the elements in a pattern would have to be remembered very precisely when bilaterally symmetric figures are briefly presented. This would suggest that symmetry detection is a process that is intensive, and quite demanding, when it appears, in fact, that vertical symmetry is detected almost effortlessly. Furthermore, the small line segments used as elements in some of the patterns presented by Locher and Wagemans would restrict the propagation of virtual lines, again making the generation of correlation quadrangles more difficult. Wagemans never makes it clear how the appropriate dots are selected to be linked by virtual lines over other possible matches (there are *n(n-1)* possible matches in a pattern, where *n* is the number of dots). If some mechanism exists to link symmetrically paired dots preferentially, this suggests bilateral symmetry has been detected, so why construct the quadrangles? The construction of correlation quadrangles, and the recognition of the higher order structure in patterns would be unnecessary if the orientation uniformity in a pattern is already recognized, as suggested by Jenkins (1983). Thus, Wagemans and co-workers have suggested a general model for detecting regularity in patterns that suffers from that generality because it does not correspond to the observation that bilateral symmetry is a special kind of structure. Vertical symmetry appears to be a form of bilateral symmetry that is special itself.

The neuroanatomical hypothesis

Mach originally proposed that the bilateral symmetry of the ocular musculature was involved in the advantage for vertical symmetry. He suggested that the bilateral symmetry of the visual system around the vertical meridian was the basis for the salience of vertical symmetry. Corballis and Beale (1976) present a lucid discussion and review of Mach's original proposal, and the extension of those ideas by Julesz (1971). Julesz noted that the symmetric structure of simple forms is easily detected, but demonstrated that symmetry in complex forms such as random dot patterns is not easily perceived unless the centre of the pattern is fixated, and the symmetry axis is vertical. This distinction between the ease of detecting symmetry in 'simple' forms as compared to 'complex' forms has been noted by many of the researchers following Julesz, and it has been taken as evidence for a two-stage process in symmetry detection, as described above. Surprisingly, there has not been an empirical test of this finding, and examination of the results from studies using random dot patterns versus outline figures reveals no systematic differences in the reaction times or accuracy reported for detecting bilateral symmetry among the two types of patterns (Corballis & Roldan, 1975; Fisher & Bornstein, 1982; Herbert et al., 1989; Masame, 1984; Palmer & Hemenway, 1978; Pashler, 1990; Royer, 1981; Zimmer, 1984). The symmetry of a pattern may be assessed in more than one stage, but it does not appear that there are differences in the salience of bilateral symmetry as a function of the type of stimulus used (although grouping elements may increase the saliency of symmetry as reported by Locher and Wagemans, 1993).

The addition to Mach's hypothesis that was made by Julesz was that the projection of a symmetric pattern to the symmetric visual system would result in the left half of the image first going to the right cortical hemisphere, and the right half of the image first going to the left hemisphere. He suggested that some point-by-point matching process occurs between symmetrically opposite loci in each cortical hemisphere. A cortical locus for symmetry detection was suggested by the observation that symmetry perception occurs after the information from both eyes has been combined (Julesz, 1971; Julesz & Chang, 1979). Julesz and Chang demonstrated that if a horizontal symmetric pattern is presented to one eye, and a vertically symmetric pattern is presented to the other the resultant percept is not symmetric. If, on the other hand, a low-pass filtered horizontally symmetric pattern and a high-pass filtered vertically symmetric pattern are presented to each eye both symmetries are perceived simultaneously. Julesz and Chang proposed that symmetry detection occurs after stereopsis, and that information from different spatial frequency channels may be combined to detect symmetry.

One link between the visual areas in each hemisphere consists of the nerve fibres running through the corpus callosum. Braitenberg (1984, 1990) suggested that vertical symmetry is detected through point-by-point matching mediated by fibres crossing over through the corpus callosum. Thus, the pattern of activation produced by one side of the visual field is mapped onto that from the other side, and symmetry is signalled by sufficient overlap in the activation produced by the hemi-patterns. Corballis and Beale (1976) suggested that the mechanism for detecting symmetry might have a subcortical substrate, but that idea has not been developed further. The current understanding of the arrangement of callosal projections from visual cortex is described next, and it is generally consistent with what would be required by the neuroanatomical hypothesis.

Research on interhemispheric cortical connections in humans suggests that there are direct links between parts of the visual cortex representing symmetrically placed regions in space. The earliest callosal projections seem to link homotopic regions of the visual cortex, linking cells located symmetrically across the vertical meridian. These conclusions have been made by extrapolating from studies of non-human primate neuroanatomy and neurophysiology, and from studies of human neuroanatomy and psychophysics. Some work on contralateral cortical projections running through the corpus callosum has been conducted in cats, where the earliest contralateral projections arise from the area 17/18 border from cells representing space near the vertical midline and the horizontal midline

(Blakemore, 1969; Hubel & Wiesel, 1967; Innocenti, 1986). Recordings from fibres running through the splenium of the corpus callosum of cats were made by Hubel and Wiesel (1967), and they found that these cells had receptive fields straddling the vertical midline. Neuroanatomical studies of macaques have indicated that area 17 has no afferent or efferent callosal projections, and the earliest callosal projections from visual areas seem to be related to the representation of space at fixation and along the vertical meridian, and arise from area 18 (Braitenberg, 1984, 1990; Choudhury, Whitteridge, & Wilson, 1965; Clark & Miklossy, 1990; Cragg & Ainsworth, 1969; Cumming, 1969; Geschwind, 1965; Glickstein & Whitteridge, 1976; Innocenti, 1986; Myers, 1962; Pandya & Seltzer, 1986; Van Essen, Newsome & Bixby, 1982; Zeki, 1969, 1970). These projections run through the corpus callosum to areas 18 and 19 contralaterally, and link cells in those areas that have receptive fields arranged symmetrically across the vertical midline (Choudhury et al., 1965; Cragg & Ainsworth, 1969; Cumming, 1969; Geschwind, 1965; Pandya & Seltzer, 1986; Zeki, 1969, 1970). Zeki (1993) suggests that there are contralateral projections from area 17 in humans, but again, he states that these arise from cells with receptive fields representing the vertical midline and these synapse on cells with receptive fields representing the vertical midline (Clarke & Miklossy, 1990). As far as the neuroanatomical hypothesis for symmetry detection is concerned, it is most important that contralateral connections exist linking areas of the brain mapping space symmetrically about the vertical midline. Debate about how early they arise in the cortical visual pathways only affects the level at which we could say symmetry detection occurs. The same mechanism would operate whether area 17 connects to area 17 contralaterally, area 17 is linked to area 18 contralaterally, or area 18 is linked to area 18 contralaterally. To reiterate, the earliest contralateral connections in visual cortex link symmetric areas of the brain representing space along the vertical meridian and the fovea. These callosal connections are limited to portions of the primary visual cortex representing space to a maximum of 3° to either side of fixation (Milner & Jeeves, 1979). Thus, the neuroanatomy of the human visual system could support the point-to-point matching required by the neuroanatomical hypothesis.

Predictions stemming from the neuroanatomical hypothesis

In its most simple form the neuroanatomical hypothesis suggests that each half of a vertically symmetric pattern is represented as a pattern of activation in each cerebral hemisphere, and the activation is matched across the vertical meridian to detect symmetry (Braitenberg, 1984, 1990; Julesz, 1971). For brief presentations of symmetric patterns the process may occur as follows: one half of a pattern presented at fixation is first processed by the contralateral cortical hemisphere; information from the other half of a pattern is first processed by the other cortical hemisphere; and the input to both halves is compared by some mechanism mapping information across the vertical midline. Julesz (1971) first described the process as occurring in this manner, and based a number of predictions on the neuroanatomical hypothesis. He suggested that symmetric random element patterns would have to be fixated for symmetry to be detected, that dilations (expansions or contractions of the hemi-patterns) would disrupt symmetry detection, and that the elements closer to the symmetry axis contribute the most to the symmetry percept. Julesz demonstrated that dilations disrupted the detection of symmetry, and that the region around the symmetry axis is important in detecting symmetry. The latter was confirmed in experiments reported by Barlow and Reeves (1979), Bruce and Morgan (1975), and Jenkins (1982). Some studies have suggested that symmetry can be rapidly and accurately detected without fixation of the axis of symmetry, as described later.

The neuroanatomical account serves as a good framework for examining bilateral symmetry detection, and the vertical symmetry advantage, because a number of testable predictions follow from it. The predictions that stem from the hypothesis are the following: the tuning of symmetry detection should be quite narrow around vertical; the vertical advantage should decrease, or disappear for brief presentations of patterns away from fixation; the corpus callosum must be intact for the vertical advantage to be expressed; and head tilts should produce a change in the most salient symmetry orientation to correspond with retinal vertical.

The head tilt prediction has been examined by Corballis and Roldan (1975), who found that the reaction times for symmetry detection were fastest for vertical symmetry as compared to symmetry at 45° and 90° from vertical, when the head was in an upright position. This vertical advantage shifted when observers made symmetry judgements with a 45° head tilt. Shorter reaction times were observed for symmetry in line with the head tilt, so retinally vertical symmetry was detected faster than vertical symmetry relative to environmental coordinates. The preference for retinally vertical patterns was not complete, but that is unsurprising given the likelihood that cyclotorsional eye movements occurred in the head tilt conditions. The general pattern of their findings was replicated by Fisher and Bornstein (1982).

The tuning of the vertical symmetry advantage for axis orientation has been examined before, but not for very small shifts in the axis orientation in relatively complex patterns. If the mechanism for detecting vertical symmetry relies on a point-to-point matching process across the vertical midline one would expect that a small shift in the orientation of the axis of symmetry would disrupt the process. The tuning of the vertical symmetry advantage should be quite narrow if the neuroanatomical hypothesis is to be accepted as an explanation for that advantage. Numerous experiments have examined the difference in symmetry detection for different symmetry orientations, but only to within 15° of vertical for random dot patterns (Wagemans et al., 1992). Zimmer (1984) has examined the detection of symmetry for 5° shifts in axis orientation of line drawings. Zimmer's results (Experiment 1, and Figure 13 of that article) suggest that the detection of symmetry changes continuously as a function of axis orientation. Conversely, the neuroanatomical hypothesis suggests that the orientation tuning should be very narrow, so one would expect a pronounced discontinuity between the detectability of vertical symmetry and symmetry at other orientations, contrary to Zimmer's findings. There are several possible accounts for the discrepancies between Zimmer's results and the predictions stemming from the neuroanatomical hypothesis. First, Julesz (1971) suggested that the detection of bilateral symmetry in relatively simple stimuli such as outline drawings does not require the point-to-point matching process necessary to detect symmetry in patterns with greater internal detail like random dot patterns. Thus, there might not be a pronounced advantage for vertical symmetry in simple stimuli. Of course, the premise that symmetry in 'simple' patterns is easier to see is questionable, as described above. Second, subjects in Zimmer's study were allowed to view the figures until they made a response, and reaction times from correct responses to symmetric patterns were the only trials analyzed, so the limits of the visual system were not tested in this study as they would have been with brief presentations using a signal detection procedure. If the task is made harder it seems reasonable to expect a greater difference in the ability to detect symmetry at different orientations. The final possibility is that observers tilted their head to detect non-vertical symmetry in Zimmer's experiment. He does not report whether a head restraint was used to restrict possible head tilts, or whether instructions were given to keep the head still, so this potential problem may or may not be relevant. If observers could make head tilts the reaction times for symmetry close to vertical would be speeded up in some cases, potentially resulting in the continuous function observed. Experiments 1 and 3 of the dissertation examined the tuning of symmetry detection around vertical.

Barlow and Reeves (1979), Masame (1983), and Saarinen (1988) have examined symmetry detection for presentation of target stimuli away from fixation, but only for a single symmetry orientation (the first two studies used vertically symmetric patterns, and Saarinen's study examined the detectability of horizontal symmetry at different eccentricities). These studies showed that symmetry is detected in the periphery, but the neuroanatomical hypothesis suggests that the difference between detecting vertical symmetry and symmetry at other orientations should be reduced when stimuli are presented off fixation relative to the difference at fixation. This question was examined in Experiments 2, 3 and 4. The detectability of vertical, horizontal and oblique symmetry was compared across a number of positions along the horizontal meridian in Experiment 2. Experiment 3 examined the detectability of symmetry for small displacements along the horizontal meridian, and Experiment 4 examined the effect of presenting stimuli away from fixation along the horizontal and vertical meridia.

In Experiment 5 two individuals born without a corpus callosum were tested to determine if they could detect bilateral symmetry at fixation, and to see if the vertical symmetry advantage was present. According to the neuroanatomical hypothesis these individuals should not detect vertical symmetry more easily than symmetry at other orientations for patterns briefly presented at fixation. The results of all five experiments were consistent with the predictions of the neuroanatomical hypothesis.

Why dots and signal detection?

Before describing the experiments, and the results obtained in them, it is necessary to make a brief digression to address some concerns that may have arisen regarding the choice of the stimuli and task in these experiments. In all the experiments described below random dot patterns served as stimuli (half of them symmetric around one axis, and half asymmetric), and they were briefly presented on a computer monitor. Subjects were asked to indicate whether the pattern of dots they saw on each trial was bilaterally symmetric about a designated axis, or if the pattern was random. Their responses were used to compute *d′* values for the particular orientation tested at a range of exposure durations and positions in the visual field.

The use of random dot patterns has a long history in research on symmetry detection, and there are a number of good reasons for using patterns composed of small dots to examine the detectability of bilateral symmetry. First, the circular dots used here do not provide information about a single orientation, so they should not bias the observer towards any one symmetry orientation. Each dot is also easily detected, so the local micropattern information does not limit the detectability of symmetry. The dots were quite small, so they provided a discrete position marker. Position information should be sufficient for symmetry to be detected, as shown by the research indicating the shape of pattern elements has little effect on detectability (Locher & Wagemans, 1993; Masame, 1985; Royer, 1981). Although the dots used in these experiments were small, they have a complex representation in the spatial frequency domain. The Fourier transform of a dot has energy at many spatial frequencies, and if symmetry detection is spatial frequency specific it is very likely that dot patterns would have energy at the bandwidth of concern (De Valois & De Valois, 1990). The use of dots spreads the symmetry information across the entire pattern in contrast to outline drawings, where all of the information is contained in the contour. Dot patterns also serve as good stimuli because a large number of different patterns can be generated using the same number of items constrained to fall within a restricted region, preventing the possibility that individual patterns are recognized with repeated presentation. The problem of salient features signalling the identity of the pattern, and thereby the presence or absence of symmetry, is avoided by using random dot patterns. If the same patterns were used at different orientations, or in different blocks of trials it is possible that observers could recognize symmetric or asymmetric members of the population of stimuli based on particular arrangements of elements or contour information (a problem for some of the studies reviewed earlier). A new pattern was generated for each trial in the present experiments, so no pattern of dots could be recognized over different trials. Finally, symmetry detection involves the solution of a correspondence problem, namely pairing the correct items on each side of the symmetry axis, and dot patterns are ideal stimuli to test such processes.

As described above, most studies of symmetry detection have attempted to maximize the number of correct symmetry identifications and measured the time required to make a symmetry judgement (Table 1). There is a problem with this approach if there are orientation dependent differences in the detectability of symmetry. If only one exposure duration is tested, vertical symmetry must be made quite easy to see so that non-vertical symmetry is also easy to detect. In this case the detection of vertical symmetry may be at ceiling, so the vertical advantage cannot be fully expressed. Floor effects could result if symmetry is made more difficult to detect, because symmetry at other orientations may then be indistinguishable from random patterns. By using a signal detection approach, specifically a yes/no procedure, and varying the exposure duration of patterns, it is possible to measure performance over a range of task difficulty, and compare the results across this dimension. In the following experiments the relative detectability of symmetry at different axis orientations was measured by calculating *d'* values for each symmetry orientation at each exposure duration. These values provide a bias-free estimate of subjects' performance (MacMillan & Creelman, 1991), and permit the comparison of the scores across the different exposure durations for a single symmetry orientation, and across symmetry orientations for the different positions and exposure durations tested. By manipulating these variables simultaneously and/or across blocks of trials, it was possible to measure each subject's ability to detect symmetry for each symmetry orientation when the task was quite difficult and relatively easy. The vertical advantage may disappear when symmetry is easily detected, as indicated by the results of Wagemans and co-workers (1991, 1992, 1993), but only Barlow and Reeves (1979) examined the detectability of symmetry at different task difficulties. Unfortunately, they only did so for vertical symmetry, so the results of the following experiments provide an opportunity to broaden our understanding of bilateral symmetry detection under different conditions. If the orientation anisotropy only occurs when the task is difficult, or if it changes with the demands made on the observer, comparisons across difficulty levels should tell us more about how symmetry is detected than would testing at one exposure duration.

Chapter 2 - Experimental Results

Experiment 1

Subjects in this experiment had to detect symmetry for six symmetry axis orientations: vertical; 10° clockwise and counterclockwise from vertical; 45° clockwise and counterclockwise from vertical; and horizontal. As described above, vertical symmetry has been shown to be most rapidly and easily detected in numerous studies, but most have only tested vertical, horizontal and oblique symmetry orientations (Corballis & Roldan, 1975; Masame, 1983; Palmer & Hemenway, 1978; Pashler, 1990; Royer, 1981). When the detection of symmetry at other orientations has been examined, the pattern of results has varied: some researchers finding differences as a function of orientation (Barlow & Reeves, 1979; Herbert et al., 1989; Masame, 1983; Zimmer, 1984); and others finding no difference (Wagemans et al., 1992, 1993). Barlow and Reeves found vertical symmetry was detected most easily, followed by horizontal symmetry, then other orientations (30°, 45°, and 60° from vertical), as did Masame. The detectability of symmetry at these "non-canonical" orientations differed little amongst each other relative to the differences between the detectability of horizontal or vertical symmetry and the oblique orientations. Zimmer found a continuous change in reaction times for symmetry detection, with vertical most rapidly detected, diagonal symmetry most difficult to detect, and horizontal symmetry was of intermediate detectability. In a reaction time task, Herbert and co-workers (1989) reported that symmetry at ±23°, ±45°, ±67°, and 90° from vertical was detected equally quickly, albeit slower than vertical. In contrast, Wagemans and co-workers have found no difference in the detectability of symmetry across all orientations (cf. Locher & Wagemans, 1993, as noted in Table 1). Most importantly, they found no vertical advantage for the detection of bilateral symmetry, which is an uncommon result (see above) and contrary to what is predicted by the neuroanatomical hypothesis. In this experiment vertical symmetry was expected to be detected more easily than symmetry at other orientations based on previous findings and the neuroanatomical proposal. In light of the inconsistencies among the results of previous studies no concrete predictions could be made as to the precise ordering of the detectability of non-vertical symmetry. However, the general pattern of results reported earlier led to the expectation that horizontal symmetry would follow vertical in salience, followed by the oblique symmetry orientations.

In this experiment, and those that follow, symmetry detection was measured across a range of exposure durations to vary the difficulty of the task, and to determine if the order of detectability of different symmetry orientations varied when symmetry was very difficult to detect compared to when it was readily detected. Thereby, the presence of the vertical advantage could be tested for across a range of exposure durations. All subjects completed this experiment before participating in any other study (except for Experiment 5), which permitted the use of a narrow range of appropriate exposure durations for each individual in the other experiments.

Method

Subjects

There were seven subjects (four of whom were male) ranging in age from 20 to 44 years. All of the subjects were faculty, graduate students, or research assistants affiliated with the Department of Psychology at the University of Western Ontario. The subjects reported that they had normal, or correctedto-normal acuity, and stereo vision.

Apparatus & Stimuli

The stimuli were presented using a Macintosh IIci computer and a Magnavox 14" high-resolution colour video display (dot pitch 0.29 mm). The computer also recorded the data from each trial. A circular sheet of black poster-board was positioned in front of the monitor screen to obscure the rectangular perimeter of the monitor. A round hole, 16 cm in diameter, was cut in the sheet to produce a boundary around the viewing area free of orientation bias. The viewing distance was 57 cm, and a combination head restraint/chin-rest was used to maintain the distance from the screen. A forehead stop and two lateral head stops on the head restraint prevented forward head movement and head tilts. All of the testing was conducted in a dimly lit room. Although the room illumination was such that dark adaptation could occur, the luminance of each target stimulus and mask was well within the photopic range and would prevent such adaptation (see next paragraph).

All of the stimuli were generated on the computer using software written in Think C (Symantec). The patterns were composed of white dots, 4 pixels (6′) in diameter, on a black background. The luminance of the background was 0.02 cd/m^2, and the luminance of the dots was 64 cd/m^2. Seventy-two dots were randomly positioned within a circular region 120 pixels in diameter (subtending 4.8° of visual angle) to form a random pattern. Symmetric patterns were generated by a similar process. Thirty-six dots were randomly positioned, and symmetric pairs were generated by reflecting the positions of the original half pattern across the axis specified for a particular trial (see

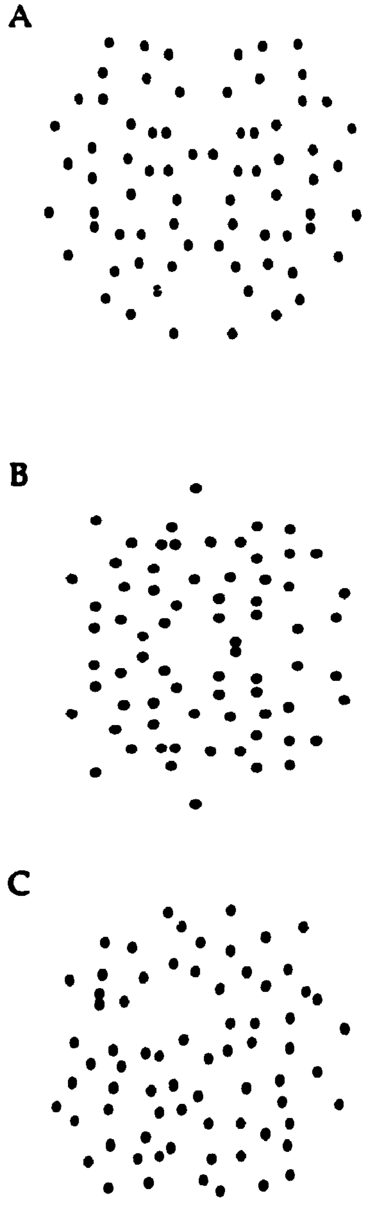


Figure 1: Schematic representations of the stimuli used in these experiments (the patterns consisted of white circular dots on a black background). A) vertically symmetric pattern; B) horizontally symmetric pattern; C) random pattern.

Figure 1). The centre of the patterns could be located at any distance from the centre of the screen along the horizontal and vertical meridians, and the exposure durations could be set to a resolution of one clock tick of the Macintosh (1 tick ≈ 16.7 ms). In this experiment patterns were always presented centred at the fixation point. The symmetric axis could be vertical, 10° clockwise or counterclockwise from vertical, 45° clockwise or counterclockwise from vertical, or horizontal. A new pattern was generated on each trial.

Pilot testing indicated that some subjects could easily detect symmetry in patterns presented for 1 tick. To make the task harder, a dense pattern of random dots was presented immediately after the target pattern. These masking patterns consisted of 360 dots of the same size as those in the target patterns randomly positioned in a circular region 160 pixels in diameter, and this masking pattern was centred around the same point as the target pattern (subtending 6.4°). The masking patterns were presented immediately following the target stimuli, and remained on screen for 10 ticks (167 ms). Following a response there was feedback in the form of a plus sign or minus sign presented for 10 ticks at fixation. The plus was presented when the response was correct, and the minus sign followed incorrect responses. A white dot centred on the monitor screen served as a fixation cue. The fixation cue appeared immediately after feedback was provided, and remained on screen until a trial was initiated by the subject.

Procedure

The stimuli in the experiment were ordered pseudo-randomly. The factorial combination of the varied stimulus parameters provided a base number for a block of trials, and each trial-type was presented once within a block of trials in a random sequence without replacement. Two factors were varied within an experimental session in the experiment: the exposure duration (4 or 5 levels depending on the subject — after testing some of the subjects, and examining their results, we found that the 1 tick exposure duration was too brief, and did not test that duration for the remaining subjects); and whether the patterns were symmetric or random — so a block consisted of 8 or 10 trials. Subjects were tested individually over 20 to 30 sessions to reach a total of 100 responses for each symmetry orientation at each presentation time for symmetric and random patterns. Thus, there were a total of 4800 or 6000 trials completed by each subject. The orientation of the symmetry axis was held constant for each session, and the subjects knew which orientation was being tested at all times. The detectability of symmetry was expected to be maximized by doing this, although previous research has shown that reaction times for symmetry detection are not affected by knowing the orientation of the symmetry axis for upcoming blocks of trials (Corballis & Roldan, 1975; Locher & Wagemans, 1993).

Forty or fifty practice trials consisting of equal numbers of random and symmetric trials at the appropriate orientation were completed before the experimental session. On practice trials the target stimuli were presented for longer durations than on the experimental trials, as well as at durations equivalent to those on experimental trials. This ensured the subjects could detect symmetry at the test orientation, and allowed them to practice responding to brief exposure durations. The results from the practice trials were not analyzed.

The subjects knew that they would see dot patterns that would be random or symmetric about an axis at a particular orientation. Subjects were instructed to fixate upon the dot visible on the screen, and to initiate a trial when ready by pressing any key on the keyboard. Their task was to indicate if they detected bilateral symmetry in the first dot pattern flashed on screen after the key was pressed. The subject pressed the "z" key to indicate that no symmetry was detected, whereas pressing the "/" key indicated the subject detected symmetry in the pattern. The subjects used the index finger of the left and right hands, respectively, to make responses. The subjects were told to respond as accurately as possible and that their reaction times would be disregarded. The *d'* statistic was computed for each symmetry orientation at the different exposure durations based on the number of hits and false alarms in each condition.

Results & Discussion

The results of this experiment are presented graphically in Figure 2. The results of the subjects have been averaged together where their performance was approximately equivalent for clarity of presentation in Figure 2A. For subjects LH, PP, and SR the results from one exposure duration were averaged (LH, 117 ms; PP, 150 ms, SR, 117 ms). The short duration line for AH, JD, KH, and LS was selected based on comparable performance, where *d'* exceeded 1 for at least one orientation (AH, 33 ms; JD, 50 ms; KH, 50 ms; LS, 83 ms). The long exposure line for those subjects was the average of the results where a *d'* up to, but not exceeding 4 was observed (AH, 50 ms; JD 83 ms; KH, 83 ms; LS, 117 ms). It is clear from Figure 2 that the same pattern of results occurs for a range of exposure durations, and across different subjects. This pattern holds whether the subjects were finding the task very difficult (with

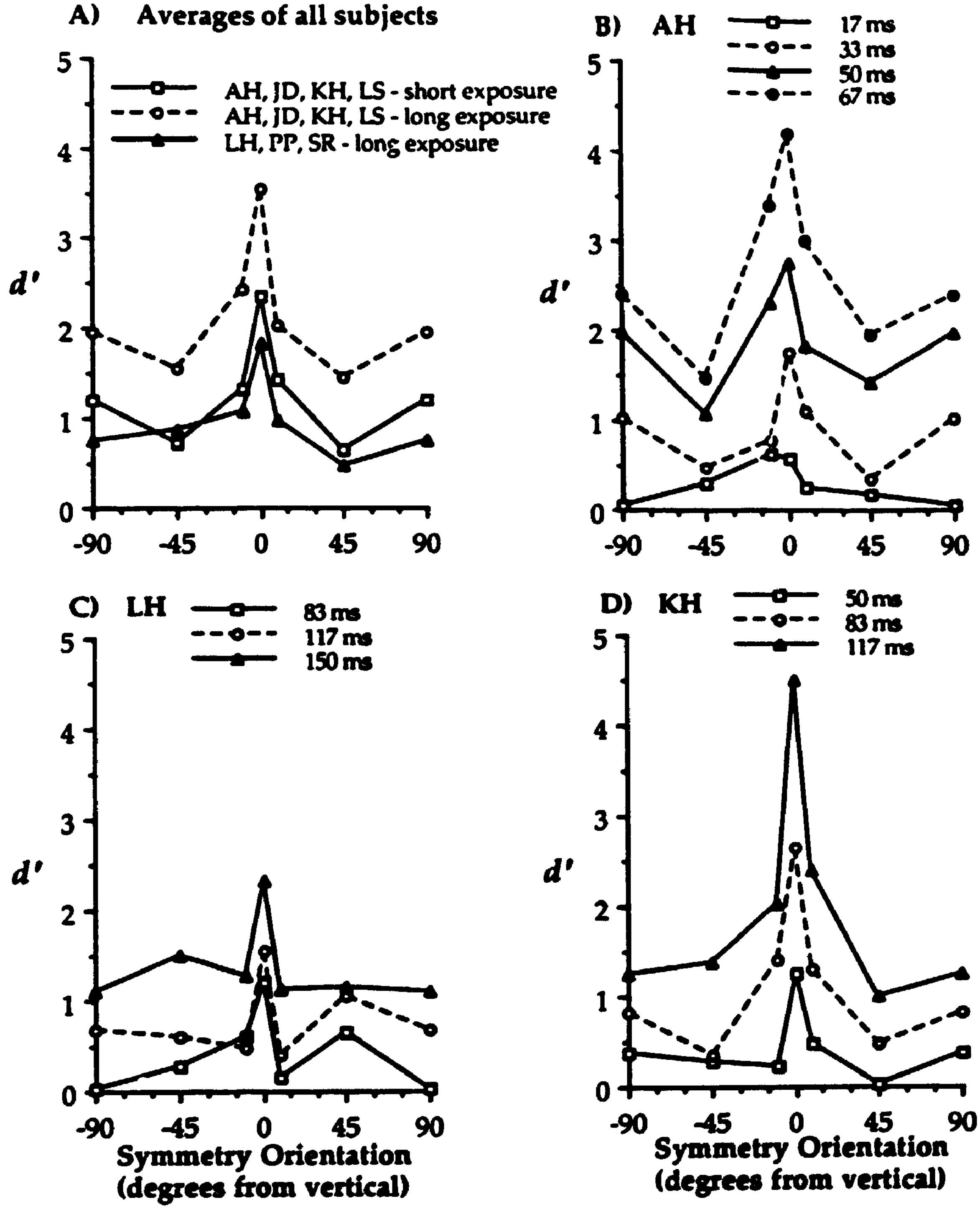
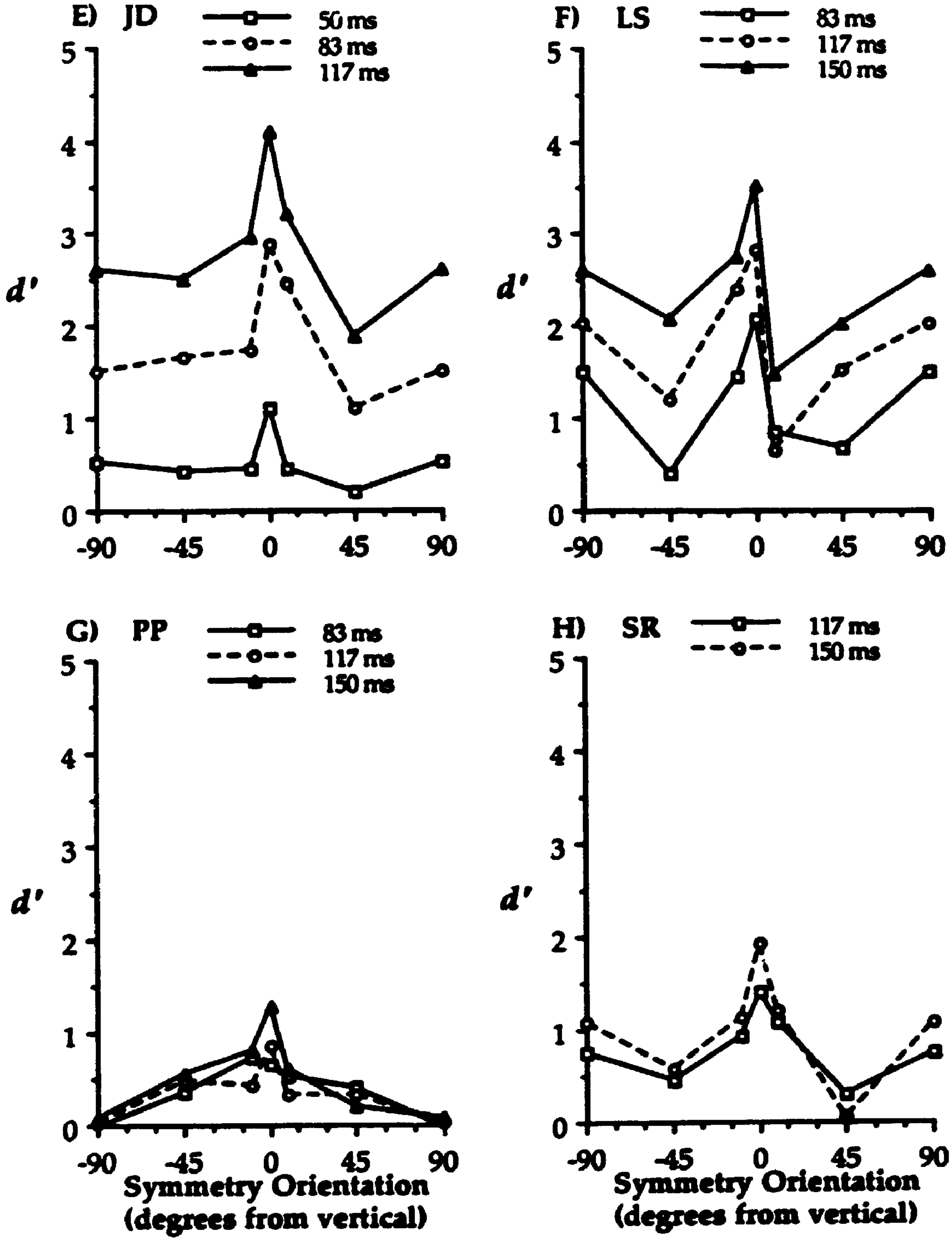


Figure 2. The detectability of bilateral symmetry plotted over the six orientations used in Experiment 1.
A) averaged results for all subjects
B)-H) results from each subject at a range of exposure durations


E) JD
50 ms
83 ms
117 ms
F) LS
83 ms
117 ms
150 ms
G) PP
83 ms
117 ms
150 ms
H) SR
117 ms
150 ms
d'
0
1
2
3
4
5
-90
-45
0
45
90
Symmetry Orientation
(degrees from vertical)

d' scores less than 1), or responding near ceiling for some symmetry orientations. Vertical symmetry was always most detectable, followed by horizontal symmetry and symmetry at 10° off vertical (clockwise or counterclockwise). Symmetry 45° off vertical appeared to be the most difficult to detect. The pattern of off-vertical symmetry detection varied slightly from one subject to the next as shown in the other panels of Figure 2 (B-H), where results from each subject are presented at different exposure durations. The results presented for each subject do not include trials where performance was at chance (*d'* values at or near zero across all symmetry orientations) or where ceiling was reached (perfect responding for vertical symmetry, resulting in infinite *d'* values). The maximum exposure duration tested was 150 ms (9 clock ticks), to prevent the possibility of eye movements, so fewer data points are presented for those subjects who required longer exposure durations to detect symmetry. As stated above, the results from the different exposure durations for the different subjects were used to reduce the range of exposure durations used in subsequent experiments.

The question of possible differences in bias in the responses across the different orientations and exposure durations was analyzed by computing *c* for each subject's results at each orientation and exposure duration. The formula for this estimate of bias is: $c = -0.5(z_{\text{hits}} + z_{\text{false alarms}})$. The values of *c* for the four longest exposure durations for each subject were analyzed as a function of orientation and exposure duration using repeated measures analysis of variance (ANOVA) . There was no significant difference in *c* as a function of symmetry orientation ($F_{(5,30)} = 1.37$, $p>.2$), or interaction between exposure duration and symmetry orientation ($F_{(15,90)} = 1.28$, $p>.2$).

There was a significant effect of exposure duration ($F_{(3,18)} = 7.54$, $p<.005$), where *c* declined for longer exposures. At briefer exposure durations the *c* values were significantly more positive than at longer exposure durations, as indicated using the Newman-Keuls procedure for tests of means. At brief exposure durations subjects were more likely to respond "no", indicating they did not see symmetry. At moderate exposure durations the average values of *c* were close to 0, indicating that subjects were not biased to respond either way. The pattern of average *c* values as a function of exposure duration was in a direction indicating that at the longest exposure durations subjects were more likely to respond "yes" a pattern is symmetric, although there was not a significant difference among average *c* values at these durations. The pattern of results is consistent with the following interpretation: when the task is most difficult, and one can not discriminate between random and symmetric patterns, there is a tendency to to see all patterns as random, and respond accordingly; and, when the task is moderately difficult, there is no bias. It should be noted that there was no difference in bias across symmetry orientations, indicating that subjects do not set a different criterion for detecting symmetry at different orientations.

The *d'*s for the seven subjects were entered into an ANOVA with six levels of one factor – the symmetry orientations tested. Two ANOVAs were completed, the first included all 7 subjects, and analyzed the data labeled as short duration for subjects AH (33 ms), JD (50 ms), KH (50 ms), and LS (83 ms) in Figure 2 and long duration for LH (117 ms), PP (150 ms), and SR (117 ms). Therefore, this analyzed the results at an exposure duration when a *d'* of one or larger was first observed. The repeated measures ANOVA resulted in a significant effect of symmetry orientation ($F_{(5,30)} = 15.84$, $p<.00005$). Tests of means revealed vertical symmetry to be more detectable than symmetry at other orientations, with no difference in the detectability of non-vertical symmetry (t-tests were used to maximize the likelihood of finding significant differences among the non-vertical orientations). The results for AH (50 ms), JD (83 ms), KH (83 ms), and LS (117 ms) labeled long duration in Figure 2A were analyzed in another repeated measures ANOVA with six levels of orientation tested. The results were the same as for the first ANOVA, there was a significant effect of symmetry orientation ($F_{(5,15)} = 8.552$, $p<.0005$), and vertical symmetry was more detectable than symmetry at other orientations, and there were no other significant differences (for all non-vertical orientations, $p>.05$).

The results clearly demonstrate that the tuning around vertical is narrower than ±10°. Symmetry at all off-vertical orientations was detected with more difficulty than vertical symmetry. The pattern of responses in Figure 2A suggests that symmetry may be detected in a vertical, ±10°, horizontal, then ±45° sequence, but the analyses did not indicate significant differences among these orientations. The salience of vertical symmetry is clearly demonstrated in Figure 2, and interestingly, vertical symmetry is more detectable even when symmetry at other orientations is being detected with relative ease at the longer exposure durations. This is apparent in the results from individual subjects (Figure 2B-H), and across subjects (Figure 2A). Note, however, that there are differences in the minimum time required to detect symmetry. A comparison of these results with those from other studies of the detectability of bilateral symmetry following brief exposure durations reveals similar patterns of responses. Barlow and Reeves (1979) found differences in the detectability of non-vertical symmetry, but these were smaller than the difference they observed for detecting vertical symmetry versus non-vertical symmetry. In Masame's (1983) study the same result was found Thus, non-vertical symmetry may not be detected differentially (as found by Herbert et al., 1989, although that was a study using reaction time as the dependent measure). The tuning of symmetry detection around vertical was further examined in Experiment 3.

The variation in the minimum exposure duration required by different subjects suggests that studies of symmetry detection using one exposure duration may be measuring observers at different levels of competence. All but one of the studies of symmetry detection reviewed earlier use one exposure duration within an experiment (Table 1). As described earlier, ceiling and floor effects may be affecting the averaged results (especially in reaction time studies), so the discrepancies in symmetry orientation preference reported in previous studies may have been a product of confounding the variable of interest, symmetry axis orientation, with task difficulty. The results of testing subjects at different exposure durations show that the order of non-vertical symmetry preferences shifts slightly from one time to the next for some subjects (the largest changes can be seen from Figure 2B, E and F, for subjects AH, JD, and LS respectively). It is likely that the selection of a single exposure duration, whether too short or too long, could affect the orientation preference observed in an experiment, and lead to a conclusion that is not borne out when testing across a range of exposure durations.

Experiment 2

In this experiment symmetric patterns were presented at nine positions along the horizontal meridian to examine whether the advantage for the detection of vertical symmetry decreased when the centre of a pattern was not at fixation. Three other studies that have examined the detection of symmetry for eccentric presentation, but each has tested only one symmetry orientation. Barlow and Reeves (1979) and Masame (1983) presented vertically symmetric patterns to subjects, whereas Saarinen (1988) presented horizontally symmetric patterns. The eccentricities tested in these studies varied, with an extreme of stimulus presentations 20° off fixation (Saarinen, 1988). Barlow and Reeves presented stimuli up to 3° off fixation, and Masame presented patterns a maximum of 2.8° off fixation. The differences in the symmetry orientations tested make it difficult to generalize from the results of these studies, but they all show that symmetry is detectable when presented away from fixation. This result contradicts Julesz' (1971) proposal that the axis of symmetry must be fixated to detect bilateral symmetry in complex patterns.

In Saarinen's study there was a small change in the accuracy of the detection of symmetry up to 4° from fixation, but a large drop in correct responses when patterns were presented 10°, 15°, and 20° from fixation. The detection of horizontal symmetry is not expected to change according to the neuroanatomical hypothesis, but this may only hold true for small shifts in the locus of presentation, because acuity decreases away from the fovea (i.e., De Valois & De Valois, 1990), which probably resulted in the attenuation observed by Saarinen. This conclusion is supported by the fact that there was a smaller drop in accuracy for M-scaled patterns in that study (M-scaled patterns consist of larger elements, scaled to cancel out the reduction in acuity at different distances from fixation). The results of the other two experiments suggest that vertical symmetry is detected for stimulus presentations up to 3° from fixation, but the pattern of *d′* values reported suggests a drop in the detectability off fixation. According to the neuroanatomical hypothesis, the vertical advantage should decrease off fixation, because the symmetry in the patterns would not project symmetrically to the visual system. Thus, the previous studies, and the predictions of the neuroanatomical hypothesis, suggest that the detectability of non-vertical symmetry should not change as much as the detectability of vertical symmetry when presented away from fixation.

The detectability of symmetry was measured for four axis orientations (vertical, horizontal, and both diagonals) at nine positions across the visual field in this experiment. The maximum eccentricity tested was 4.8° to the left and right of fixation. The same method was used as in Experiment 1, holding the symmetry orientation constant through each block of trials, but the patterns were presented at all nine positions across the horizontal meridian within each block. The exposure durations for each subject were selected based on their performance in Experiment 1 in an attempt to equate the detectability of symmetry across subjects.

Method

Subjects, Stimuli & Procedure

Four of the subjects from Experiment 1 completed this experiment. The apparatus, stimuli and general procedure were the same as in Experiment 1. The only difference in the experimental parameters was that the target and masking stimulus could appear at any of nine positions across the monitor screen. The patterns were presented at fixation, and with the centre of the pattern 1.2°, 2.4°, 3.6°, and 4.8° to the left and right of fixation along the horizontal meridian. The outer edge of the most peripheral of the masking patterns abutted the edge of the aperture in the cardboard disk centred over the monitor screen. Subjects were given practice prior to each experimental session, and each session consisted of 20 blocks of the factorial combination of each position, 2 or 3 exposure durations, and the presence or absence of symmetry in the targets. Five sessions were run for each symmetry orientation, and four symmetry orientations were examined: vertical; horizontal; and ±45° from vertical. The exposure durations for each subject were determined based on that subject's performance in Experiment 1. The shorter of the exposure durations was one where the subject had difficulty detecting symmetry in the first experiment, and the longer was a duration where symmetry was being detected relatively well for a range of symmetry orientations. One hundred random and 100 symmetric trials were completed for each symmetry orientation at each of the positions tested. Thus, there was a total of 7200 trials per exposure duration.

Results & Discussion

The results from this experiment are displayed in Figure 3. The results for some subjects at the shorter exposure durations are not presented because the functions were essentially flat, consisting of *d′* values near zero. Examination of the figure suggests that symmetry at the four orientations was detected differently as a function of the locus of presentation. At fixation, vertical symmetry was most detectable, followed by horizontal, and then the two diagonal orientations (except for PP, who detected the horizontal and diagonal symmetries with equal facility). For patterns presented away from fixation there is a general decrease in the detectability of symmetry, replicating the results of previous studies, as described above (Barlow & Reeves, 1979; Masame, 1983; Saarinen, 1988).

A 4 (symmetry orientation) by 9 (presentation position) repeated measures ANOVA of the results from four subjects (AH at 50 ms, JD at 67 ms, LS at 83 ms, and PP at 117 ms) indicated a significant interaction between orientation and position ($F_{(24,72)} = 2.098, p<.01$). There were also main effects of orientation ($F_{(3,9)} = 31.68, p<.00005$), and position ($F_{(8,24)} = 14.374$, $p<.00005$). Tests of simple main effects indicated an effect of symmetry orientation at each position, and an effect of position for each orientation. A further 4 by 9 repeated measures ANOVA was conducted on the results for three of the subjects at longer exposure durations (AH at 67 ms, LS at 117 ms, and PP at 150 ms). The same pattern of significant effects was observed. There was a significant interaction between orientation and position ($F_{(24,48)} = 2.445, p<.005$), a significant effect of orientation ($F_{(3,6)} = 11.714, p<.01$), and a significant effect of presentation position ($F_{(8,16)} = 10.125, p<.0001$). Again, simple main effects analysis indicated significant effects of orientation at each position, and significant effects of position for each symmetry orientation.

A number of analyses were conducted to tease apart the observed interaction between orientation and position, and to examine specific aspects of the results as they pertain to the predictions of the neuroanatomical hypothesis. First, the detectability of symmetry at fixation for the four symmetry orientations was examined. The results for the four subjects at the shorter exposure durations were compared in one ANOVA, and the results from three of them at longer durations were analyzed in another ANOVA.

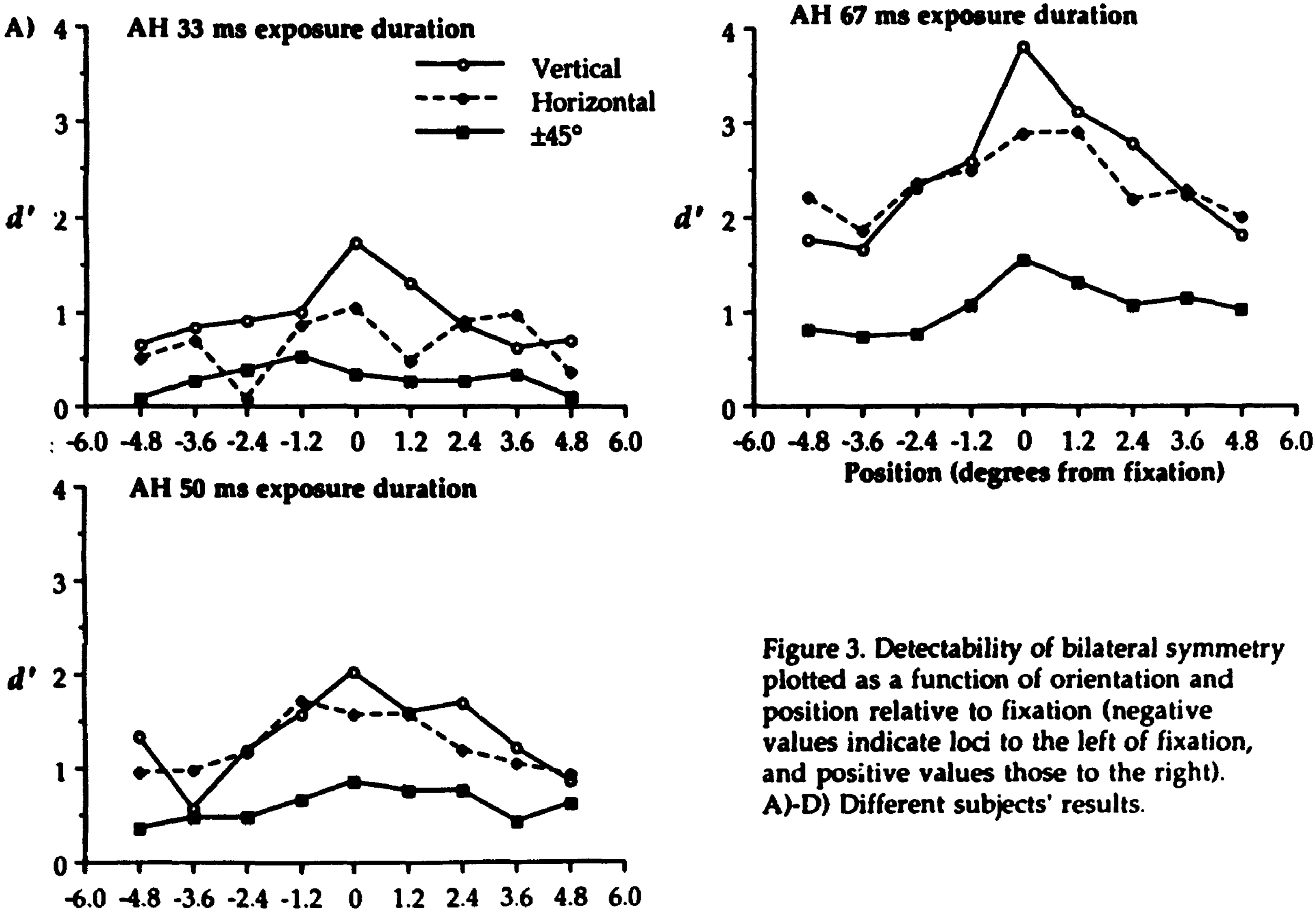
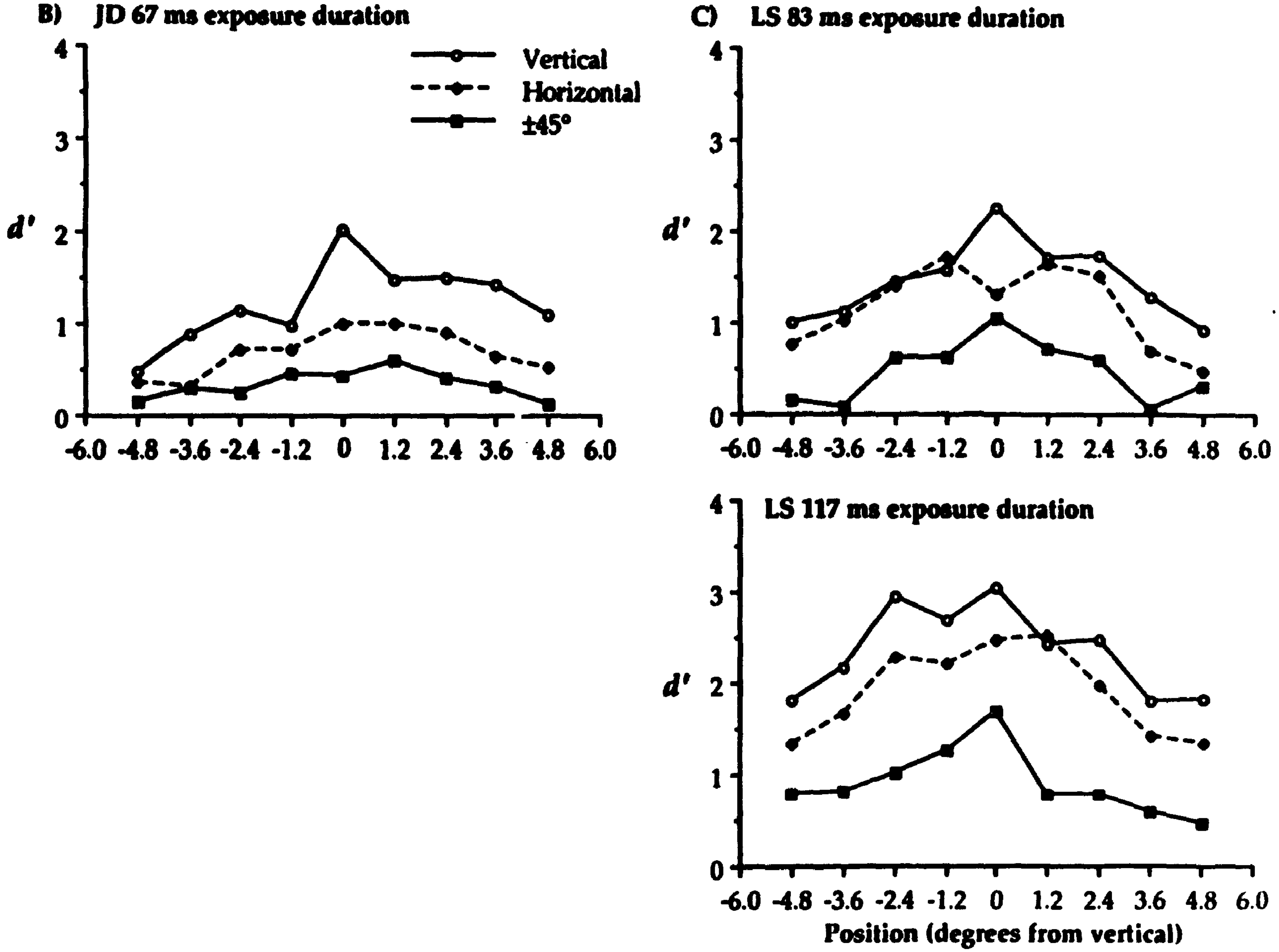
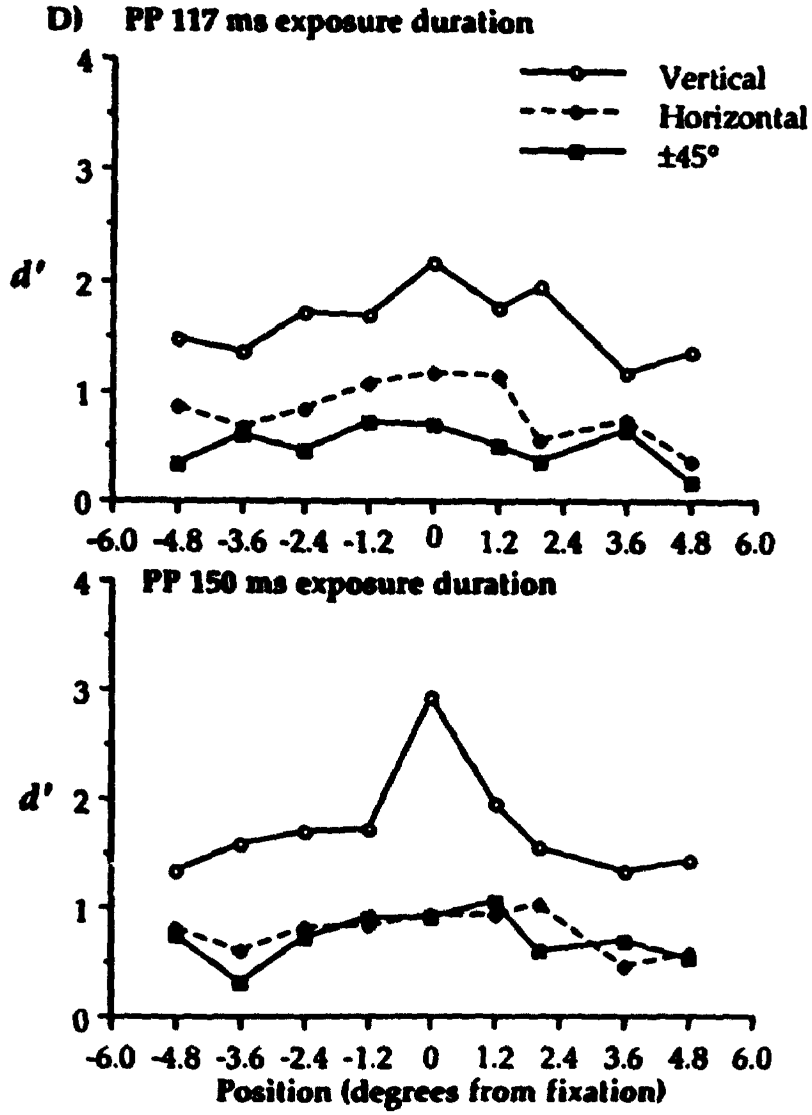


Figure 3. Detectability of bilateral symmetry plotted as a function of orientation and position relative to fixation (negative values indicate loci to the left of fixation, and positive values those to the right). A)-D) Different subjects' results.

B)
JD 67 ms exposure duration
Vertical
Horizontal
±45°
d'
4
3
2
1
0
-6.0 -4.8 -3.6 -2.4 -1.2 0 1.2 2.4 3.6 4.8 6.0
C)
LS 83 ms exposure duration
d'
4
3
2
1
0
-6.0 -4.8 -3.6 -2.4 -1.2 0 1.2 2.4 3.6 4.8 6.0
LS 117 ms exposure duration
d'
4
3
2
1
0
-6.0 -4.8 -3.6 -2.4 -1.2 0 1.2 2.4 3.6 4.8 6.0
Position (degrees from vertical)


D)
PP 117 ms exposure duration
Vertical
Horizontal
±45°
d'
4
3
2
1
0
-6.0
-4.8
-3.6
-2.4
-1.2
0
1.2
2.4
3.6
4.8
6.0
PP 150 ms exposure duration
d'
4
3
2
1
0
-6.0
-4.8
-3.6
-2.4
-1.2
0
1.2
2.4
3.6
4.8
6.0
Position (degrees from fixation)

The first repeated measures ANOVA resulted in a significant effect of symmetry orientation at fixation ($F_{(3,9)} = 20.275$, $p<.0005$), where, on average, vertical symmetry was more detectable than horizontal symmetry, and both vertical and horizontal were significantly more detectable than symmetry ±45° from vertical (as indicated by tests of means using the Newman-Keuls procedure). The repeated measures ANOVA for the longer exposure durations also resulted in a significant effect of symmetry orientation ($F_{(3,6)} = 14.35$, $p<.005$). Vertical symmetry was easier to detect than the three other symmetry orientations ($p<.01$), which did not differ from one another significantly ($p>.05$).

The next series of analyses examined the detectability of vertical symmetry across the nine positions tested. As above, separate repeated measures ANOVA were conducted for results from shorter and longer durations. The analysis of the results from the brief exposure durations revealed a significant effect of presentation position ($F_{(8,24)} = 12.751$, $p<.00005$). Post-hoc analysis indicated that vertical symmetry was more detectable at fixation than at any other position (once more, the Newman-Keuls procedure was used, and all effects reported were significant to at least the .05 level in this and all of the following analyses reported). Vertical symmetry presented at 1.2° and 2.4° to the right of fixation was easier to detect than vertical symmetry 3.6° and 4.8° to either side of fixation. Vertical symmetry 1.2° and 2.4° to the left of fixation was easier to detect than vertical symmetry presented 4.8° to either side of fixation. The repeated measures ANOVA for the three subjects at longer exposure durations produced similar results ($F_{(8,16)} = 9.738$, $p<.0001$). Vertical symmetry at fixation was significantly easier to detect than vertical symmetry at any other position. Vertical symmetry presented 1.2° to the left or right of fixation was more easily detected than vertical symmetry 3.6° and 4.8° to the left or right of fixation, and vertical symmetry was more easily detected 2.4° from fixation than 4.8° from fixation. This pattern of differences is in accord with the individuals' results presented in Figure 3.

A final pair of repeated measures ANOVA was conducted to examine the detectability of symmetry at fixation and in the periphery. The *d'* for symmetry 2.4°, 3.6°, and 4.8° to the left of fixation for a given symmetry orientation were averaged to form a composite score of detectability in the periphery. An average score was also computed for the three equivalent loci to the right of fixation. This reduced the number of means to be compared from 36 in the first analyses reported for this experiment, to 20. A decrease in detectability with increased eccentricity was expected for all symmetry orientations, as described earlier. The use of these composite *d'* and the subsequent reduction of comparisons allowed for an examination of the vertical advantage itself – how does it change away from fixation? A 4 (symmetry orientation) by 5 (position) repeated measures ANOVA was conducted for the results at the shorter and longer durations. For the shorter durations there was a significant interaction between orientation and position ($F_{(12,36)} = 2.904$, $p<.01$). There was also a significant effect of orientation ($F_{(3,9)} = 32.129$, $p<.00005$), and of position ($F_{(4,12)} = 24.009$, $p<.00005$). Analysis of simple main effects indicated significant effects of orientation at each position ($p<.0005$), but position effects for vertical and horizontal only ($p<.0005$). Tests of means indicated vertical symmetry at fixation was significantly more detectable than symmetry at any other orientation and/or position (including vertical symmetry presented eccentrically). Thus, there was a vertical advantage at fixation. Vertical symmetry at every other position was also more detectable than symmetry ±45° from vertical at any position ($p<.05$). Both horizontal and vertical symmetry were significantly more detectable than diagonal symmetry for the composite positions ($p<.05$). In summary, examination of Figure 3 suggests there was a vertical advantage across all positions tested for some subjects, but the advantage is reduced for symmetry detection off fixation.

The ANOVA of the longer durations resulted in similar significant effects. There was a significant orientation by position interaction ($F_{(12,24)} = 2.261$, $p<.05$), and effects of orientation ($F_{(3,6)} = 11.287$, $p<.01$) and position ($F_{(4,8)} = 13.854$, $p<.005$). Simple effects analysis revealed effects of orientation at fixation and the two far peripheral composites ($p<.01$). There was also a significant effect of presentation position for vertical and horizontal symmetry only ($p<.01$). Tests of means resulted in a similar pattern to that described for shorter exposure durations. Vertical symmetry was most detectable at fixation, and the advantage was reduced away from fixation ($p<.05$). In general there was a vertical, horizontal, then diagonal sequence of ease of detectability at all positions, with vertical detectability reduced to be equivalent to horizontal off fixation.

These four sets of analyses demonstrated that vertical symmetry was most detectable at fixation, with a reduction in detectability off fixation, as expected. Furthermore, symmetry at any orientation was more difficult to detect the further it was presented from fixation. In conjunction with the pattern of results presented in Figure 3, the analyses indicated that the vertical advantage is tuned to within ±1.2° from fixation. Figure 3 suggests that the advantage for the detectability of vertical symmetry over other orientations disappears away from fixation for some subjects (AH & LS), and is quite reduced for others (JD & PP). Horizontal symmetry was as detectable as vertical symmetry for AH and LS for all loci away from fixation. The drop in symmetry detection with presentation away from fixation is greatest for vertical symmetry in agreement with the prediction derived from the neuroanatomical hypothesis. The results are consistent with the findings reported by Saarinen, where there was relatively little change in the detectability of horizontal symmetry with peripheral presentation for displacements up to 4° from fixation. In the present experiment the detectability of off-vertical symmetry changed less than the detectability of vertical symmetry as a function of position along the horizontal meridian. In the following experiment a smaller shift in presentation away from fixation was examined.

Experiment 3

The results of Experiments 1 and 2 demonstrated that the vertical symmetry detection advantage is preserved for symmetry orientations at least to within 10° of vertical, and for presentation of stimuli to within 1.2° from fixation. In this experiment the vertical symmetry advantage was examined more closely. Subjects were tested at one of five symmetry orientations for five different positions within a session. The symmetry orientation was varied in 5° steps, from 10° counterclockwise to 10° clockwise from vertical, and the stimuli were presented so that the centre of the pattern was 0.6° and 1.2° to the left or right of fixation, or at fixation. Barlow and Reeves (1979) examined the detectability of vertical symmetry for displacements of as little as 0.2° from fixation. They reported mixed results, but there was no systematic decrease in the detectability of vertical symmetry for displacements 0.2° and 0.4° from fixation for the two subjects they tested. Masame (1983) tested symmetry detection for a minimum displacement of 0.7° from fixation, and found vertical symmetry was detected as easily there as it had been at fixation. The peripheral displacements of patterns tested by Saarinen (1988) were a minimum of 2°, and he found virtually no change in the detection of horizontal symmetry relative to fixation at this locus. The results of this experiment extended these earlier experimental manipulations across a number of axis orientations for small displacements from fixation.

This experiment was performed in two ways. First, subjects were tested in a manner like that used in Experiments 1 and 2 (they saw patterns that were random or symmetric about a single possible orientation within a block of trials), then the experiment was repeated with a change in the ordering of trials, such that all five symmetry orientations were presented within a block of trials. Thus, the subjects did not know the precise orientation of the symmetry they would see on each trial. This manipulation was performed to control for anticipatory head positioning. It is possible that a subject in the single orientation condition, knowing the symmetry orientation to be tested in a block of trials, would position his or her head at a slight tilt in the appropriate orientation, thus aligning retinal vertical with the tested symmetry axis. The lateral head stops on the chin-rest were constructed with foam pads at the temples, and it is possible small head movements could occur even if the subject was trying to maintain a vertical head orientation at the start of a block of trials. If head movements were occurring in the first part of this experiment it was expected that the *d′* values would be higher for the oblique orientations when symmetry orientation was blocked as compared to the second part, where symmetry was not blocked. The results from each part of the experiment are described separately below.

Experiment 3A - Blocked Condition

This experiment was conducted in the same manner as the previous two experiments. Subjects saw random or bilaterally symmetric patterns, and only one symmetry orientation was presented during a block of trials.

Method

Subjects, Stimuli & Procedure

Three subjects were tested in this experiment. The same apparatus was used as in the previous experiments. The only difference in this experiment was the range of symmetry orientations and eccentricities tested. The symmetry axes tested were vertical, ±5° from vertical, and ±10° from vertical. Stimuli were presented at fixation, and 0.6° and 1.2° to the left and right of fixation. For each position there were 100 symmetric trials at each symmetry orientation and 100 random trials, and each orientation was tested in separate blocks of trials. A total of 5000 trials were run at each exposure duration. Practice trials at the appropriate exposure durations were conducted prior to each session of experimental trials, as described for Experiment 1.

Results & Discussion

The results are presented in Figure 4. The *d′* values for detecting symmetry ±5° and ±10° from vertical were averaged for clarity of presentation. Across the subjects vertical symmetry was best detected at fixation, followed by symmetry ±5° from vertical, then symmetry ±10° from vertical. For subjects AH and KH the vertical advantage decreased with presentation of stimuli 0.6° to the left or right of fixation.

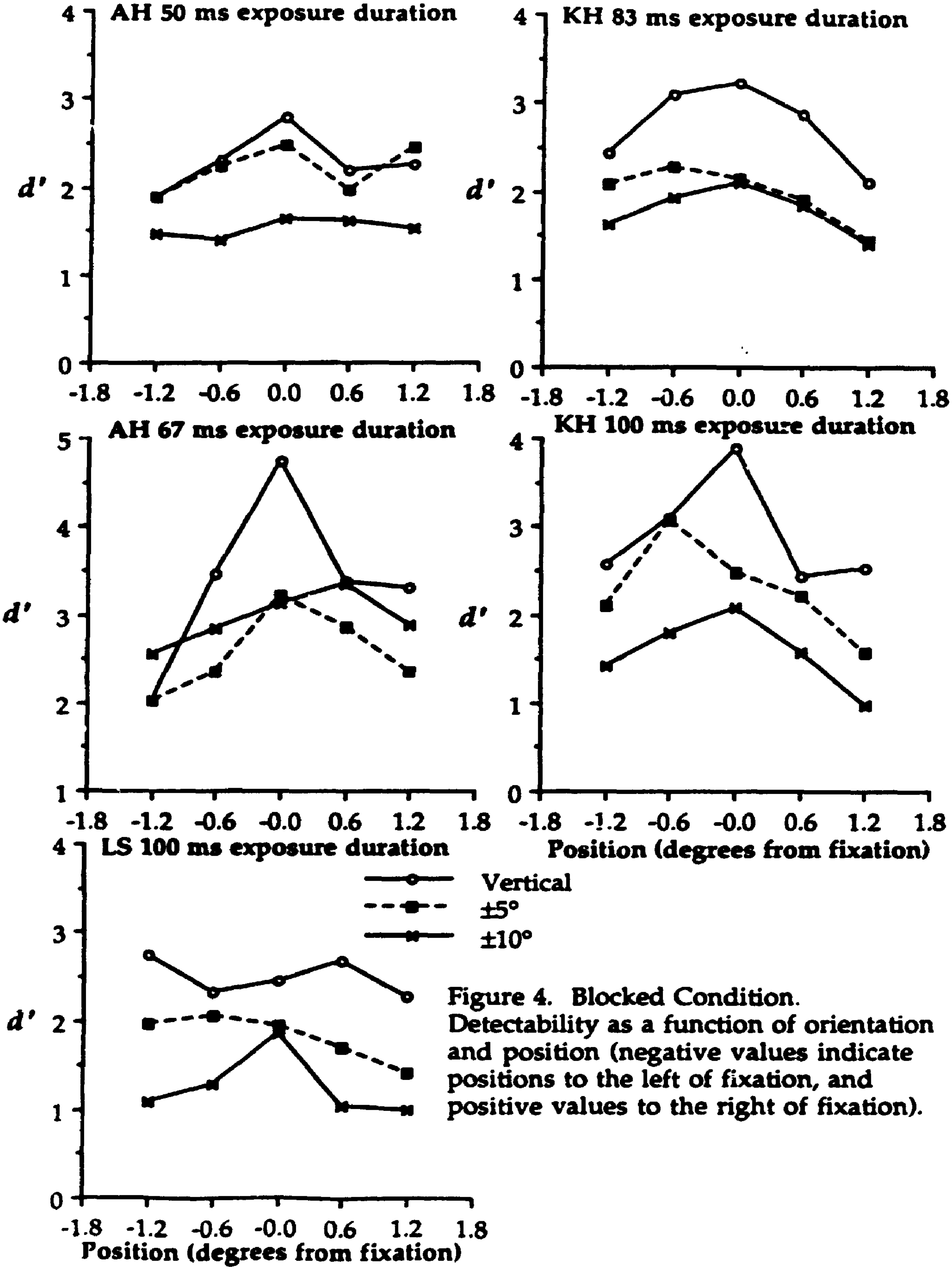


Figure 4. Blocked Condition. Detectability as a function of orientation and position (negative values indicate positions to the left of fixation, and positive values to the right of fixation).

The results of this experiment suggest that there is narrow tuning of symmetry detection around fixation and around the vertical axis. In this experiment the variations in presentation positions were equivalent to displacement of the pattern one half pattern radius (1.2°) and one quarter pattern radius (0.6°) to the left or right of fixation. Despite the small shift in the centre of the patterns away from fixation the vertical advantage appears to be diminished for some subjects (Figure 4).

A 5 (orientation) by 5 (position) repeated measures ANOVA was conducted for the results of the three subjects (AH at 50 ms, KH at 83 ms, and LS at 100 ms). The interaction was not significant ($F<1$). There was a significant effect of symmetry orientation ($F_{(4,8)} = 14.426$, $p<.001$) and a trend for a position effect ($F_{(4,8)} = 3.273$, $p<.1$). Vertical symmetry was more detectable than symmetry at ±5° from vertical, and these three symmetry orientations were more detectable than symmetry at ±10° from vertical ($p<.05$). Another 5 by 5 repeated measures ANOVA was conducted on the d' for two subjects at longer exposure durations (AH at 67 ms, and KH at 100 ms). The interaction between orientation and position was significant in this analysis ($F_{(16,16)} = 2.673$, $p<.05$). Simple effects analysis revealed an effect of symmetry orientation at fixation, 0.6° to the left of fixation, and 1.2° to the right of fixation. Tests of means indicated that vertical symmetry at fixation was more detectable than symmetry at any other position and/or orientation ($p<.05$). Vertical symmetry at 0.6° to the left of fixation was more detectable than symmetry at 10° from vertical at 1.2° to the left and right of fixation ($p<.05$). The main effect of orientation ($F_{(4,4)} = 5.786$, $p>.05$) and the main effect of position ($F_{(4,4)} = 2.823$, $p>.1$) were not significant.

The results from the different subjects suggest that the tuning of symmetry detection around vertical is quite narrow, to within 5° of vertical. At the longer exposure durations the results from subjects AH and KH indicated that the presentation of symmetry 0.6° from fixation along the horizontal axis reduced the detectability of vertical symmetry.

Experiment 3B - Unblocked Condition

In this part of the experiment symmetry orientation and position were varied within a block of trials. Subjects were required to make a binary decision, symmetric or not, for each pattern, but the symmetry could be at any one of five orientations.

Method

Subjects, Stimuli & Procedure

Four subjects were tested in this experiment, three of whom had been tested in the blocked condition. The experimental set-up was identical to the blocked condition, except that the ordering of the trials was such that all five symmetry orientations, and the five positions, were presented in each block of trials. There were 100 symmetric trials run for each orientation, and an equal number of random and symmetric trials were run in total. Again, there were 5000 trials for each duration, the same as in the Blocked condition. Likewise, a series of practice trials was run before each experimental session, as described earlier. To compute the *d′* values in this experiment the results from random trials were pooled, because false alarms could not be paired with a single orientation in each block of trials, as was the case in the preceding experiments. When a subject responded that a pattern was symmetric when it was really random there was no way of knowing at what orientation the apparent symmetry had been seen. Thus, the most conservative procedure was to use the same false alarm rate for computing *d′* for all symmetry orientations. The pooled false alarm rate was based on the errors made on the 500 random trials at each position across the visual field.

Results & Discussion

The results are presented in Figure 5. Note that the *d′* values for vertical symmetry may be underestimated in this condition, because the false alarm rate was computed across all symmetry orientations. The effect of pooling the false alarm rate would be to underestimate it for symmetry that is difficult to detect, and overestimate it for easily detected symmetry. Thus, the *d′* for vertical symmetry, which appears to be most easily detected, would be reduced by the pooled false alarm rate, and the *d′* for symmetry at ±5° and ±10° from vertical may be artificially inflated by using this pooled false alarm rate. It seems reasonable to assume that the majority of false alarms would be misidentification of the random pattern as symmetric about some oblique orientation, not vertical. The effect of using this pooled false alarm rate would be to reduce any difference in *d′* scores that existed, which operated against the hypothesis that vertical symmetry should be more detectable at fixation, and it should elevate the *d′* values for non-vertical orientations, again contrary to what was expected.

Figure 5 indicates that vertical symmetry was more detectable than the other orientations at fixation, although symmetry at ±5° from vertical was detected almost as well for all four subjects. Symmetry ±10° from vertical was the least detectable. The pattern of symmetry detectability was not much different when stimuli were presented at fixation or 0.6° to the left or right of

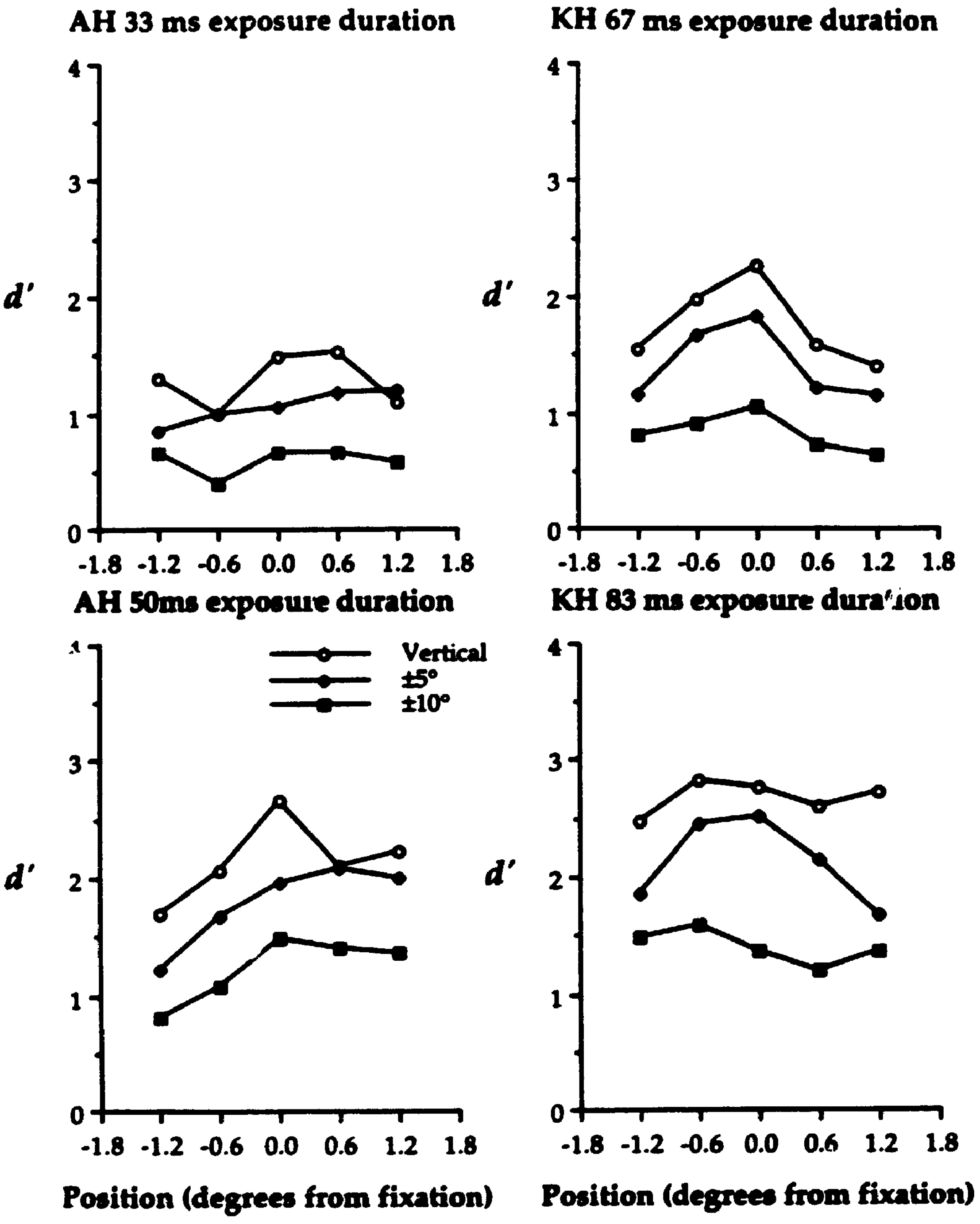
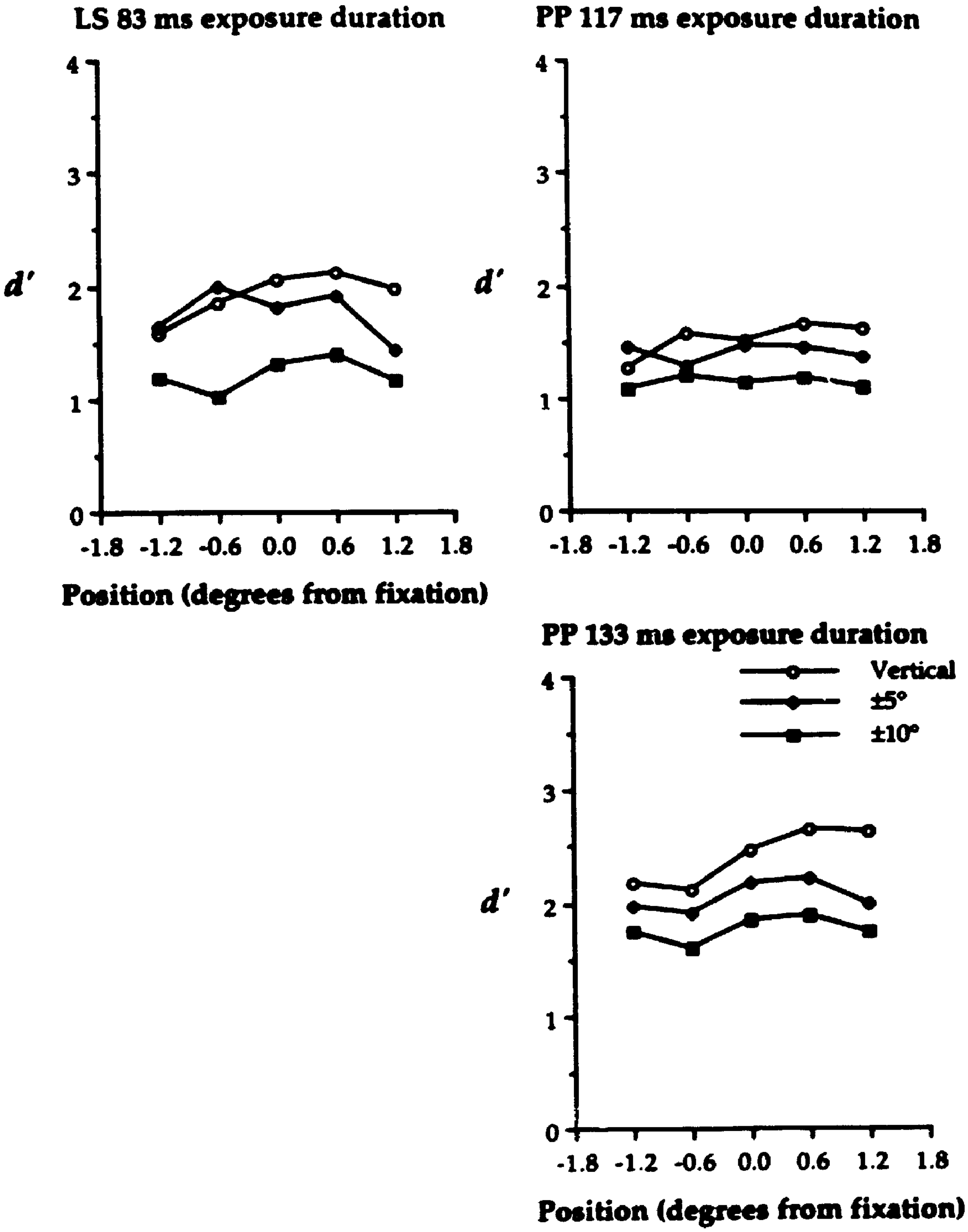


Figure 5. Results from Experiment 3 (Unblocked Condition).
Detectability as a function of position and orientation.
Points to the left of fixation are represented by negative values.


LS 83 ms exposure duration

PP 117 ms exposure duration

PP 133 ms exposure duration

fixation. The *d'* from each subject for each orientation and position combination were submitted to a 5 by 5 repeated measures ANOVA. The results from four subjects were analyzed at brief exposure durations (AH at 33 ms, KH at 67 ms, LS at 83 ms, and PP at 117 ms). There was no significant interaction between orientation and position ($F<1$). There was a significant effect of symmetry orientation ($F_{(4,12)} = 7.903$, $p<.005$). Tests of means indicated that the detectability of symmetry ±5° from vertical did not differ significantly from vertical, but symmetry at these three orientations was more easily detected than symmetry at ±10° from vertical. There was a trend for an effect of position ($F_{(4,12)} = 2.841$, $p<.1$).

The results from longer exposure durations for three subjects (AH at 50 ms, KH at 83 ms, and PP at 133 ms) were entered into a 5 by 5 repeated measures ANOVA. There was no significant interaction between orientation and position ($F_{(16,32)} = 1.625$, $p>.1$), and no significant effect of position ($F_{(4,8)} = 1.753$, $p>.2$). There was a significant effect of symmetry orientation ($F_{(4,8)} = 21.987$, $p<.0005$). Vertical symmetry was most detectable, followed by symmetry ±5° from vertical, then symmetry ±10° from vertical. This pattern is consistent with the individual results presented in Figure 5.

The important result of this condition was that it indicated that preparatory head rotations are unlikely to have produced the differences in the results observed in the Blocked condition. If such head rotations had occurred, the *d'* scores for the near-vertical orientations should have been less different from vertical in the Blocked condition than in the Unblocked condition, whereas the reverse was observed in these experiments. Thus, it seems fair to conclude that the tuning of symmetry detection is quite narrow, probably less than ±5° around vertical. The vertical, ±5°, to ±10° preference order observed in both parts of this experiment indicates that the orientation tuning of the vertical advantage is narrow.

Barlow and Reeves (1979) showed that symmetry was detected in patterns where symmetric dot pairs were not positioned perfectly. Vertical symmetry was detected when symmetrically paired dots were imperfectly positioned (symmetry was detected when one dot of a pair was up to 16′ from the correct location). Thus, the mechanism that detects symmetry tolerates a relatively large amount of error in the positioning of symmetric pairs (one fifth of the pattern width in that experiment). With this in mind, it is not surprising that near vertical symmetry would be almost as detectable as vertical symmetry; a process similar to that tolerating some smear in the precise positioning of symmetric elements may result in near vertical symmetry being indistinguishable from vertical symmetry. Across the subjects tested in this study it seems that the vertical tuning is within ±5° of vertical, although there may be individual differences in the range of orientations that are indistinguishable from vertical.

Jenkins (1982) showed that observers do not use all the information in a dot texture when deciding if it is symmetric or not. He found that observers were only sensitive to the information provided by symmetric dot pairs in a region extending 1.1° to either side of the axis of symmetry for vertically symmetric patterns presented at fixation. Furthermore, he reported that complete accuracy was reached when a symmetric strip of dots was only 0.31° wide. This finding confirmed Julesz′ (1971) prediction that elements closer to the axis of symmetry contribute most to the symmetry percept, as described earlier. The results of the present experiment are in basic agreement with

Jenkins' findings that there is a small region around the centre of the pattern where symmetric elements contribute most to the detection of symmetry. Nonetheless, the results also demonstrate that symmetry is detectable when there are no symmetrically paired elements at fixation (or within a narrow region around fixation). Symmetry may be most easily detected at fixation as shown in Experiment 2, but when no symmetric pairs are presented at fixation it is still possible to detect symmetry. This conclusion is also supported by the finding that symmetry could be detected in dot patterns having only the outer third of each hemi-pattern organized symmetrically (Barlow & Reeves, 1979). This suggests the detection of symmetry does not require the presence of symmetric internal detail (which is also obvious from experiments using line drawings as stimuli, Palmer & Hemenway, 1978; Zimmer, 1984), but symmetric information near fixation may be most important when it is present.

Experiment 4

Thus far, peripheral presentation of target patterns has been restricted to displacement along the horizontal meridian both in the present experiments and in previous studies of symmetry detection. The neuroanatomical hypothesis in its simplest form suggests that displacement of target patterns along the vertical meridian should not disrupt the vertical symmetry advantage. The stimuli would still be presented along the vertical midline, so matching across the cortical hemispheres should not be disrupted. This simple model does not correspond to the known organization of the human retina and visual cortex. First, the foveola is a small circular region, and if patterns are presented outside it they would be perceived at a lower resolution. Second, neuroanatomical studies have indicated that primate area V1 has no direct callosal projections, and the earliest callosal projections from visual areas seem to be related to the representation of space at fixation, and 2-3° around fixation (Braitenberg, 1990; Cragg & Ainsworth, 1969; Cumming, 1969; Geschwind, 1965; Milner & Jeeves, 1979; Pandya & Seltzer, 1986). Therefore, if the earliest arising contralateral connections mediate the vertical advantage, presentation of the patterns above or below fixation should disrupt the vertical advantage. In this experiment subjects had to detect symmetry at four different axis orientations, and at five positions across the visual field along the horizontal or vertical meridian. Each symmetry orientation was tested separately, and subjects ran sessions where target patterns were presented at different loci along the vertical midline separately from sessions where the patterns were presented along the horizontal meridian.

There is a problem with examining the detectability of vertical symmetry for presentation at different positions along the vertical midline. Vertical symmetry is still present at fixation for vertically symmetric patterns displaced less than the pattern radius from fixation. Thus, any overlap of the target patterns with fixation would result in symmetric elements being presented at fixation, so there should be little or no change in the detectability of vertical symmetry with vertical displacements of less than a pattern radius. In this experiment the patterns were presented 2° and 4° above and below fixation, so vertical symmetry overlapped fixation for the smaller displacements. The 2° displacement was expected to result in little change in the detectability of vertical symmetry relative to its detectability at fixation.

Method

Subjects, Stimuli & Procedure

Three subjects completed this experiment. The apparatus was the same as for the previous experiments. The stimuli were presented at fixation, and 2° and 4° to the left and right of fixation in the horizontal displacement conditions, or 2° and 4° above and below fixation for vertical displacement of the patterns. As before, the masking stimulus was presented centred around the same locus as the target stimulus, and feedback was provided at fixation. Subject AH completed the experiment with three exposure durations randomly interleaved — 33, 50, and 67 ms. The other two subjects were tested at two exposure durations — 67 and 83 ms. The symmetry orientations tested were vertical, horizontal and 45° clockwise and counterclockwise from vertical. Subjects ran 4 sessions of 25 blocks of randomly ordered trials for each symmetry orientation for each of the horizontal and vertical displacement conditions. This resulted in 100 symmetric and 100 random trials for each orientation at each position across the visual field (at fixation a total of 200 of each trial type were run). A total of 5000 trials were run for each exposure duration. The order of experimental sessions was random, and each testing session was preceded by a practice block of 60 trials. As before, the results from practice trials were not analyzed.

Results & Discussion

The results from all subjects are presented in Figure 6. The results for symmetry at 45° clockwise and counterclockwise from vertical are averaged for each subject for clarity of presentation. The results were analyzed in a sequence analogous to that used for Experiment 2. First the results from the three subjects were analyzed in two 2 (exposure duration) by 4 (symmetry orientation) by 5 (presentation position) repeated measures ANOVAs, one for horizontal displacements, and the other for vertical displacements. The two exposure durations for AH were 33 and 50 ms, for JD and KH they were 67 and 83 ms. A complicated pattern of significant effects was obtained from both analyses, partly because of a main effect of exposure duration in each case (horizontal displacement – $F_{(1,2)} = 35.536$, $p<.05$; vertical displacement – ($F_{(1,2)} = 68.932$, $p<.05$) and an interaction between exposure duration and orientation (horizontal displacement – $F_{(3,6)} = 9.375$, $p<.05$; vertical displacement – $F_{(3,6)} = 9.758$, $p<.05$). Both significant effects made it difficult to interpret the contribution of the orientation and position to the detectability of symmetry. For this reason, the results at each exposure duration were analyzed separately for horizontal and vertical displacements so that the relationship (if any) between symmetry orientation and presentation position could be determined.

First I will describe the results for the analysis of horizontal displacements (a 4(orientation) by 5(position) repeated measures ANOVA in each case). The short duration results (AH at 33 ms, JD and KH at 67 ms) resulted in no significant interaction ($F_{(12,24)}<1$). There was a significant effect of symmetry orientation ($F_{(3,6)} = 75.518$, $p<.00005$), which was expressed in higher average d' for vertical symmetry than horizontal symmetry, with both of these orientations significantly easier to detect than diagonal symmetry. There was a trend for a main effect of position ($F_{(4,8)} = 3.687$, $p<.1$). For longer exposure durations (AH at 50 ms, JD and KH at 83 ms) the results were similar. There was no significant interaction between orientation and position ($F_{(12,24)} = 1.404$, $p>.2$), and a significant effect of symmetry orientation ($F_{(3,6)} = 56.005$, $p<.0001$), where vertical symmetry was more detectable than horizontal symmetry, and both were more detectable than symmetry at °45° from vertical. In this case there was a significant effect of presentation position ($F_{(4,8)} = 6.242$, $p<.05$), where symmetry detection was better at fixation than at 2° to either side of fixation, and symmetry presented at those three positions was significantly easier to detect than symmetry present at 4° to the left or right of fixation.

The results from the analysis of the *d'* for vertical displacement are similar at the shorter exposure durations. There was no significant interaction between orientation and position for vertical displacements ($F_{(12,24)} = 1.58$, $p>.1$), a significant orientation effect ($F_{(3,6)} = 28.792$, $p<.001$), and a significant effect of presentation position ($F_{(4,8)} = 7.141$, $p<.01$). The orientation effect was expressed as a vertical symmetry detection advantage over horizontal and diagonal symmetry (the detectability of non-vertical symmetries did not differ significantly). The position effect was that symmetry was more detectable at fixation than at 4° above or below fixation. For the longer exposure durations there was a significant interaction between orientation and position ($F_{(12,24)} = 2.719$, $p<.05$). Simple effects analysis revealed an effect of orientation at each position (detectability of vertical greater than horizontal, greater than ±45°), and an effect of position for vertical symmetry only ($F_{(4,8)} = 23.957$, $p<.0005$). These effects were reflected in the significant main effect of orientation ($F_{(3,6)} = 200.251$, $p<.00005$), and position ($F_{(4,8)} = 17.276$, $p<.0005$).

Further analysis of the results was conducted to examine specific predictions of the neuroanatomical hypothesis. First, vertical symmetry was expected to be more easily detected at fixation than off fixation, both for horizontal and vertical displacements. An ANOVA comparing *d'* across the five positions for vertical symmetry indicated that it was more detectable at fixation than at 2° or 4° off fixation for horizontal displacements. For vertical displacements, the detectability of vertical symmetry at fixation and 2° above or below fixation were not significantly different, and vertical symmetry at all three of those positions was more easily detected than at 4° above or below fixation. This result was consistent with the predictions made earlier, since part of the vertically symmetric patterns overlapped fixation at the 2° vertical displacements.

The following is a summary of the results of the analyses. First, there were no systematic differences in detecting symmetry at either of the oblique orientations. The results from the horizontal displacement are consistent with those from Experiment 2 (compare Figures 3 and 6 for subjects AH and JD). The detectability of symmetry at all orientations was reduced as patterns were presented further from fixation. Vertical displacement of the patterns resulted in basically the same pattern of responses as for presentation of stimuli at different positions along the horizontal meridian. Presentation of symmetry at the highest and lowest positions clearly disrupted the vertical symmetry advantage. The intermediate positions produced little change in the detectability of vertical symmetry. This result occurred because the target patterns overlapped the fixation point for 2° offsets, so vertical symmetry was still present at fixation, despite vertical displacement of the pattern. The same effect was not observed for horizontal symmetry when patterns were shifted 2° (as in the present experiment) or 2.4° (in Experiment 2) along the horizontal meridian. The presence of horizontal symmetry at fixation did not result in any increase in the detectability of symmetry at that orientation relative to vertical symmetry, and the advantage of horizontal symmetry over symmetry ±45° from vertical was not affected by eccentricity. The absence of an advantage for detecting horizontal symmetry after small horizontal displacements reemphasizes the salience of vertical symmetry, and suggests that whatever mechanism confers the vertical advantage does not generalize to other symmetry orientations.

From these results we cannot determine with precision the size of the region within which vertical symmetry is best detected, but vertical and horizontal displacement disrupted the detection of symmetry similarly for non-vertical symmetry, and for vertical symmetry at the extremes of the eccentricities tested (4°). The fall off in detectability with eccentricity was similar along the horizontal and vertical midlines as is evident by comparing the results for both vertical and horizontal displacement in this experiment (Figure 6), and examining the results of Experiment 2 (Figure 3). Furthermore, the general level of competence exhibited by the subjects differed little for horizontal and vertical displacements. The results indicate that vertical symmetry is easily detected when there is minimal symmetric structure at fixation. When the patterns were displaced vertically only a small part of the vertically symmetric pattern overlapped fixation, but the detectability of vertical symmetry remained almost unchanged from when patterns were presented centred at fixation. As mentioned above, the same is not true of horizontal symmetry, which is best detected at fixation, but its salience changes little as compared to the detectability of vertical symmetry off fixation.

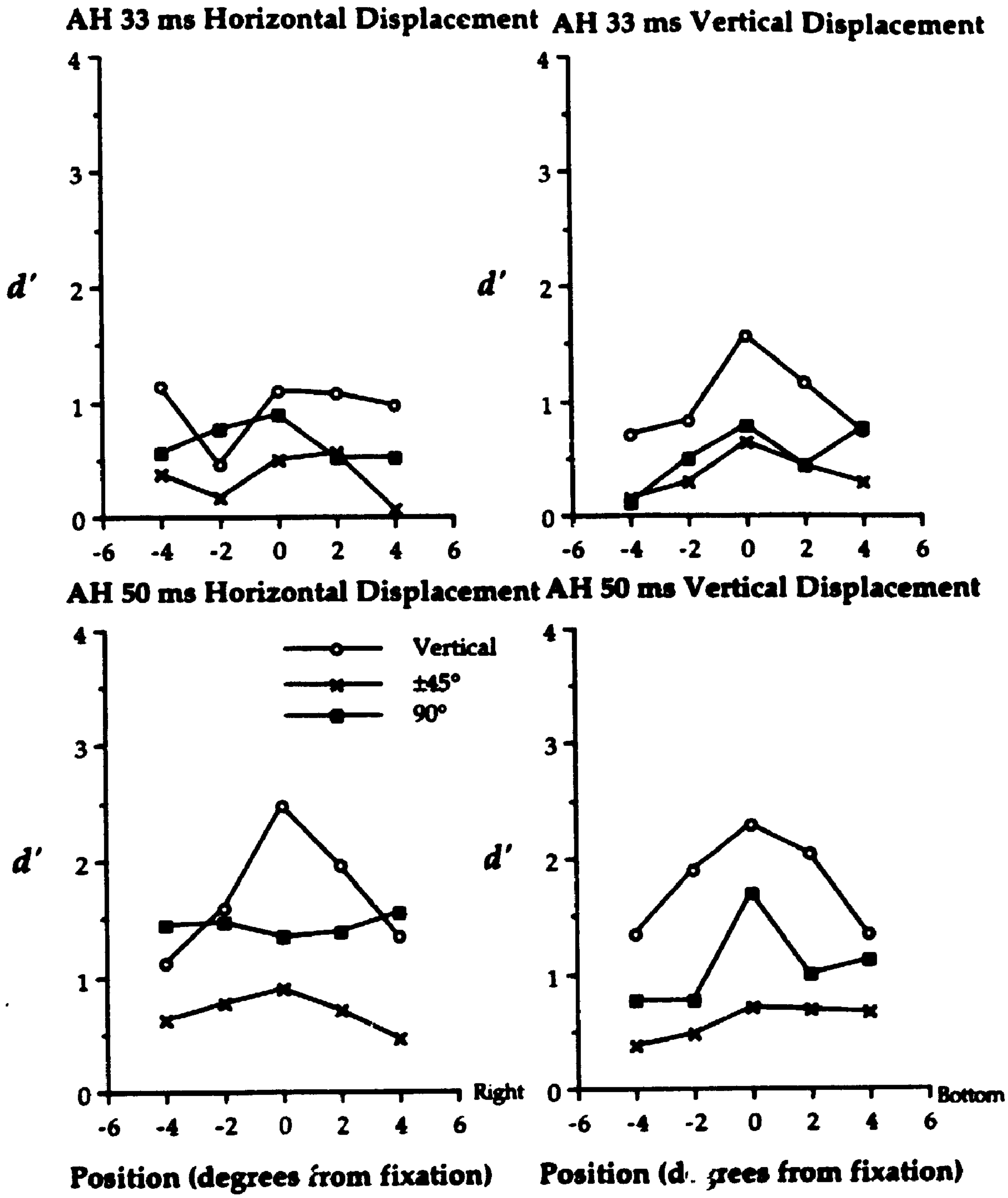
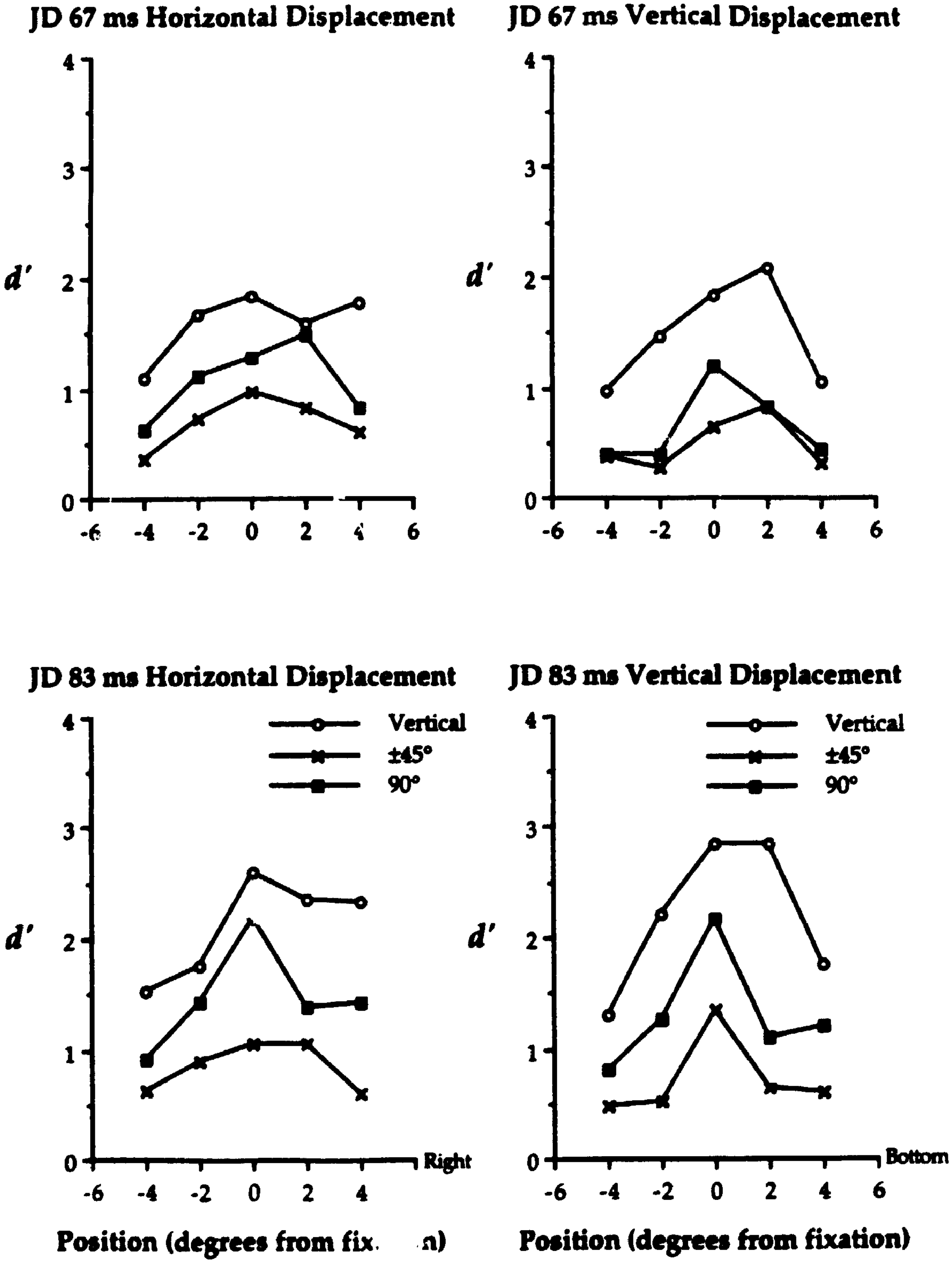


Figure 6. Detectability plotted as a function of symmetry orientation and pattern position for three subjects.

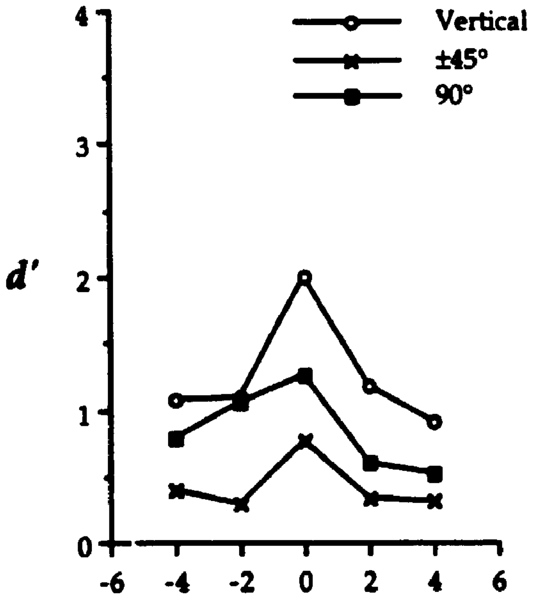


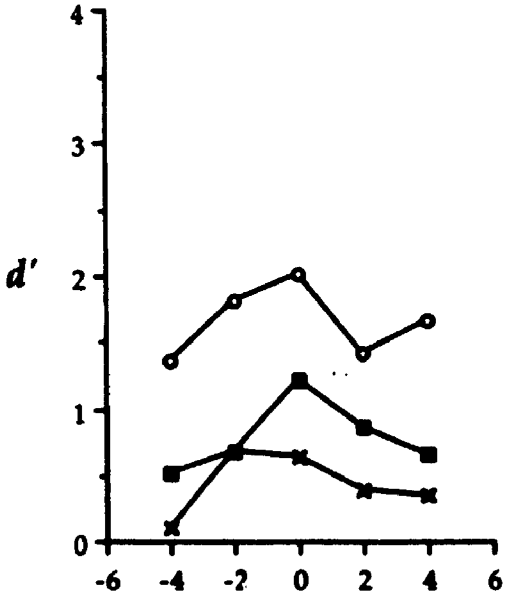
JD 67 ms Horizontal Displacement

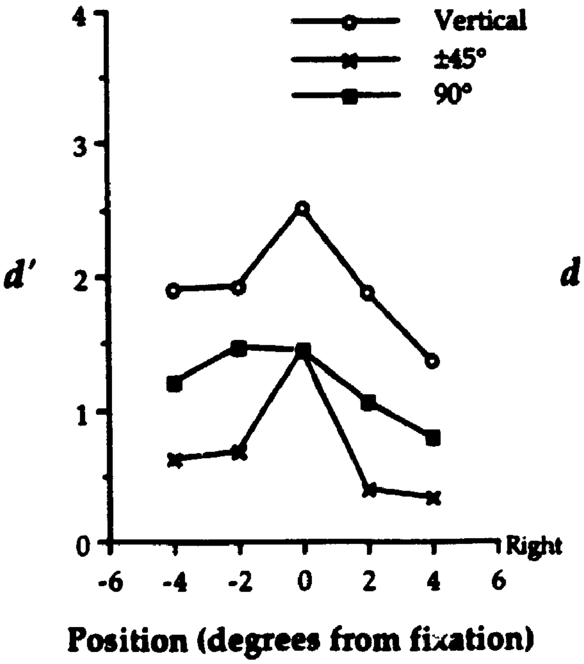
JD 67 ms Vertical Displacement

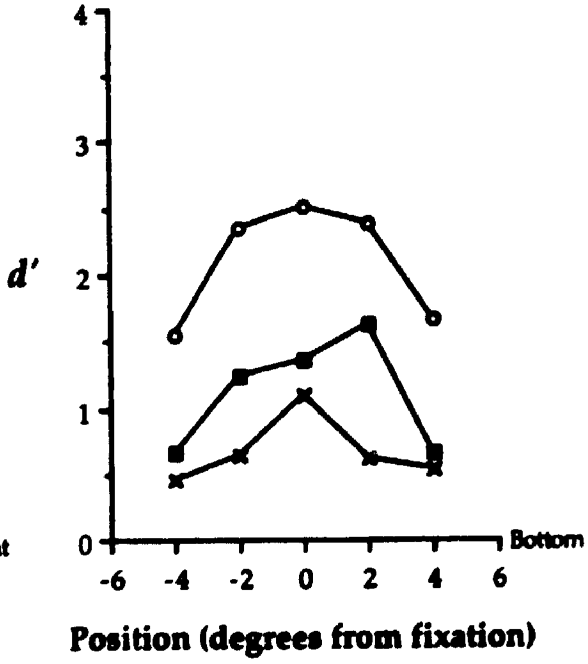
JD 83 ms Horizontal Displacement

JD 83 ms Vertical Displacement


KH 67 ms Horizontal Displacement


KH 67 ms Vertical Displacement


KH 83 ms Horizontal Displacement


KH 83 ms Vertical Displacement

Again, this experiment demonstrated that there is little influence of practice on symmetry detection. The *d'* values reported for vertical symmetry do not differ systematically across the four experiments for each subject, and the detectability of horizontal and oblique symmetry was similar across Experiments 1, 2 and 4 (subject AH and JD completed all three of these experiments, and their results can be compared directly from Figures 2, 3 and 6). The differences in the detectability of bilateral symmetry at a particular orientation across the three experiments were much smaller than the differences observed for the range of exposure durations and positions tested within an experiment.

Experiment 5

As mentioned earlier, according to the neuroanatomical hypothesis it was expected that the absence of the corpus callosum would impair the detection of vertical symmetry at fixation. The present experiment was conducted on two individuals born without a corpus callosum. They performed a symmetry detection task similar to that used in the experiments reported above. The two acallosal subjects were expected to detect symmetry presented off-fixation comparably to normal subjects, but for patterns displayed at fixation the vertical advantage should be absent. In general, acallosal individuals have been found to perform tasks requiring integration across the vertical midline more slowly than individuals with normal callosal development, but to an equivalent level of proficiency (Ettlinger, Blakemore, Milner & Wilson, 1972, 1974; Lassonde, Sauerwein, McCabe, Laurencelle, & Geoffroy, 1988). Thus, the acallosal subjects might require longer exposure durations than control subjects to detect symmetry as well as those controls.

As far as we know, the only neuroanatomical difference between normal brains and acallosal brains is that the corpus callosum is absent in the latter. This leads to some differences in the gyri along the medial surface of the cortex where the corpus callosum is normally found, but in general, the gross anatomy of the brain is similar for individuals born with a corpus callosum and those born without (Loeser & Alvord, 1968; Shoumura, Ando, & Kato, 1975). Furthermore, there are a number of cases of callosal agenesis that were only detected post mortem, suggesting that the congenital absence of the corpus callosum is not always a severe impairment (Loeser & Alvord, 1968; Slager, Kelly, & Wagner, 1957).

Method

Subjects

Two subjects[1] born without the corpus callosum were tested, along with two age, and sex-matched control subjects. M.G. is a male aged 22 at time of testing. M.G. was first seen by a neurologist at the age of 4 because of chronic enuresis, delayed acquisition of speech, and motor incoordination. Pneumo-encephalography performed at the time showed complete agenesis of the corpus callosum, and this diagnosis was confirmed five years later by a computerized tomography (CT) scan. Subject S.G. is a woman aged 30 at time of testing. A CT scan revealed complete callosal agenesis in this subject, who is otherwise asymptomatic (Jakobson, personal communication; Lassonde et al., 1988). Both of these subjects had been tested previously in a variety of perceptual studies, and had experience with holding fixation while

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[1] Two other acallosal subjects were tested. At exposure durations less than 200 ms they responded at random, whereas they had been able to see symmetry when permitted unlimited viewing of patterns. Consequently, their results are not reported.

performing visual tests. The two control subjects were tested using the same basic procedure. They were matched to the acallosal subjects with respect to age, general intellectual ability, sex, and socioeconomic status.

Stimuli & Procedure

The experimental procedure for these subjects was similar to that described in the four previous experiments, with the following differences. The stimuli consisted of random and symmetric patterns made up of 50 dots, and there was no masking pattern presented after the target pattern. A Macintosh II computer was used for stimulus generation and to control the experiment, and the stimuli were presented on a Radius 21" high-resolution, grey-scale monitor. The stimuli subtended 2° of visual angle, and were presented at fixation, and 4° to the left or right of fixation. The subjects received extensive practice, both to familiarize them with the procedure, and to reach exposure durations that were below 200 ms. All *d'* values were computed based on 30 random and 30 symmetric trials per orientation and position. The trials were ordered such that only one symmetry orientation (vertical, diagonal, or horizontal) was presented per session. The experimenter sat with the subjects to ensure that they were able to perform the task, and to set up blocks of trials for the subjects. The exposure durations that were used were selected based on each subject's performance over a number of practice trials. The two control subjects detected symmetry quite easily following a minimum of practice, and were tested at an exposure duration of 33 ms (2 clock ticks). M.G. and S.G. were tested at several exposure durations, but a full set of results was only obtained for an exposure duration of 167 ms (10 clock ticks). The two acallosal subjects required a longer period of practice as compared to the control subjects. Their main difficulty was in coping with the brief presentation of the targets, and having to respond after the target had disappeared. The instructions given to the subjects were the same as those given in the experiments described above. They were to fixate on the dot presented on the screen, and press a key when they were ready to respond. The subjects in this experiment responded on the numeric keypad of the keyboard using one hand. Pressing the "0" key indicated no symmetry was detected in the dot pattern, and pressing the "." key indicated the subject had seen symmetry. The behaviour of all subjects was quite similar once they had gotten used to the task; they responded at a uniform rate to the stimuli, and proceeded quite briskly through each block of trials.

Results & Discussion

The results from this experiment are presented in Figure 7. The results from each of the acallosal subjects are presented beside those of their respective control subject. The control subjects found the task relatively easy, as indicated by the high *d'* values. Subject R, the control for M.G., performed at ceiling for horizontal and vertical symmetry presented at fixation. He made no errors for detecting horizontal and vertical symmetry at fixation, so the *d'* values were estimated based on a 99% hit rate to generate points for his graph. Nonetheless, across the two control subjects the detectability of symmetry decreased away from fixation, as observed for most subjects in the previous studies, and the difference in the detectability of symmetry with respect to orientation is reduced away from fixation. The two acallosal subjects demonstrate a very different pattern of responses. The detectability of vertical symmetry at fixation was lower than that of horizontal symmetry at fixation for S.G.. This pattern of responding was not observed in any of the preceding experiments.

The results of this experiment were analyzed in two separate ANOVAs, one for the acallosals, and one for the controls. The small number of subjects precluded a between-subjects ANOVA, and there were a priori reasons for expecting a difference between the acallosals and controls. The results of a 3 (orientation) by 3 (position) repeated measures ANOVA for the control subjects resulted in a main effect of orientation ($F_{(2,2)} = 223.759$, $p<.005$), no significant effect of position ($F_{(2,2)} = 3.209$, $p>.2$), and no significant orientation by position interaction ($F<1$). Vertical symmetry was detected significantly more easily than horizontal and diagonal symmetry, and horizontal symmetry was more detectable than diagonal symmetry. This pattern of results differs from that obtained for the acallosal subjects, where neither the orientation by position interaction, nor the main effects approached significance.

The results of these analyses must be interpreted cautiously, because there were two subjects per group and far fewer trials completed than for the preceding experiments. In conjunction with the striking differences in the shapes of the functions for the acallosals (especially S.G.) it seems safe to conclude that the absence of a corpus callosum disrupts the detectability of vertical symmetry at fixation. None of the subjects tested in the preceding experiments found vertical symmetry more difficult to detect than horizontal symmetry at fixation. When horizontal symmetry was easily detected in Experiments 1, 2 and 4, the detectability of vertical symmetry was higher. S.G. shows a complete reversal of the pattern of symmetry detection at fixation as compared to both control subjects, and subjects tested in the preceding experiments. This study indicates that individuals born without a corpus callosum do not detect vertical bilateral symmetry normally at fixation. Regardless of any differences in the arrangement of contralateral connections that exist in the brains of these individuals, it is clear that they do not detect bilateral symmetry like individuals with an intact corpus callosum. This result is in agreement with the predictions derived from the neuroanatomical hypothesis. It also suggests that any subcortical links between the left and right sides of the brain are not sufficient to mediate the vertical symmetry detection advantage, contrary to a suggestion made by Corballis and Beale (1976).

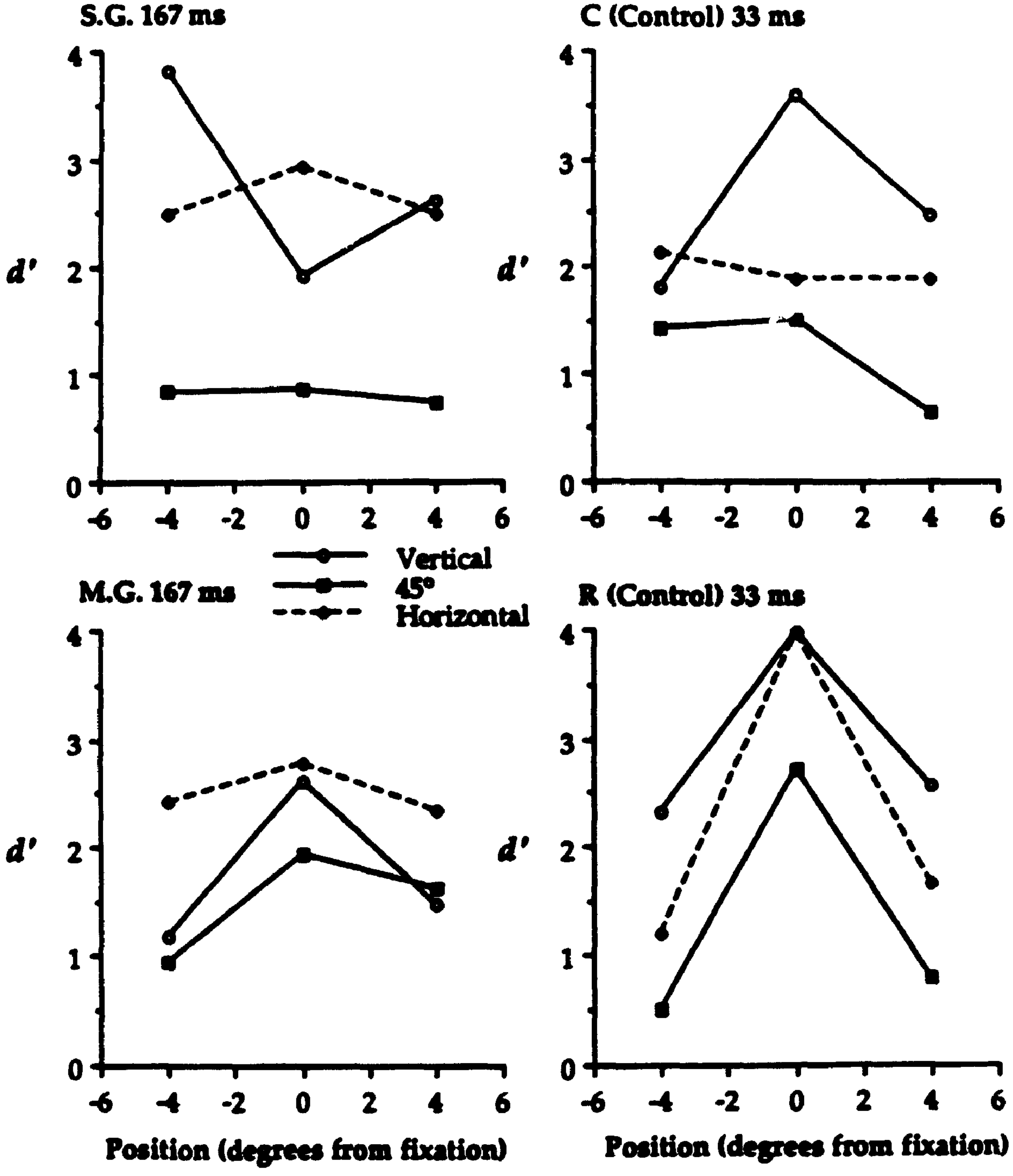

Figure 7. Comparison of acallosal subjects and controls. Detectability of symmetry at different orientations is plotted over the three positions tested (negative values represent loci to the left of fixation, positive values to the right).

Chapter 3 - General Discussion and Summary of Findings

The results of all five experiments were consistent with the predictions derived from the neuroanatomical hypothesis. As expected, the detectability of symmetry was superior for vertical symmetry as compared to symmetry as little as 5° clockwise or counterclockwise from vertical. Experiments 1 and 3 demonstrated that the detectability of vertical symmetry differs from that of orientations close to vertical, because the *d'* values decreased for detecting symmetry within ±5° of vertical. This was observed for individual subjects and across subjects. The vertical advantage was found to be dependent on the position of pattern presentation relative to fixation. Experiments 2, 3 and 4 showed that the detectability of vertical symmetry is highest at fixation compared to the detectability of symmetry at other orientations, but the magnitude of this advantage decreased with presentation of patterns off fixation. Presentation of vertically symmetric patterns as little as 0.6° off fixation reduced the vertical symmetry advantage, whereas the detection of symmetry at other orientations was relatively unchanged by presentation off fixation. Experiment 4 provided evidence that the detectability of symmetry changes in the same way for horizontal and vertical displacement of patterns. The pattern of performance exhibited for vertical displacement was consistent with the neuroanatomical hypothesis because any part of the axis of a vertically symmetric pattern presented at fixation results in the vertical advantage. Finally, there was evidence consistent with Braitenberg's (1984, 1990) proposal that the corpus callosum is involved in the vertical symmetry advantage. Experiment 5 demonstrated that individuals born without a corpus callosum do not express the vertical advantage at fixation.

How the results relate to our general understanding of symmetry detection

Bilateral symmetry was found to be detectable for presentation of patterns up to 4.8° from fixation along the horizontal axis, and 4° above or below fixation, contrary to the predictions of Julesz (1971). He suggested that symmetry was difficult, or nearly impossible, to detect when the axis of symmetry (or the centre of the pattern) of random dot patterns is not presented at fixation. Furthermore, symmetry at different orientations was also detectable in the periphery. Presentation times were always less than 167 ms on experimental trials, so eye movements occurred after the target patterns were presented and had disappeared or been masked. As stated earlier, these results are consistent with previous studies of eccentric symmetry detection, but extend those findings because the detectability of more than one symmetry orientation was examined in the periphery. There is a decrease in the detectability of symmetry away from fixation, but it was relatively small, and was observed only in some of the subjects (Figure 3). Symmetry is still detected in the periphery, and bilateral symmetry detection is affected more for vertical than other symmetry orientations.

Fahle and Popp (1989) observed a left visual field advantage for symmetry detection, and a small increase in detectability for presentation of patterns slightly away from fixation. The latter result was not observed in the present experiments; there was no central performance drop. Barlow and Reeves (1979), Masame (1983), and Saarinen (1988) did not find any improvement in symmetry detection for patterns presented away from fixation, nor did they report any visual field differences. There was no evidence of visual field advantages in the present experiments. Some subjects detected symmetry better on one side than the other, but this was not consistent. Subjects AH, JD, KH, LS, and PP participated in at least two of Experiments 2, 3, and 4, and Figures 3, 4, 5, and 6 provide no evidence for a visual field superiority across the different experiments. In fact, if there were any differences in detectability between symmetry detection for patterns presented to the left or right of fixation, it would favour the left hemisphere (AH & JD, Figure 3; AH, Figure 4 & 5). Troscianko (1985) found visual field differences for symmetry detection, but these were dependent on properties of the stimuli used, because the hemispheric advantage shifted from left to right in different experiments. Collectively, these previous findings, the results of eccentric presentation in Experiments 2, 3, and 4, and the performance of the acallosal subjects, lead to the conclusion that bilateral symmetry can be detected when first presented to only one cerebral hemisphere, and there is little evidence for hemispheric specialization for bilateral symmetry detection.

The results for detecting symmetry at opposite, but equal, orientation shifts from vertical were also equivocal. Symmetry at each of ±5°, ±10°, and ±45° from vertical was equally detectable across different exposure durations, subjects and experiments. There were some differences among opposing orientations (for example, subjects AH, LH, JD, LS, & SR, in Figure 2), but these were fleeting, and much smaller than the differences observed for different orientations. This result is also in agreement with previous research, where no systematic differences have been reported for opposing orientations.

The present studies also replicate a number of other findings concerning the detection of bilateral symmetry regardless of axis orientation. Practice effects were negligible once subjects became accustomed to the brief exposure durations and the masking of the target patterns. In order to perform Experiments 1 to 4 a subject ran a minimum of 46,400 trials, not including practice trials prior to each experimental session. There was no systematic change in the *d′* values across the experiments for any symmetry orientation at a particular exposure duration as can be seen by comparing the results for each subject across the different experiments. This replicates findings reported by Cohen and coworkers (1986), and Royer (1981). It could be argued that any practice effects may have occurred over the course of Experiment 1. An analysis of the *d′* over the first half of the trials compared to the values obtained over the last half revealed a practice effect dependent on exposure duration. At shorter exposure durations their was no increase in *d′* from the first half of the trials to the last. For the two higher exposure durations across subjects the detectability of symmetry improved as a function of practice. The practice effect did not interact with symmetry orientation, so it did not affect the order of detectability of symmetry. In the present experiments, bilateral symmetry could be detected at brief exposure durations, even when the target patterns were followed by a dense masking pattern of random dots. Subjects with relatively little symmetry detection experience (compared to the subjects in the other experiments) performed near ceiling for 33 ms exposure durations in Experiment 5. These results indicate that the symmetry detection mechanism is fast and efficient, as demonstrated by others (notably by Barlow & Reeves, 1979).

Clearly, the results of these experiments indicate that the detection of bilateral symmetry does not rely on the mechanism mediating the vertical symmetry advantage alone. Symmetry is still detected off fixation, and for different axis orientations. The means by which we detect symmetry when the axis is off-vertical and/or off-fixation appears to require more time to operate, and is less accurate. The results of previous studies using accuracy and reaction time as dependent measures corroborate this conclusion (Corballis & Roldan, 1975; Herbert et al., 1989; Palmer & Hemenway, 1978; Pashler, 1990; Royer, 1981; Zimmer, 1984). Finally, this general symmetry detection mechanism may not depend on the existence of callosal connections, because the acallosal subjects could detect symmetry in patterns presented away from fixation. The acallosal subjects may have some functional connections between the cortical hemispheres (e.g., Lassonde et al., 1988; Loeser & Alvord, 1968; Milner, 1994; Slager et al., 1957), so one cannot be certain that symmetry can be detected by mechanisms operating solely within a cortical hemisphere, but the speed and accuracy of symmetry detection suggest that the mechanism must operate early in the visual system.

Further evidence in support of a general symmetry detection mechanism stems from research on other animals' ability to detect symmetry. Birds have been shown to discriminate between symmetric and asymmetric forms (e.g., Swaddle & Cuthill, 1994), but the neuroanatomy of their interhemispheric connections is unlike primates, because birds do not have a corpus callosum (Benowitz, 1980; Remy & Watanabe, 1993). It is possible that different symmetry detection mechanisms have evolved in parallel across different animals, but it is also likely that humans detect symmetry the same way other organisms do except for vertical symmetry. The vertical symmetry advantage may be a characteristic conferred by the presence of a corpus callosum and overlapping visual fields, and therefore, may be unique to primates. The pattern of symmetry detection as a function of orientation and eccentricity has only been examined in humans thus far, so one can only speculate about the similarities and differences across species.

Implications for other symmetry detection proposals

To date, the proposals for the detection of symmetry have suffered from a lack of generality. Most account for the results from experiments reported in the articles accompanying the proposals, but the results from different studies are often contradictory, and this has led to the proliferation of different accounts for symmetry detection. As mentioned earlier, the common feature of the proposals that have been made is that symmetry detection appears to be a multi-stage process, including an initial rapid phase then a slower, more detailed analysis of the patterns (Jenkins, 1982; Palmer & Hemenway, 1978; Royer, 1981; Zimmer, 1984). The results of the present experiments do not contribute to arguments for or against a multiple stage process. The general pattern of results corresponded to previous findings, where there is an orientation anisotropy, but bilateral symmetry is detected easily and rapidly for a range of axis orientations and positions in the visual field.

Wagemans and co-workers (1992, 1993) have presented the most recent model for symmetry detection, and the results of the present studies bear on the predictions derived from that model. One of the findings that the model is based on is that there are no differences in the detectability of bilateral symmetry for different symmetry axis orientations (Wagemans et al., 1992, 1993). All other studies of symmetry detection that have examined the ability to detect bilateral symmetry at different orientations have reported at least a difference in the ability to detect vertical symmetry and symmetry at other orientations tested (Table 1). In the present studies there was a difference in the detectability of vertical symmetry and symmetry at other orientations, and an indication that symmetry at 45° from vertical is less detectable than horizontal symmetry in Experiments 1, 2 and 4 (replicating Barlow & Reeves, 1979; Palmer & Hemenway, 1978; Zimmer, 1984, and other studies mentioned earlier). The differences in symmetry detection as a function of orientation observed here and previously indicate some modification of the correlation quadrangle mechanism may be necessary if it is to account for the way humans detect bilateral symmetry.

Two further problems with the model were described earlier: first, it accounts for the detection of many types of pattern regularity using the same mechanism, but the empirical evidence suggests there are qualitative differences in the detectability of different kinds of symmetry; and second, it seems to be formulated to account for the results of tests with dot patterns only, whereas bilateral symmetry is detected in a variety of stimuli, and the vertical advantage is found consistently with the different stimuli. Mach proposed that vertical symmetry was salient because of the vertical symmetry of the ocular musculature, and made this prediction based on observations made using patterns composed of large irregularly shaped blobs (Mach, 1897). Julesz (1971) adopted Mach's hypothesis, and based his proposals on observations he made using symmetric dot patterns. Braitenberg (1990) illustrated his points using patterns composed of randomly oriented line segments. This variety of patterns and the consistency of obtaining the vertical advantage suggest that the matching of activation in symmetric loci across the vertical midline may not depend on pattern type.

To summarize, not only is vertical bilateral symmetry special, but bilateral symmetry in general may not be perceived in the same way as other forms of symmetry, and the correlation quadrangle approach argues the opposite. These problems with the model suggested by Wagemans and co-workers must be dealt with, but there is the possibility that they have described a way in which bilateral symmetry is detected away from fixation and when the symmetry axis is not vertical. Whether this model is specific to bilateral symmetry, or only describes the detection of other types of symmetry will require further examination.

Locher and Wagemans (1993), Barlow (1980), Bruce and Morgan (1975), and Julesz (1971; Julesz & Chang, 1979) have all proposed that symmetry detection may follow decomposition of images into their spatial frequency components, and the matching of large scale structure across an axis. This may be what occurs, and it would be consistent with the neuroanatomical account assuming that cells tuned to different spatial frequencies may be linked across the corpus callosum. The output of low-frequency tuned cells may have higher weighting than those tuned to higher frequencies (Marr, 1982; Watt, 1987). Spatial filtering may also be involved in detecting non-vertical symmetry, but the absence of direct connections between homotopic regions across the vertical midline early in the visual system may slow that process and make it less accurate. The detectability of spatially filtered symmetric patterns could be examined in an attempt to resolve this issue.

A possible account for the means by which bilateral symmetry is detected would run as follows. The detectability of vertical symmetry at fixation is enhanced by the direct connections between cells representing symmetric regions in space, which may be independent of spatial frequency. The presence of symmetry in line with that of the visual system is somehow signalled directly by the activation of symmetrically located cells. For non-vertical or non-fixated patterns a possible mechanism would be one analogous to that proposed by Marr (1982) for stereopsis. The output of low frequency operators could provide an estimate of the location of symmetric regions in an image, and this could direct more fine-grained analysis of the image to test for symmetry. The first, rapid stage, may be one where a pattern is sampled at a low spatial frequency (Barlow, 1980), and this is followed by a slower, detailed inspection process to search for matches between elements or contours making up the image. Of course, this explanation is speculative, and the orientation selectivity of the system would have to be accounted for. The results of studies of symmetry detection using spatially filtered patterns may provide some answers here.

In conclusion, the neuroanatomical hypothesis for symmetry detection was supported by the results of these experiments. Vertical symmetry is special, and this may be a product of vertical symmetry in the visual system. The experiments also demonstrated that symmetry away from fixation, and at different orientations, can be detected. Although not as detectable as vertical symmetry, non-vertical bilateral symmetry is clearly a salient form of pattern structure. The neuroanatomical hypothesis may account for the salience of vertical symmetry at fixation, but it is mute with respect to the detection of non-vertical symmetry, as discussed above. Experiments 2, 4, and 5 demonstrated a clear vertical, horizontal, then diagonal order of preference in bilateral symmetry detection. Although the results of Experiment 1 were not as clear, on average, the same order was found (Figure 2A). A variety of accounts for the ordering of symmetry orientations have been proposed, as described earlier, but the means by which bilateral symmetry is detected in general remains unknown. Further examination of the stimulus parameters affecting symmetry detection should shed further light on the topic.

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