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EYE DESIGN FOR DEPTH AND DISTANCE PERCEPTION IN THE PIGEON: AN OBSERVER ORIENTATED PERSPECTIVE

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ABSTRACT: The perception of the distance of objects with respect to an observer (egocentric distance) and the perception of the relative distance (depth) between external points was found to be optimised in the pigeon visual system according to the optical and retinal constraints of the eye. Each of these perceptual capacities is mediated by different binocular mechanisms in the frontal field, both of which appear to be designed for a stationary world. This is particularly evident in the egocentric distance estimation that occurs during the reaching movement when pecking. Here both the saccadic nature of the head movement and the convergence eye movements appear to allow constant retinal stimulation. This system of vergence signal alone is inadequate for depth perception which is instead mediated by retinal disparity. Stereopsis in the pigeon appears to be more effective for pattern decoding than for absolute spatial perception.

Any system faced with interpreting the relative position of objects in space must do so within a frame of reference. Thus, the perception of the relative distances between external points (depth perception) must interact with the observer orientated perceived egocentric distance of those objects (distance perception).

The distinction between depth and distance perception is important, as their interrelationship will only be attained through knowledge of the mechanisms underlying each capacity. The current popular literature on spatial perception has emphasized the role of depth information as a major linking feature in visual perception (Barlow, 1981) or an independent channel of visual processing in mammalian and primate systems (Livingston & Hubel, 1987). Physiologically, this scheme is based primarily on retinal disparity as the underlying mechanism of stereopsis (Hubel & Livingston, 1987). However as Foley (1980) has pointed out, retinal disparity alone cannot tend the true perception of the metric of visual space from an observer perspective. This is all the more so when one considers the limited range of

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stereopsis (less than 450 meters in man) and paradoxically by impli-
cation, its relevance to close range observer orientated activity.

Interestingly, birds also have the capacity for stereopsis. Neurons
responsive to horizontal retinal disparity have been recorded in the
owl (Pettigrew & Konishi, 1976) and kestrel (Pettigrew, 1979; see
also Fox, Lehmkuhle & Bush, 1977). More recently, using behav-
ioural psychophysics we have demonstrated the presence of a binocu-
lar depth mechanism in the pigeon. This mechanism appears inde-
pendent of absolute distance (McFadden & Wild, 1986) and allows
very fine acuity (McFadden, 1987).

Thus stereopsis or at least local stereopsis, is not restricted to
mammals, primates or even predatory type species as suggested long
ago by Ramon-y-Cajal (1899) and by Elliot Smith (1928, 1930) and his
school. Nor can it be said to have evolved along with increased fron-
tality as has been repeatedly claimed (Johnson, 1901; Le-Gros Clarke,
1962; Bishop, 1981).

Hughes (1977) argues that binocular vision is at least universal
among mammals, and stereoscopy not justifiably regarded as absent
from any mammal possessing a binocular field. Fox (1978) takes this
view further in proposing his proletarian hypothesis in which he pro-
poses that stereopsis is not an emergent capacity bestowed on a rela-
tively small number of elite animals, but may be a fundamental at-
tribute of vertebrate vision.

Given that stereopsis does not give a direct useful measure of the
distance of objects with respect to the observer, one could speculate
that it serves primarily as a pattern decoder aiding in accurate object
recognition. This view would thus ascribe the evolution of stereopsis
in terms of common fundamental attributes of the visual world,
rather than peculiarities associated with particular lifestyles and
their related pressures.

How local stereopsis may contribute to spatial perception in the
pigeon requires a thorough understanding of the dynamics of avian
visual processing capability (both optically and neurally) within dif-
ferent sectors of visual space. Such information can be gained by mea-
suring the static extent of the cyclopean and binocular retinal fields
and relating this to eye-movements and fixation capacity; determin-
ing the areas of visual space surveyed by the various retinal spe-
cialisations; determining the refractive properties of the eye for dif-
ferent directions of visual space in the context of the range of
accommodation, and through the use of behavioural psychophysics,
determining the capabilities of information processing in different
sectors of the visual arena.

This paper attempts to examine each of the above approaches as
applied to the pigeon visual system and in particular, with respect to

mechanisms which allow the accurate perception of the position of objects in space with respect to either an arbitrary fixation point (depth perception) or the animal itself (absolute distance perception).

1. THE BINOCULAR FIELD OF THE PIGEON

There is no dispute regarding the presence of binocular overlap within the visual field in the pigeon, however there has been much discussion over the absolute size and position of this binocular field.

To define a binocular field, one must do so in terms of a fixation plane as the absolute size of the binocular field will increase as the distance from the eye to the fixation point decreases. For this reason, binocular fields are normally defined in terms of the straight forward position, in which the visual axes of the two eyes are parallel. In the human, this means that both fovea are fixated on a point at infinite distance relate to the interocular separation.

In the pigeon, the angle between the two foveae is approximately 135° due to the lateral placement of the eyes. Therefore, it is extremely unlikely that the eyes could converge the 60-70° necessary to allow the two foveae to simultaneously observe a point in space. That is, the two lateral foveal axes cannot intersect.

However, the pigeon has a retinal specialisation in the temporal retina called the area dorsalis (Galifret, 1968). Thus, the straight forward position in the pigeon we define as when the two frontal visual axes, corresponding to the direction of the area dorsalis, are parallel (Figure 1). We have measured the binocular field with reference to this primary eye position (McFadden & Reymond, 1985).

The dimensions of the binocular field have been also measured by others for various fixation positions either using optical criterion by determining the point in the nasal visual field at which the pupil slit just approaches zero width, (Martinoya, Rey & Bloch, 1981; Jahnke, 1984) or on retinal based criterion. In the retinal mapping technique, the edge of the retinal binocular field is determined by mapping the points in the nasal visual field at which a bright light shone into the eye just fails to elicit a retinal reflex (Martin & Young, 1983; McFadden & Reymond, 1985).

It would be expected that the studies based on pupil appearance would predict a larger binocular field than the retinal reflex studies as the extent of the retina is less than the potential offered by the optics, although in some birds this mismatch is more pronounced on the nasal margin of the eye (Martin, 1984).

The family of curves in Figure 2 shows each of the binocular fields from the studies mentioned above. It should be noted that it
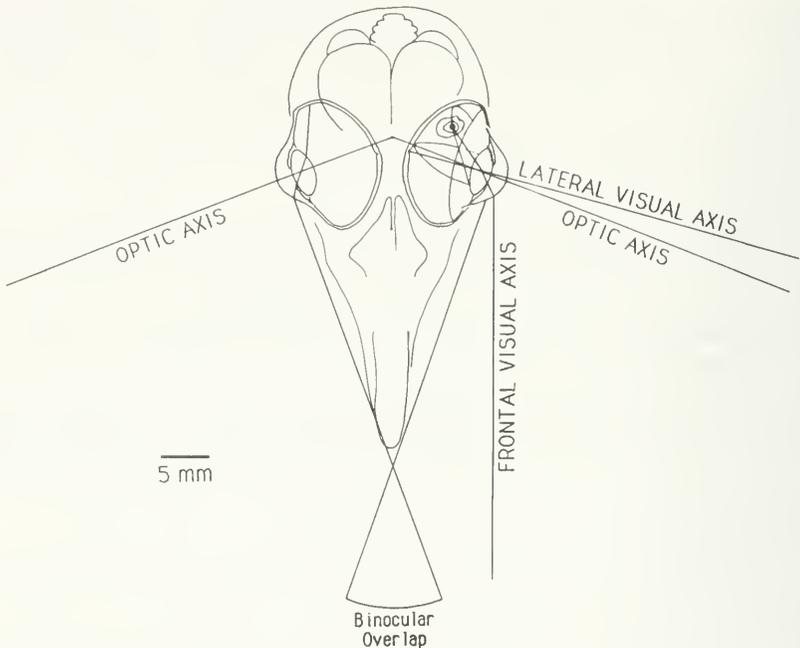
FIGURE 1. Diagrammatic view of the straightforward position in the pigeon. This is defined as when the frontal visual axes are parallel and theoretically viewing a point at infinity. The ringed dot on the retina represents the position of the area dorsalis. The fovea is represented by the depression in the retina which is intersected by the lateral visual axis.

incorporates a number of different breeds of pigeon and the techniques are based on either the optical or retinal based criterion. The optical estimates have not controlled for eye movement and are not corrected for the primary eye position. Thus the absolute size of the fields varies from study to study. Nonetheless, there is a surprising degree of similarity in terms of the overall symmetry of the binocular field with respect to the position of the beak. The peak width appears to occur at about 10° below the eye beak axis which is defined in Figure 3. Such symmetry about the eye beak axis suggests that the binocular field may be used during pecking.

Much of the discussion in the literature has centred on where maximum binocularity occurs. Thus, Martinoya et al. (1981) described the plane containing both optical axes by determining the angle at which both pupils appear to have their long axes parallel. However, this technique assumes that the eyes do not undergo vertical fixation movements with respect to the eye beak axis, and thus can-
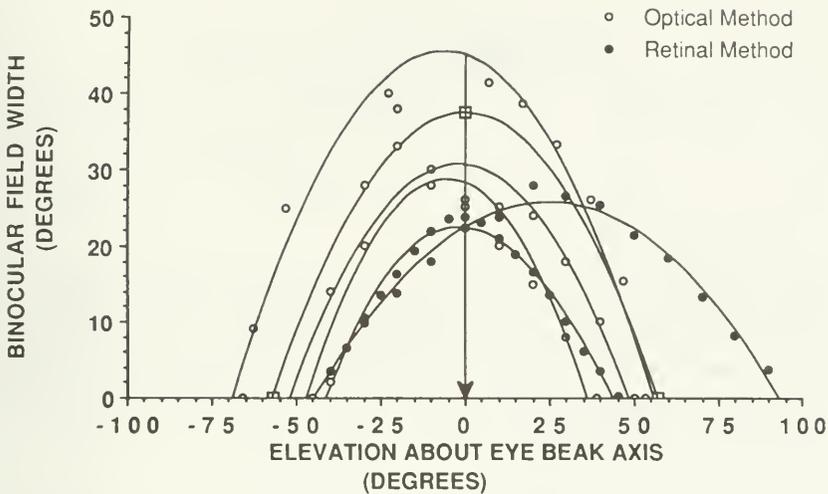
FIGURE 2. Binocular field width as a function of elevation in order from top curve to bottom are from: Martinoya et al. (1981); McFadden & Reymond (1984) corrected for the straight forward position, shown by the square symbol; the homing pigeon and blue Altenburg Trumpter from Jahnke (1984); Martin & Young (1983), rightmost curve; and McFadden & Reymond (1984) uncorrected for deviation. The arrowed line shows the eye beak axis. Data are fitted with 2nd order polynomial functions.

not effectively predict the relative position of the optical axes plane. Indeed, when the eyes are immobilised immediately following an intramuscular injection of xylazine and ketamine, the planes containing both optic axes also approximately contain the eye beak axis (Martin & Young, 1983; McFadden & Reymond, 1985).

Maximum binocularity has been also taken to mean the maximum width of the binocular field. This measure can be dependent upon whether body features such as the feathering and cere interfere with the visibility of the reflex or pupil slit. Although it cannot be denied that intrusions into the absolute field of view have functional significance, it does not allow one to determine if eye geometry alone varies between different breeds of birds as proposed by Jahnke (1984).

The measure of maximum width of the binocular field is critically dependent upon the fixation point. We have shown that the maximum retinal binocular field width is 37° when the eyes are in the straight forward position viewing an infinite fixation point.

Table 1 depicts the range of maximum widths found by various authors using retinal or optical criterion. As expected, the optical measures tend to be larger than the retinal measures (see Figure 2).
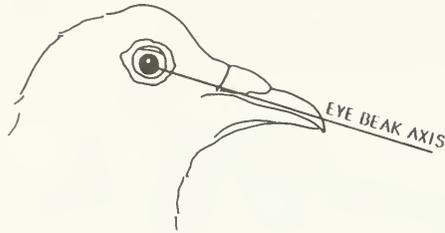
FIGURE 3. The eye beak axis lies parallel to straight edge of the upper mandible of the beak and goes through the centre of the pupil. The distance that the axis is displaced above the line of the beak is exaggerated for the purposes of illustration. However, the eye beak axis is not necessarily coincident with the line of the beak, but lies slightly above in the feral pigeon.

The latter are surprisingly consistent when the fixation point used is taken into consideration.

Thus, if a pigeon was converged for fixating an object at a viewing distance of 15 cm, the F1 distance routinely used when pecking at grain (see section 6), then the patch of ground being viewed simultaneously by both eyes would be about 9 cm in diameter. This size is presumably sufficient to allow resolution of figure from ground stereoscopically and perhaps implies that when the bird moves to F1 during pecking at patches of grain (Goodale, 1983) binocular vision is available to aid in the discrimination.

2. EYE MOVEMENTS AND BINOCULAR VISION

The pigeon has a sophisticated array of eye movements despite the tightness of the orbital fit. Nye (1969) has described small monocular eye movements resembling impulses, drifts, flashes and tremors. All are of relatively low amplitude.

Of relevance to the role of binocular vision, vergence eye movements have also been found, elicited during the peck response (Martinoya, Le Houezec & Bloch, 1984). There is no question that such eye movements will modulate the extent of the binocular field as the distance to the fixation point decreases. However, it is possible that their role is primarily to maintain an image over a constant area of the retina.

The size of the vergence eye movements elicited during pecking has been measured relative to either the maximum divergence that occurs immediately after the peck or the total convergence relative to a scotopic rest position (Bloch, Rivaud & Martinoya, 1984; McFadden,

TABLE 1
Maximum Binocular Field Widths

Max. Width	Source	Conditions
Retinal		
24°	Walls, 1942	"Upon full convergence", unspecified technique.
24.3°	Martin & Young, 1983	Under ketamine, uncorrected for drug induced deviation.
24.°	McFadden & Reymond, 1985	Under ketamine/xylazine, uncorrected for drug induced deviation.
37°	McFadden & Reymond, 1985	Straight forward position, infinite fixation point, corrected for drug induced deviation.
Optical		
42°	Martinoya et al., 1981	Unmonitored vergence state, possibly fixation on camera at 28 cm.
28-40°	Jahnke, 1984	Unmonitored vergence state, flash at 28 cm, field limited by head silhouette.

Lemeignan, Martinoya & Bloch, 1986). The scotopic rest position is the absolute constant position that the eyes adopt when a pigeon is left in the dark for 20 minutes. It is unknown whether the scotopic rest position is equivalent to either the position of the eyes immediately following death or to the straight forward position.

Relative to the scotopic rest position, vergence movements can be up to 17° in each eye. If the scotopic rest position is equivalent to the

straight forward eye position as defined in Section 1 and shown in Figure 1, then 17° of convergence in each eye would allow fixation at a distance of 3.9cm. Since the distance from the eye to the tip of the beak is about 3.7cm, at maximum convergence the object of regard would be just in front of the beak. Although each eye is independently mobile, evidence for binocular fusion is provided by the striking and precise temporal synchrony of these vergence movements. Not only does each eye converge in short bursts, but the initiation of each burst appears coordinated in time (Bloch et al. 1984). In addition, the amount of convergence is linearly related to the distance of the fixation point.

The Influence of Binocular Feedback on Convergence Eye Movements

The mechanism underlying these apparently coordinated eye movements is modulated if binocular interaction is removed either physically or neurally. Physical intervention can be induced by the placement of a binocular field occluder in front of one eye only (Figure 4). It should be noted that this technique does not produce any true blind spots in the visual field at distances beyond the beak but simply removes binocular feedback. Under these conditions, eye convergence still occurs (Martinoya et al. 1984). Figure 5 shows the data from Martinoya et al. (1984) replotted so that normal convergence can be directly compared to that which occurs when binocular feedback is blocked. It can be seen that as the eye gets closer to the grain, the amount of convergence increases linearly. However, the line of best fit under normal viewing conditions ($y = -1.99x + 32.3$) is significantly less than the regression line under conditions when binocu-

BLOCKED VISUAL FIELD
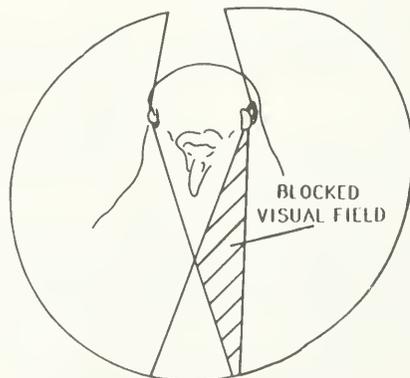
FIGURE 4. Diagrammatic representation of the effect of placing a moon shaped occluder in front of the binocular field of one eye.
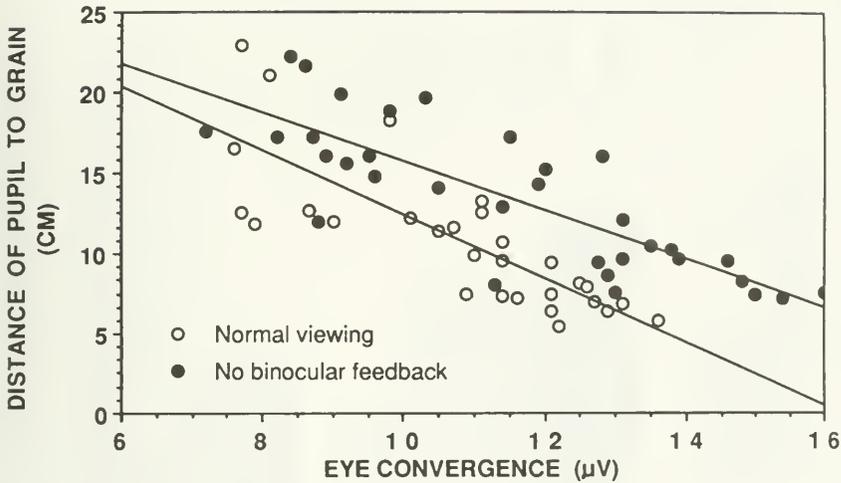
FIGURE 5. Eye convergence (μV $\times$ 10^{-2}) plotted as a function of distance while pecking at a single grain. Data taken from Martinoya et al. (1984) and fitted with regression lines.

lar feedback is blocked (y $= -1.5$x $+ 30.84$) (Analysis of Covariance; $F = 15.8$; df $= 1,60$; $p < .01$). Deprived of binocular feedback, the oculomotor system appears to over-converge as if deprived of modulatory inhibitory control.

A similar picture emerges when binocular interaction is removed neurally by the creation of a split brain preparation (McFadden et al. 1986). This technique involves cutting the major commissures that join the two half brains and measuring the vergence eye movements during pecking before and after surgery. One of the major commissures of relevance is the dorsal and ventral supraoptic decussation (DSO) which lies just above the optic chiasm. Evidence has implicated the DSO in mediating interocular transfer of pattern discriminations in the pigeon (Meier, 1971; Burkhalter & Cuenod, 1978). The DSO is also believed to help integrate binocular information in the thalmofugal pathway which is thought to be analogous to the genticulate-striate pathway in mammals and primates (Karten, Hodos, Nauta & Revin, 1973; Pettigrew & Konishi, 1976).

Figure 6 shows the change in eye convergence in 5 birds caused by cutting the DSO compared with 4 birds in which other commissures were cut, but DSO remained intact. Rather than removing convergence, the effect of creating the DSO split brain preparation was to cause an increase in convergence. The difference in amount of convergence before and after surgery was much greater in the DSO lesioned group ($t = 2.8$, df $= 7$, $p < .05$).
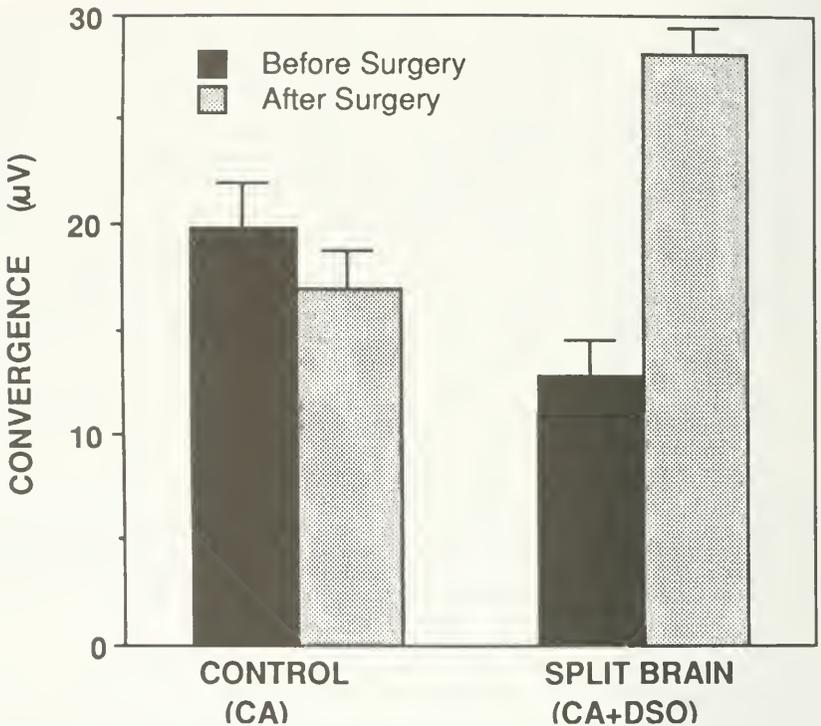
FIGURE 6. The effect of cutting the supraoptic commissure (DSO) compared with cutting the anterior commissure (CA) on eye convergence ($\mu V \times 10^{-2}$). Bars show the standard error.

Not only does interference in binocular neural integration cause an increase in convergence, but it also affects pecking accuracy. The peck error in 9 adult pigeons before and after split brain surgery is shown in Figure 7. Normally, peck accuracy decreases as seeds become large and unmanageable, but is best for smaller seeds like millet and wheat ($F = 10.6$; df $= 3,66$; $p < .01$). Pecking accuracy also decreases markedly as a result of cutting all the major commissures (anterior commissure, supraoptic commissure, tectal and posterior commissures) ($F = 9.8$; df $= 2,66$; $p < .01$). The deficits shown in Figure 7 were permanent since pecking accuracy was measured up to one year after the split brain surgery and after the birds had had much pecking practise under the new perceptual conditions.

Thus, it can be seen that eye movements in the pigeon could allow binocular fixation and possibly fusion in an area of visual space as large as $37 + 17 + 17 = 71°$ for near objects. These eye movements are disrupted when binocular feedback is inhibited either physically or neurally. Surprisingly, in both cases, convergence ap-
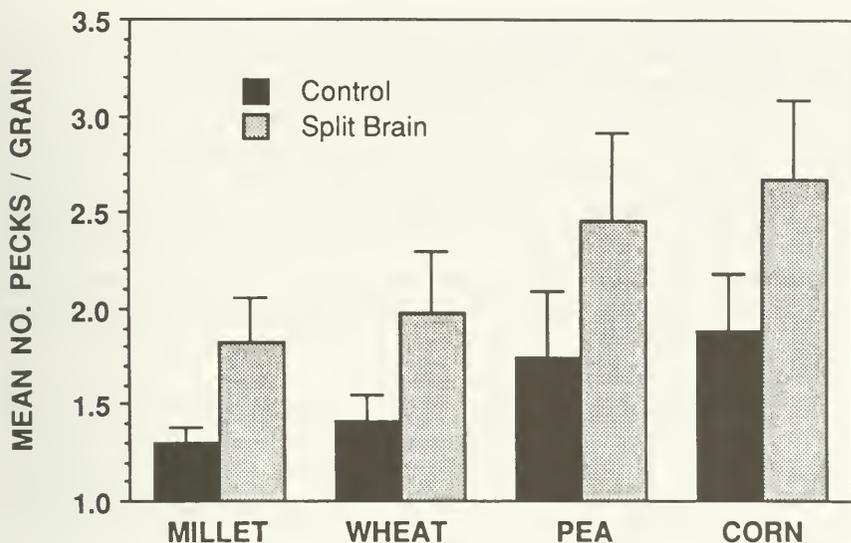
FIGURE 7. Pecking accuracy for different seed sizes before (Control) and 1 year after surgery (Split Brain) in which all the major commissures were cut. Bars show the standard error.

pears to increase as if there is dis-inhibition of vergence control. The convergence eye movements are correlated with the position of grain during the peck response. The vulnerability to interference with binocular interaction is not only seen in the vergence system but is also reflected in the accuracy of the reaching movement during pecking. Before we examine the role of the vergence system in mediating distance perception during pecking, it would be of relevance to understand the retinal and optical characteristics associated with this frontal binocular area of the pigeons visual space.

3. THE AREAS OF VISUAL SPACE SURVEYED BY THE RETINAL SPECIALIZATIONS

It has been noted since Rochon-Duvingneaud (1943) described the 'visual trident' (see Walls, 1942) that birds have the remarkable feature of two separate retinal specialisations allowing high resolution over much of the retina. These specialisations are characterized by increased cell density and in many birds (for example—hawks, eagles, kingfishers and hummingbirds) are both accompanied by foveae. The fovea is a high acuity pit within the retina (see Snyder & Miller (1978) for an interesting discussion of a possible optical advantage of the foveal pit).

In the pigeon with its laterally placed eyes, it is a central area of the retina which subserves the lateral visual field that is accompanied by a fovea. The pigeon fovea is quite deep (see pictures in Chard & Gundlach, 1938; Galifret, 1968; Clarke & Whitteridge, 1976) and more developed than in the human eye (Walls, 1942). The horizon in the plane of the foveae appears well served by an almost streak like density distribution of the displaced ganglion cells (see Fig. 3 in Hayes & Holden, 1983).

The second specialisation occurs in the superior temporal retina, and aids detection in a more frontal downward direction. The precise projection of this 'area dorsalis' as it has been called (Galifret, 1968) is in dispute and will be addressed below.

It has often been proposed that such a dual visual system offers not only the advantages of lateral detection in a panoramic system (eg. predators), but also a capacity for possible parallel processing of visual information closer at hand (e.g. during feeding) (Walls, 1942; Catania, 1964; Bloch & Martinoya, 1983).

4. LOCATION AND CHARACTERISTICS OF THE RETINAL SPECIALISATIONS

The presence of a distinct fovea in the pigeon retina has long been known. Viewed with an ophthalmoscope, the pigeon fovea appears as a bluish ring that has a dark spot in the centre and placed just up from the tip of the pecten. Due to their easy visibility to the experienced observer, the foveae can be accurately mapped in relation to their position in the visual field. The foveal axis lies close to the optic axis (within 5°). Each foveal visual axis is slightly nasal with respect to the centre of each uniocular visual field. With the eyes in the primary position we have found that the angle between the two foveal axes is 147° (see Figure 1).

It is intriguing to note that laser lesions of the central fovea in the pigeon does not have much effect on their visual acuity of grating patterns as measured behaviourally (Blough, 1973). This may be due to the use of other cell rich areas of the retina. A ganglion dense strip posterior-superior to the pecten was described by Whitteridge in 1965 (see Binggeli & Paule, 1969). The distribution of cells within the internal granular layer (nuclei of the muller fibres, horizontal, bipolar and amacrine cells) were mapped by Galifret (1968). In addition to the central area surrounding the fovea, he found the cells to be densely packed at a posterior-dorsal position which he called the area dorsalis. He also noted that the area dorsalis could be assimilated in the 'red field', an area of pigeon retina which contains a high density of red and orange oil droplets.

Staining and mapping of the ganglion cell layer also produced this characteristic distribution (Binggeli & Paule, 1969) with the area dorsalis estimated to contain $36 \times 15 \times 10^3$ cells/degree (Hayes & Holden, 1983).

The amacrine and bipolar synaptic densities do not parallel the cellular densities of the amacrine and bipolar cells, however the highest synaptic densities in the inner-plexiform layer occur in the red field, even higher than that found at the fovea (Yazulla, 1974).

Figure 8 shows the data from the various studies superimposed relative to the angle of the pecten. There is no doubt that in terms of
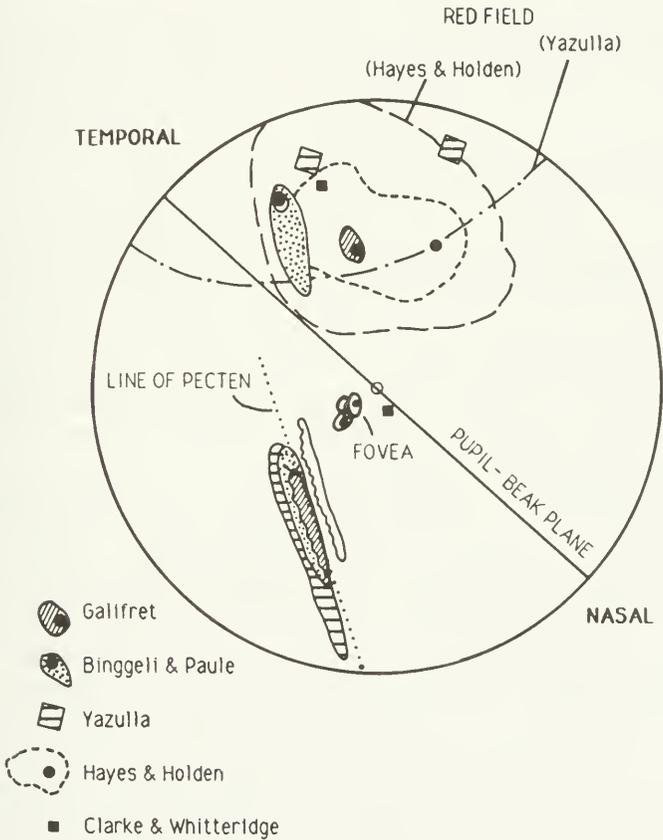
FIGURE 8. Retinal map of the combined data superimposed relative to the angle of the pecten for peak cell densities of: the internal granular layer (Galifret, 1968); ganglion cells (Binggeli & Paule, 1969; Hayes & Holden, 1983); synaptic density (Yazulla, 1974); and tectal magnification (Clarke & Whitteridge, 1976). The large dashed line and dash-dot line represent the borders of the red field found by Hayes & Holden and Yazulla respectively.

cell density, the presence of an 'area dorsalis' consistently appears in a similar retinal area. This quadrant of the retina also contains the red field, although there is no empirical evidence as to the significance, if any, of the coincidence.

The question remains as to where this area dorsalis projects within the visual field. There have been frequent suggestions that it may subserve the frontal field (Clark & Whitteridge, 1976; Galifret, 1968; Goodale, 1983; Bloch et al., 1984; McFadden & Reymond, 1985). Determining its precise projection reflects the difficulty of accurately ascertaining the projection of retinal landmarks not visible ophthalmoscopically.

Only one study has attempted to directly address this question. Hayes, Hodos, Holden & Low (1987) examined the transclearal image formed by light shone from fixed visual field positions into the eye dissected in situ in post mortem pigeons. They concluded that the area dorsalis receives input from the lower visual field (the ground) and not necessarily from within the binocular field.

In such a preparation one is faced with interpreting how the post mortem eye relates to the dynamics of a surprisingly mobile eye in real life (see Martin, 1986). One might need to consider the effects of corneal and optical degradation and the eye deviation that is concomitant with death (approximately 12° from the primary position). It is also known that each eye can converge about 15° when a bird is observing grain prior to pecking (well before F1) (Bloch et al. 1984; McFadden et al., 1986). In addition, vertical and cyclorotational eye mobility have not yet been explored.

All these concerns reflect the difficulty in relating static eye maps to the behaviourally active bird. For example, in the composite cell density maps of Gallifret (1968), Binggeli & Paule (1969), Yazulla (1974) and Hayes and Holden (1983) shown in Figure 8, the projection of the various retinal features can only be ascertained if eye position is defined. Thus in Figure 8, eye position is defined roughly with respect to the angle of the pecten (32° below the eye beak axis). The plane containing the eye beak axis is marked and shows that the superior temporal quadrant of the retina does contain some interesting attributes that lie near this plane. The centre of the binocular field at the elevation of 10° below the eye beak axis stretches 18.5° from the projection of the edge of the retina when the eyes are in the stright forward position. At full convergence, the centre of the binocular field will lie 36° from the projection of the edge of the retina. The whole retina from edge to edge encompasses 169° of visual space. This means that in Figure 8 the *centre* of the binocular field 10° above the eye beak plane will lie 38° in from the edge of the retina. This is very close to the collection of high cell density attributes in this quadrant of the retina.

5. OPTICAL CHANGES OVER THE VISUAL FIELD

The regional specialisations seen in the avian retina are also to some extent mirrored in the refractive properties and optical characteristics of the eye. Various studies have speculated or concluded that the pigeon is myopic in the frontal field and emmetropic (Nye, 1973; Bloch & Martinoya, 1983) or even hypermetropic (Catania, 1964; Millodot & Blough, 1971) in the lateral visual field.

The pigeon eye is regarded as asymmetric both in shape and refractive properties. Variation in the posterior-nodal distance (PND) can be seen in the early insitu cross-sectional drawings by Chard & Gundlach (1938) and Gundlach, Chard & Skahen (1945), when the temporal PND is smaller than the nasal retina. One may expect that modification may occur as a result of the histological process. The opposite effect has been measured in the chick retina where the PND in the horizontal visual field is consistently longer in the temporal compared to the nasal retina (see Figure 9(c) in Schaeffel, Glasser & Howland, 1988). It is possible that the PND varies as a function of elevation as well as with the nasal-temporal direction.

A trend toward myopia in the superior and nasal retina was described within a relatively central retinal area using standard retinoscopic techniques in an anaesthetized pigeon (Millodot & Blough, 1971). Using electroretinographic optometry, again in anaesthetized pigeons, and the principle of conversion of optical defocus into lateral shift of the image of a grating, Fitzke, Hayes, Hodos & Holden (1985) escape the hypermetropic artifact associated with off axis retinoscopy (Glickstein & Millodot, 1970) which would arise if variation occurs in the origin of the light reflex over different eccentricities. Fitzke et al. (1985) conclude that refractive state varies systematically between upper and lower visual field, with the eye progressing from an emmetropic state on the horizon (35° above the eye beak axis) to 5 diopters (D) myopic at more negative elevations. In the nasal to posterior retinal direction, the data indicate little refractive change ($-1D$ to $+0.5D$ respectively). Unfortunately the data was only extended to within 23° of the edge of the binocular field itself, and thus the refractive state within the binocular field was not measured.

The overall refractive state of the pigeon eye is also modulated by its accommodative capacity. Accommodation in the pigeon is mediated by the ciliary muscle which in birds is striated (Gundlach et al., 1945). Both the cornea and lens participate in the accommodative response, with the corneal component having a proportionately greater role in the lower range of accommodation (Martin, 1987; Schaeffel & Howland, 1987). Estimates of the range have varied from 12D (Gundlach et al., 1945) to 5D (Levy & Sivak, 1980).

Points in the binocular field are likely to be imaged through the

peripheral optics. It is possible that such accommodative range may not necessarily act equally at the peripheral margins of the cornea and lens, dependent on the relative rate of curvature and the structural elasticity. If such differences do exist, then it is possible that the frontal field maybe more limited in its available depth of field.

Behavioural Measures of the Near and Far Point of Accommodation

The near point of accommodation can be estimated by measuring the visual acuity of the pigeon at different viewing distances. In the frontal binocular field, visual acuity (square wave grating acuity) was best at a distance of 10 cm and became progressively poorer at greater viewing distances. In contrast, the visual acuity at a distance of 10 cm in the lateral field was 3.5 times worse than frontal acuity but improved at greater viewing distances (Bloch & Martinoya, 1982).

It is clear that differences exist between the frontal and lateral fields in terms of visual acuity measures. At least a partial role of the optics in mediating this distinction can be assumed, and the near point of accommodation in the binocular field is likely to be less than or equal to 10cm. The peck response of the pigeon indicates that the near point could be as close as 5.6 cm, as the grain is not normally observed closer than this distance. As discussed in Section 7, it appears that the far point of accommodation in the frontal field or at least the greatest distance in which stimulus control occurs for distance discrimination may be less than 20cm.

6. BINOCULAR DISTANCE PERCEPTION DURING PECKING

Birds use their feet and mandibles to reach for and manipulate objects within close visual range. In the pigeon, pecking at small grains is an accurate motor action, intimately tuned to the size and distance of the seed (Zeigler, Levitt & Levine, 1980). The peck response is stereotypical between and within individual birds, and is characterised by fast saccadic head movements interspersed with fixation stops. From the last of these fixation stops the eyes begin to close and the beak opens simultaneously, so that at the inflexion point in the peck movement the eyes are fully closed and the beak opened exactly the amount needed to effectively grasp the seed. Grasping the seed is followed by a series of backward head movements accompanied by complex manidibulation and swallowing motions.

Despite the apparent ballistic nature of parts of this pecking movement, it is irresistible to propose that distance perception aids

the accuracy of this movement and is provided by visual feedback in the early stages of the peck sequence. We have attempted to examine the validity of this hypothesis and determine the type of visual cues used. Certainly it is true to say that if visual feedback is completely blocked during the peck response, then the accuracy of this movement is very poor indeed. This is not to say that successful grasping attempts are not made by blind birds, but the low probability and learning required lead one to suggest that this may be due to reliance on recall of spatial maps.

The saccadic head movements accompanying the peck response were first noted by Smith (1974) and Hodos, Leibowitz & Bonbright (1976). We have found that in the adult trained pigeon pecking at grain, the head is moved 6.6–6.9 cm in 20-40 milliseconds. The head velocity is thus conservatively estimated at 165 cm/sec. Maintaining a steady image over a constant retinal area under these conditions may be difficult and is likely to be accompanied by retinal slip. However the flow field has yet to be modelled.

The fast saccadic head movements are also interspersed with fixation stops and have been described in detail by Goodale (1983). He found that the characteristic stereotyped responses occurred when both operantly discriminating the presence of a small black dot on a vertical key (by pecking at the dot) and when pecking at patches of mixed grain.

The absolute time spent at each of the last two stationary fixation stops (labelled F1 and F2) was between 100-200 milliseconds depending on the precise condition. This is 5-10 times longer than that spent in each movement phase, and could possibly allow enough time for visual computation of spatial attributes of the pecking scene.

In order to examine egocentic distance perception, we have chosen pecking at a single grain of millet (3mm in diameter) since the accuracy of this movement can be ascertained with more certainty than the factors controlling the behavioural response under operant conditions.

Correlation of Peck Accuracy with the Fixation Positions

The experiments were done with 6 adult birds each given 10 trials/day (1 seed/trial) for 18 successive days. Enlarged images of the right hand side lateral view were taken at a luminance of 2 log cd/m^2 through a measurement grid with a video camera with a fast shutter speed ($1/1000$ th sec). Frame by frame video analysis revealed a number of interesting attributes of the normal peck response. We had previously found that peck accuracy is poorly developed in young birds with peck accuracy starting as high as 50 pecks/grain but improving with practice (see also Graf, Balsam & Silver, 1985). In adult birds,

accuracy in the single grain 'pick-up' test also improves, even though the birds have had much natural pecking practice. The improvement over time is shown in Figure 9. The data were fitted by an exponential function of the form:

$$y = 0.4e^{-x/2.83} + 1.31$$

indicating a rate of change with a time constant (t) of 2.83 days (training sessions) and levelling off to 1.3 pecks/grain. Pecking in the pigeon is not perfect, with a residual error evident even in highly trained birds. The error rate for peck accuracy is surprisingly high at 30%. Analysis of 61 initial pecking errors revealed that 44% were due to inaccurate grasping with the tip of the beak, 36% due to pecking short of the target and only 20% due to orientation error, most of which was composed of lateral misalignment.

As previously mentioned each peck is accompanied by a series of head fixations and in the above birds the last two stationary positions prior to contact of the beak with the grain were measured. Initially, the distance from the centre of the pupil to the grain of millet was 9.8cm at F1 (n = 60, S.D. = 1.1) and 5.68cm at the last fixation position F2 (n = 60, S.D. = 0.4). These values are very close to that found by Goodale (1983) for pecking at patches of grain. More interestingly, the absolute position of the fixation point increased as a function of
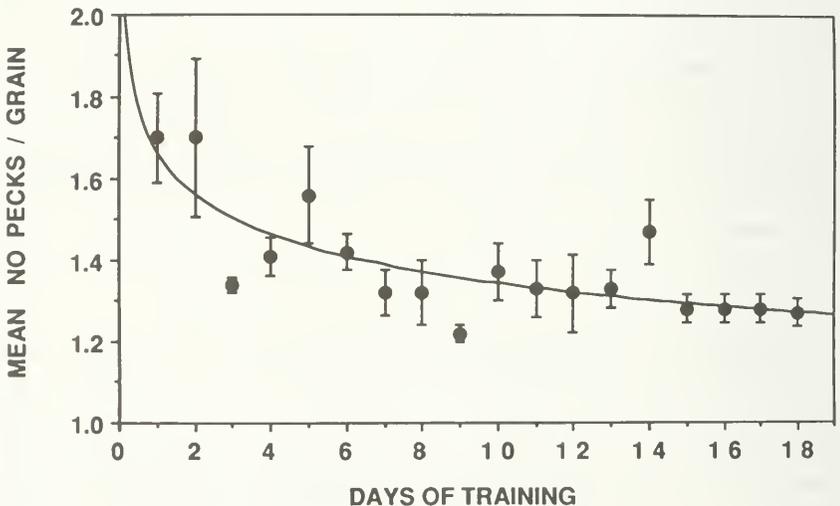
FIGURE 9. Mean improvement in pecking accuracy as a function of training (10 trial/day) in 6 adult pigeons. Bars show the standard error. Data is fitted with an exponential function.

practice. This is shown in Figure 10. Exponential fits to the data gave equations of the form:

$$y = -3.49e^{-x4.41} + 13.41 \qquad \text{for F1, and}$$

$$y = -0.97e^{-x/2.56} + 6.55 \qquad \text{for F2.}$$

Thus the final fixation positions adopted after 180 trials of training and when pecking error was minimal was F1 = 13.4cm and F2 = 6.6cm. The rate of change in pecking accuracy (t = 2.8 days) was most highly correlated with the time constant of the last fixation position F2 (t = 2.6 days) rather than F1 (t = 4.4 days). It should be noted that the variance is always less at the last fixation stop (F2) than the preceding stop (F1). However, it is the case that one or two fixation stops sometimes occur prior to F1, and it is possible that they may sometimes be included in the data if F1 is skipped. There is no question that F1 and F2 are coupled in tandem (for example, see the peaks repeated for both F-stops on days 7 and 9). The position of F1 does ultimately predict how far to move to get to F2.

These data show that the position of the head at the stationary fixation points is correlated with the accuracy of the outcome of the peck movement. Surveillance of the visual scene at F1 allows the computation of how far or for how long the head should be moved to reach F2. If F2 is not at the correct position, then the bird will generally underestimate the distance of the seed.

The Role of Binocular Feedback in Pecking

Interestingly, if binocular feedback is removed by blocking the overlap of one eye (see Figure 4), then pecking accuracy is significantly retarded ($t = 1.4$, df = 16, $p < .01$) (Figure 11). Under such conditions, the bird can eventually learn to partially overcome the effects of not having access to binocular cues. Clearly, the distance estimation is not simply based on one method but uses a variety of strategies, one of which is binocularly based.

Although the bird has difficulty in accurately grasping the target seed without binocular stimulation, examination of the stationary fixation points adopted under such partial monocular occlusion revealed a general resilience to being affected at all. Only a small but permanent decrease was often seen in the position of F1 (Figure 12A) but no change was evident at F2 (Figure 12B). This means that when deprived of binocular vision the target was often viewed at a closer distance during the early components of the peck movement.

The short peck often seen under conditions in which binocular stimulation is removed is an obvious feature if the target is viewed

A
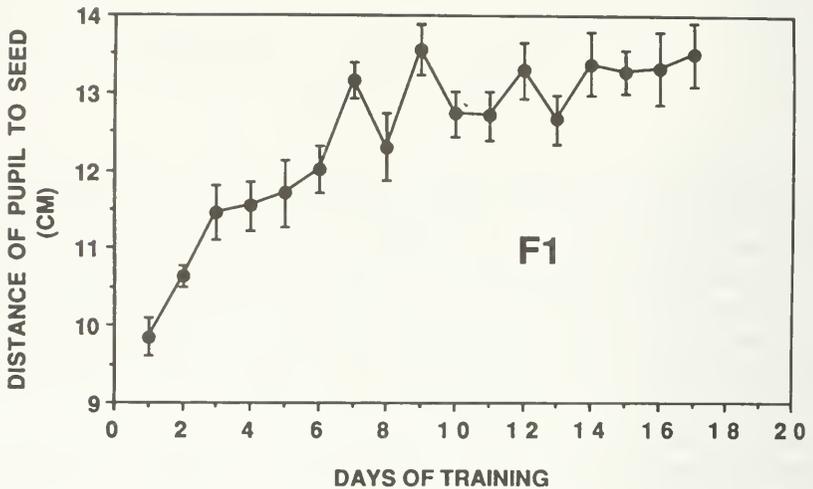
B
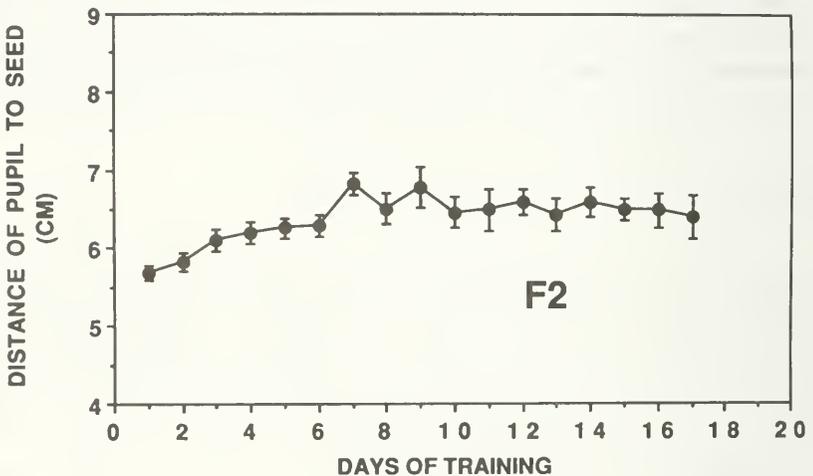
FIGURE 10. The mean fixation positions adopted by 6 birds when pecking at a single grain of millet as a function of amount of practice at: (A) the initial fixation position F1; and (B) the final fixation position F2. Standard error bars are shown.

through prisms (Figure 13). Here the virtual image is closer than the real image of the seed, and the bird uses the fused binocular image rather than the monocular image through each prism. If the bird was not using the fused binocular image then pecking would have been at
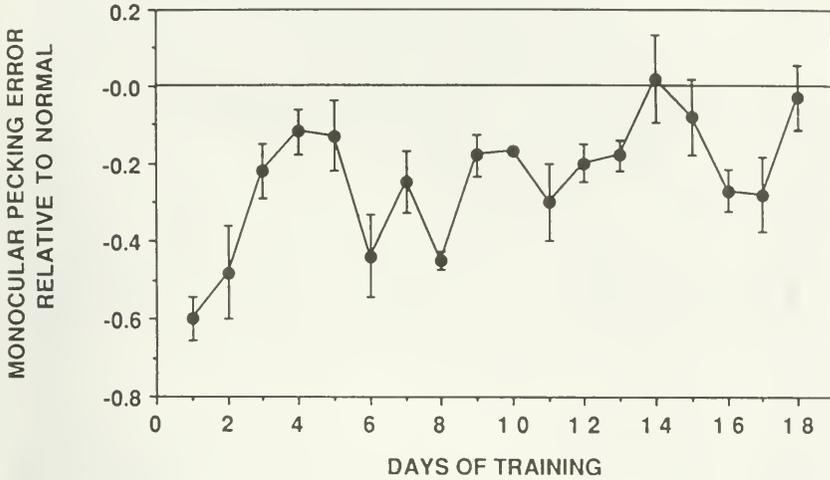
FIGURE 11. Mean difference in the pecking error for 6 birds between normal viewing conditions and conditions of monocular occlusion in which the binocular field of one eye was blocked. The eye chosen for occlusion was left in half of the birds and right in the remainder. Data falling below the line marked as -0.0 shows the increase in pecking error due to occlusion. Bars show the standard error.

the correct depth but displaced laterally. Interestingly, adaption to the prisms does eventually occur.

It is clear that distance perception is employed during the peck movement. It is also true that the seed is preferentially imaged binocularly at distances of approximately 10cm. As previously mentioned, the convergent eye movements which accompany the peck movement could result in maintaining constant retinal stimulation of the object being fixated at the stationary F-stops. The amount of convergence elicited at a fixation point could act as the means to compute the travel distance required to get to F2, the last strike position.

Such a mechanism is also used by the praying mantis to strike at moving prey with its forelimbs (Rossel, 1983). Like the pigeon pecking at grain, the mantis computes the equivalent of the convergence angle between the two eyes and uses it to estimate the egocentric distance to the prey object.

7. BINOCULAR DEPTH PERCEPTION

Relating the position of a point in space to an egocentric body position is quite different to perceiving the world in three dimensions
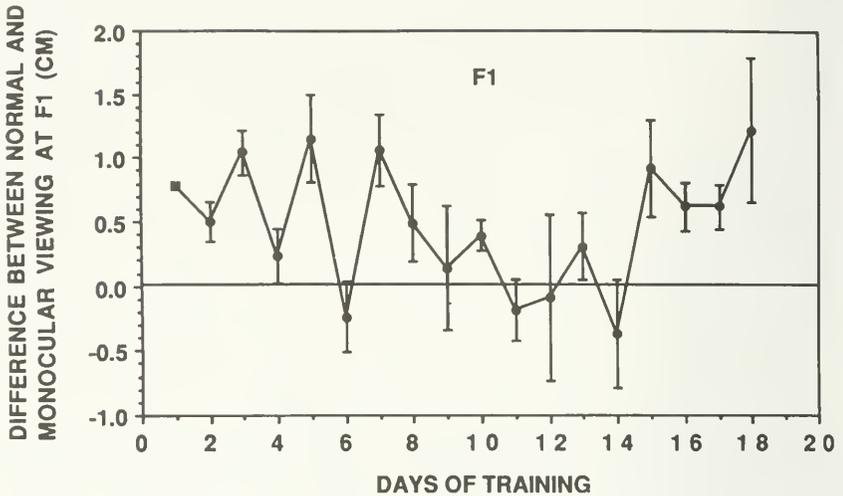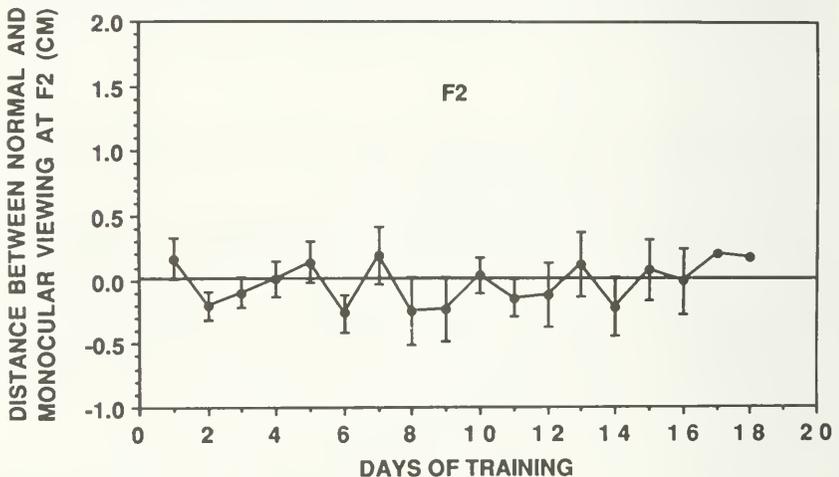
FIGURE 12. Effect of blocking binocular feedback on head fixation position for (A) F1 and (B) F2. Positive values indicate that the centre of the pupil was closer than normal to the seed. Negative values indicate that the eye was further away than normal. Bars show the standard error of the data.

FIGURE 13. Video frame image of a peck at a single grain of millet with prisms in front of both eyes (base out, 10 diopters). (A) Image at the last stationary fixation point F2. Note that the eye beak axis is

lined up with the centre of the grain. The distance from the centre of the pupil to the grain is 5.3cm. (B) Image of moving bird at the inflexion point in the peck movement in which the distance of the seed was underestimated by 5mm. Such short pecks were common in birds wearing prism spectacles. The fully opened eye of this particular frame also demonstrates the interference that was occasionally seen in the eye closure that normally accompanies the peck. In normal viewing, the eye always begins in close after F2 and is fully closed by the time the beak contacts the seed.

independent of the observer position. To this end both motion paral-
lax and stereopsis provide that extra dimension. Stereopsis relies on
convergence to facilitate fusion and provide the stimulus for horizon-
tal retinal disparity.

Within the frontal binocular field we have found that the pigeon
can use local stereopsis to estimate the relative position of objects in
its visual space (McFadden & Wild, 1986). We demonstrated that the
bird can discriminate the presence of depth between two arrays of
elements (black triangles of random size and orientation) only under
binocular viewing conditions. The binocular depth acuity for perceiv-
ing small displacements between two planes in space is best when a
distinct shape (such as a circle) is the emergent binocular stimulus.
Under these conditions, the stereoacuity is 1 minute of arc, a value
approximately matched to the photoreceptor density (McFadden,
1987). These measurements were done at a viewing distance of ap-
proximately 10cm. In previous work, we have been unable to obtain
binocular perception beyond 18-20cm when using stereoscopic stimuli
10mm in depth, despite extensive fading procedures. The mean num-
ber of trials for 4 birds in which no learning was evident was 4,680
(S.D. = 327). Just as the spatial visual acuity as measured with grat-
ings appears to be distance dependent (Bloch & Martinoya, 1982)
there also appears to be a limit to the best stereoscopic range within
the frontal field.

We have also measured distance and relative distance perception
in a task in which retinal image size was available as a major cue in
addition to enforced binocular viewing. This was achieved by the ap-
paratus shown in Figure 14. The bird was required to break a photo-
cell beam after which a brightly lit white disk (3.5cm in diameter)
was shown down a tunnel directly in front of the bird. The distance of
the target could be varied. Initially each bird was required to peck
the left key once if the disk was present and the right key if the disk
was withdrawn to 200cm (effectively absent). Correct responses were
rewarded with grain presented in the food hopper directly below the
tunnel entrance. The task was relatively difficult as the key response
had to be made after the head was withdrawn from the viewing tun-
nel and discrimination choice was based on the memory of the disk
position. Nevertheless, the task was learnt after 35 and 18 daily
sessions (96 trials/session) in two birds. Both birds were then tested
with the target presented at progressively greater distances (Figure
15A). After repeated testing, it was found that difficulty with the dis-
crimination occurred at a target distance of 18cm. At this distance
the target subtended 11°. When the viewing distance was 23cm the
presence of the disk could not be related to a correct key pecking
strategy. It is possible that the frontal field is perceptually limited in
terms of the distance at which objects can be discriminated. It is also
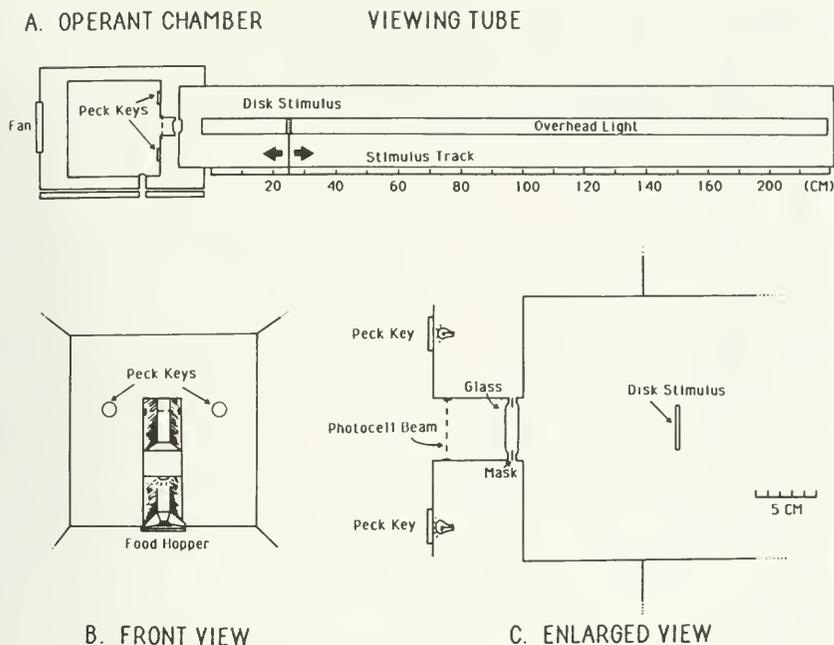
FIGURE 14. Apparatus used for measuring relative distance perception in the pigeon. (A) Top view in cross section showing the viewing tunnel attached to the operant chamber. The stimulus target was a white disk 3.5cm in diameter and could be moved on the stimulus track up and down the tunnel. (B) View of the front pecking wall as seen by the pigeon. (C) Enlarged view of part of A, showing the photocell beam and the tunnel behind it which the bird was trained to place its head in order to view the stimulus.

possible that accommodation is not adequate at distances of approximately 20cm in the frontal field.

It was also of interest to find that when both birds were tested at a viewing distance of 13cm for the smallest distinction that could be discriminated between two disk positions, the resultant mean relative distance threshold was 5.4cm (Figure 15B). This is equivalent to 4.4° in terms of the minimal discriminable difference in the size of the disk. Clearly, when forced to deduce the depth between two target positions based on comparing egocentric distance estimates, the resultant acuity is very much poorer than when access to binocular disparity is facilitated (retinal disparity was not available as the two target positions were not presented simultaneously). If the egocentric distance estimator in the frontal field was based on a vergence signal
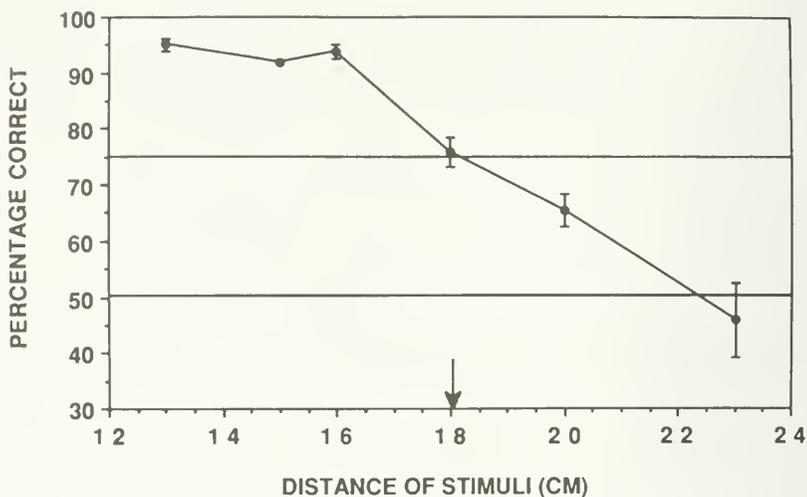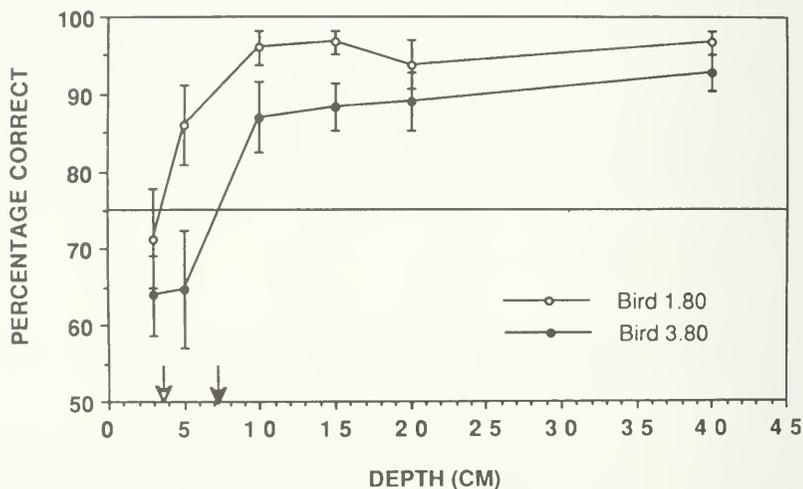
FIGURE 15. Mean performance of two birds trained in the apparatus shown in Figure 14. (A) Threshold for discriminating the absolute distance of the disk stimulus placed at various viewing distances from the eye. (B) Threshold for discriminating the relative distance between two disk positions, one of which was always placed at 13cm from the eye and the other placed at a further 3, 5, 10, 15, 20 or 40 cm. The threshold is taken halfway between perfect (100%) and chance (50%) performance. Standard error bars are shown.

as implied in the pecking studies, then this signal alone is inadequate for producing accurate relative distance perception. In contrast, retinal disparity, although alone it is not particularly useful for egocentric distance estimation, is a high resolution mediator for external depth perception.

GENERAL DISCUSSION

The finding that eye convergence is intimately linked to peck accuracy in a common reaching task in the pigeon and is binocularly sensitive at distances of approximately 13cm matches the optics of the pigeon's eye in which refractive state is relatively myopic in the frontal visual field and the depth of field may be limited. However, this vergence signal alone is relatively weak as an estimator of the relative positions of objects and is ineffective at distances greater than 20cm in the frontal field. Here we see that local stereopsis appears to be much more effective and raises the suggestion that this capacity which appears on the surface to be relatively independent of egocentric distance may be more useful for discriminating small distinctions in depth such as in objects viewed against a textured background. The resultant breaking of camouflage would be an effective means of pattern decoding in a stationary world.

Of course, there is little doubt that motion plays an prominent role in visual perception given the propensity for pigeon visual centres to contain motion cells (Donovan, 1978) and the spatial domain during flight. However, the need for stationary analysis of visual space should not be underestimated. In the pigeon, even during walking, head bobbing motions act to keep the spatial array constant (Friedman, 1975; Frost, 1978). So too, the converging eye movement that accompanies the peck response may result in maintaining the image of the grain on a constant area of the retina. As we have seen, the area dorsalis may well be such a candidate, with its high density resolution capacity.

Interaction between the vergence system mediating egocentric distance perception and stereopsis aiding in depth perception is likely to occur if depth constancy is an emergent feature of pigeon spatial vision. Perceptual constancies are more likely to be involved in the 'what' rather than the 'where' distinction proposed by Schneider (1969) and Ingle (1973). We are presently investigating this possibility, and such comparative studies may shed light on the evolution of visual pathways. Livingston & Hubel (1987) have suggested that depth perception is phylogenetically older than the capacity for colour and high resolution form perception developed in the parvocellular system of the primate geniculocortical visual system. The apparent

involvement of the supraoptic decussation in mediating distance perception in the pigeon visual system implies that such information is carried at least in part by the thalmofugal system rather than the more primitive and more prominent tectofugal pathway. It is perplexing to see that the same neural mechanisms may have convergently evolved in different species but by different pathways. The matching of the neural mechanisms may only serve to remind us that all species are constrained by similar physical properties of the spatial array.

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