

BINOCULAR DEPTH PERCEPTION IN THE PIGEON

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By means of a discrete-trial simultaneous discrimination procedure, pigeons were trained to respond differentially to visual arrays that were identical except that one of them contained a circle displaced in depth when viewed stereoscopically. Performance was severely disrupted when one eye was occluded. The monocular deficit was peculiar to the depth task, inasmuch as no such decrement was seen on a pattern discrimination. The results imply that presence of the displaced circle was discriminated on the basis of a binocular cue. It was also found that pigeons could discriminate the direction of the displacement. Discrimination of depth was independent of the global form and still occurred when elements of the array were randomly displaced in depth. Performance was not disrupted when the absolute convergence angle of the depth stimulus was changed. The cue that consistently accounted for the behavior seen was the detection of the relative angles of convergence—that is, the retinal disparity of the two planes in depth. Thus, despite the lateral position of the eyes of the pigeon, a small binocular field mediates the binocular discrimination of near objects in depth.

Key words: binocular vision, depth perception, stereopsis, convergence, key peck, pigeon

The pigeon has a sophisticated visual system (for a review, see Emmerton, 1983). Its laterally placed eyes allow panoramic vision that extends some 340° (Walls, 1942/1967). In addition, there is a small region of binocular overlap (Martinoya, Rey, & Bloch, 1981). The lateral and frontal fields of view are characterized by separate retinal specializations. The lateral field of view is served by a fovea and many yellow oil droplets (Galifret, 1968); the retina projecting to the frontal field contains numerous red oil droplets. Within the red area is located the area dorsalis, which is characterized by a high cellular density and synaptic complexity (Binggeli & Paule, 1969; Galifret, 1968; Yazulla, 1974) comparable to the fovea. Thus, the area dorsalis defines the frontal visual axis and the fovea defines the lateral visual axis. The refractive state of the eye also varies with eccentricity. It has been found that the pigeon is myopic in the frontal field and possibly hypermetropic in the lateral field (Bloch & Martinoya, 1982; Blough, 1973; Catania, 1964; Millodot & Blough, 1971; Nye, 1973).

The physical distinctions between the two fields of view support the original suggestion by Walls (1942/1967) of a functional separation in which panoramic vision in the lat-

eral field aids in the detection of a distant target (possibly a predator), while the frontal field of view is tuned to close-range activities such as pecking. The frontal field is also binocular, and the question arises as to whether the binocular quality of the frontal field has a role in the discrimination of the relative distance (depth) or absolute distance of near targets. Recent evidence has suggested that binocular cues are involved in pigeons' judgments of near frontal distance (Martinoya & Bloch, 1981).

The binocular cues known to mediate visual localization of objects are stereopsis and convergence. If the two eyes converge and fixate upon a single point in space, the convergence angle formed between the lines of sight to the target may be used to estimate one's egocentric distance from the fixated point. However, in order to determine the relative distance or depth between the fixated point and another point in space, one needs to be sensitive to the difference between the two angles of convergence. This is theoretically equivalent to correlation of the horizontal retinal disparity and is the basis of stereoscopic vision.

It is possible that the accurate spatial localization seen in pigeons' pecking at grain (Zeigler, Levitt, & Levine, 1980) is based upon these binocular visual cues. The position of the grain during the stereotypical phase of the pigeon's peck response (Goodale, 1983; Hodos, Leibowitz, & Bonbright, 1976) is correlated with the center of the binocular field and

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the projection of the area dorsalis (McFadden & Reymond, in press). Furthermore, coordinated convergent eye movements are elicited by stimuli presented in the binocular field (Martinoya, Le Houezec, & Bloch, 1984).

In order to ascertain whether the pigeon has a binocular mechanism (either stereopsis and/or convergence) for spatial localization, we used stimuli that could be maximally discriminated on the basis of binocular cues to depth. The stimuli were based on a clinical test of stereoacuity in young children devised by J. Frisby (see Hinchliffe, 1978). Apart from its simplicity and versatility, this test has the distinct advantage over haploscopic devices, including random dot stereograms, in that red/green or polarized goggle systems are not required. The difficulty of using such devices with animals arises from the impossibility of perfectly matching perceived color achieved via a filter with the spectral sensitivity of the bird. The dichoptic polarization system is also apt to produce luminance changes as a function of head-tilt (Covey, Parkinson, & Warnick, 1975). The Frisby real-depth target consists of two arrays of elements, each array confined to one of two parallel planes in space. Unlike haploscopic devices, these targets maximally stimulate the binocular system. Thus, not only retinal disparity but also convergence can potentially aid the discrimination.

In the following experiments it was found that pigeons were able to discriminate depth in the Frisby stimulus, and that this discrimination was dependent upon binocular vision.

EXPERIMENT 1: THE BINOCULAR DEPTH DISCRIMINATION

The aim of this experiment was to discover whether the pigeon could discriminate depth from nondepth using the Frisby stimuli. Because of the nature of the stimuli, fast acquisition of such a discrimination would be evidence that binocular cues are involved in the bird's perception of depth.

METHOD

Subjects

The subjects were 24 experimentally naive feral pigeons (*Columba livia*). The mean 100% body weight was 353 g ($SD = 50$ g). Each bird was maintained at 80% of its free-feeding weight during the experiment.

Apparatus

The pigeons were trained in a modified Lehigh Valley operant chamber (type BRS/LVE). The front wall (45 cm wide and 49 cm high) contained two clear Perspex keys (4.7 by 4.7 cm). These were horizontally separated by 1.5 cm and mounted 18 cm above the floor. The access to the grain dispenser was located 5 cm above the cage floor midway between the response keys. The interior of the chamber was painted flat white and was illuminated by a 45-W lamp mounted in the center of the ceiling (45 by 30 cm). The chamber was ventilated by a fan placed in the back left corner; the fan also produced masking noise.

Behind the front wall was mounted a sliding bracket that contained three glass stimuli, the outer two being identical. The bracket glided behind two apertures that matched the pecking-key apertures (see Figure 1). This enabled two different stimuli to be positioned behind the two response keys. The distance from the pecking key to the front face of the stimuli was 2 cm. Each stimulus was back-illuminated by five 0.17-A 28-V lamps, evenly diffused through a white, translucent, Perspex screen. The luminance of each stimulus as viewed through the response key and measured with a standardized photometer was $2.7 \log \text{ cd/m}^2$.

Stimuli

Three sets of stimuli were used for three different discriminations. They were all based on a standard depth task (SDT) in which the discrimination was between a two- and a three-dimensional stimulus. The two stimuli comprising the SDT were identical when directly viewed from a stationary position with one eye. However, under binocular conditions, the positive stimulus (S+) contained a circle displaced in depth; pecks on this key produced food. No such form was present in the negative stimulus (S-); pecks on this key did not produce food. Both stimuli were made from a high contrast positive film that had been photographically reproduced. The edges of the film were attached to the surface of a piece of glass that was optically clear and measured 48 by 65 mm. The thickness of the glass was 10 mm. The edges of the stimuli were masked by a lip on the bracket in which they were contained. The negative stimulus

consisted of an array of random-sized triangles placed onto the front side of the piece of glass (Figure 2a). The positive stimulus consisted of an identical array of triangles but divided into two components such that a center circular portion of the array (containing only whole triangles) was displaced onto the back of a piece of optically clear glass. The remaining surround was on the front of the same piece of glass (Figure 2b). Hence, the image present was of a circle displaced 10 mm in depth behind the surround.

The second discrimination procedure examined transfer of performance from the SDT to a relative depth task (RDT). In the RDT, both stimuli contained a circular patch of the array displaced in depth, but the direction of the displacement differed. The positive stimulus (S+) was the same as that used in the SDT. The negative stimulus was identical to S+, except that the surround portion of the array was displaced onto the back of the glass leaving the center circular array on the front of the glass. Thus, in the relative depth task, both stimuli appeared identical when viewed from a direct stationary position with monocular vision. However, with both eyes open, it was apparent that the S+ contained a circle floating behind the surround while the S- contained a displaced circle in front of the surround.

In humans, discrimination in the standard depth task occurs easily on the basis of binocular vision. However, the discrimination also is possible through the use of movement-produced monocular cues. One such cue is interposition. When the depth stimulus is viewed from an oblique angle, triangles at the edge of the displaced circle may disappear behind others. The third discrimination procedure examined behavior with respect to simulated monocular cues that would occur in this situation. The negative stimulus remained the same as in the standard depth task. The positive stimulus was made with the same random-sized triangle arrays, but placed only on the front face of the stimulus. The center circular portion of the array was moved relative to the surround as if the depth stimulus were viewed from an oblique angle (Figure 2c). Thus, the new S+ simulated monocular cues to depth, such as object overlay and/or a static image produced during motion parallax, but no binocular cues were present.

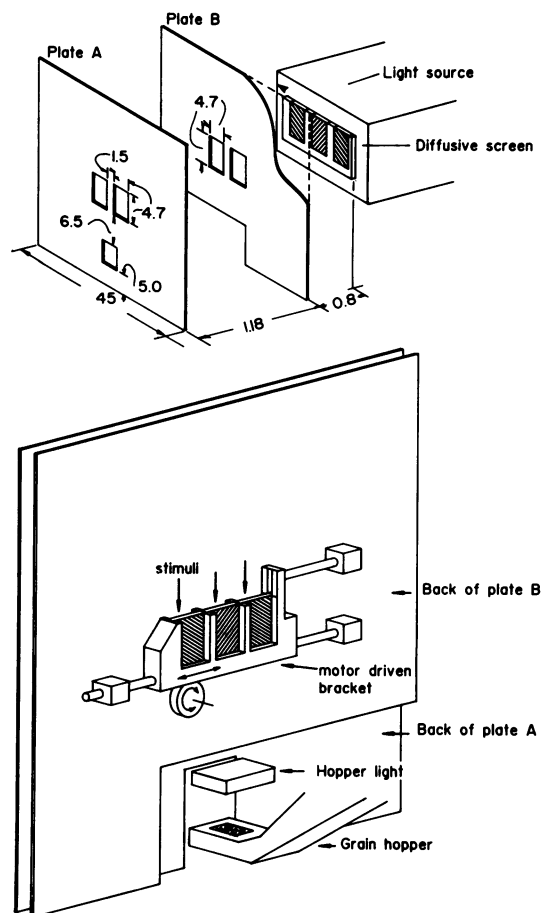


Fig. 1. Exploded view of the apparatus (not to scale), with distances in centimeters. Plate A is the front wall of the experimental chamber. The stimuli were inserted in the motor-driven bracket fixed to the back of Plate B.

Procedure

Pecks on either response key were first hand-shaped; then an autoshaping procedure was used to produce pecking on each key alternately after it was illuminated. A single peck on the illuminated key resulted in 3-s access to the grain dispenser. Food was delivered automatically if the subject did not peck the lighted key within 11 s. Subjects were given 60 trials per day until they reliably pecked the illuminated key without error (i.e., never pecked the nonilluminated key) for 3 successive days.

After completion of the preliminary training, a simultaneous discrete-trial discrimination was introduced. Here, S+ and S- stim-

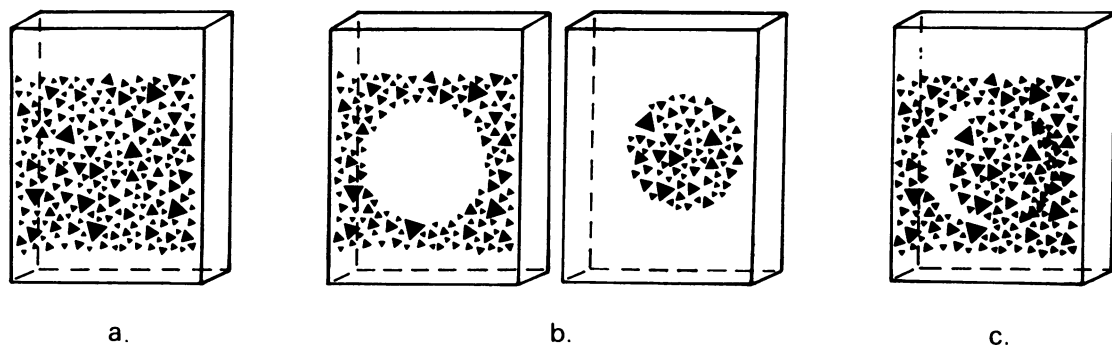


Fig. 2. Stimulus configurations used in the standard depth task (SDT). Panel a: the negative stimulus (S-) for the SDT; Panel b: the front and back faces of the positive stimulus (S+) for the SDT; Panel c: a simulation of S+ that contains only monocular cues to depth. The circle could be displaced either to the left or the right according to the side key on which it was presented. No binocular cues were present, inasmuch as both triangle arrays were in only one plane on the front of the glass stimulus. This stimulus and that shown in Panel a were used for the interposition simulation control.

uli were presented simultaneously behind different illuminated keys, and were switched between trials according to a computer-generated quasi-random sequence. The stimuli were always made to move the same distance between trials even when the move resulted in the stimuli resuming their original positions. In this latter case, the stimulus bracket moved to the halfway position and without delay glided back to the original position. This was done to obviate discrimination on the basis of any noise produced by movement of the stimuli.

All stimuli were cleaned carefully with soft lens tissue soaked in acetone. This was done prior to their introduction into the stimulus bracket at the beginning of each daily session. The stimuli were remade every two weeks with new photographic films, and three separate sets of stimuli were available for random selection. Thus, it was not possible for discrimination to occur on the basis of dirty marks or other irrelevant features of a stimulus.

The beginning of each trial coincided with simultaneous onset of both the houselight and the keylights. A peck on the S+ turned out the keylights, turned on the feeder light, and resulted in the food dispenser being presented for 3 s. A peck on the S- resulted in a 3-s timeout, during which the operant chamber was dark. Responses on the S- key also initiated a correction procedure in which the trial was repeated until the bird eventually pecked the S+ key. A correct response in a repeat

trial resulted in illumination of the feeder light but was never accompanied by delivery of grain or counted as a correct response. A 3-s intertrial interval followed the termination of access to the grain or illumination of the feeder light. During this period the chamber was dark and the stimuli were moved to the next position.

The number of correct responses, not including correction trials, was computed as a percentage of the total number of trials. Daily sessions of four blocks of 24 trials per block were given until a bird's average performance over the four blocks exceeded 90% correct in three successive daily sessions. To check for discrimination on the basis of nonvisual extraneous cues, all birds were tested for one session on a standard control. During this session, the two stimuli were identical, but reinforcement was correlated with one of them as if it were the positive stimulus. After reaching criterion on the standard depth task and passing the extraneous cue control, all birds were given one additional session on the standard depth task. Performance during this session always remained above 90% correct. The birds were then described as having completed criterion on the SDT.

Four of the pigeons (numbers 35, 37, 39, & 40) were subsequently tested for transfer on the relative depth task until performance was again 90% correct during three successive sessions on this new discrimination. Similarly, after reaching criterion on the standard depth

task, another 4 birds (numbers 40, 45, 53, & 55) were tested for one session (96 trials) on the simulated monocular cue discrimination.

RESULTS AND DISCUSSION

Acquisition of the Standard Depth Task

All birds reached criterion on the SDT. A linear regression was fitted to each individual learning curve of Experiment 1 and it was found that the mean correlation coefficient (Pearson's r) was 0.9 ($SD = 0.05$). This indicates that the learning curves can be approximated by a linear function. The mean number of sessions to criterion (SN) was 10.6 ($SD = 3.8$) and the mean slope of the regression line (SL) was 6.0 ($SD = 2.9$). Learning rates varied as a function of the month of the year in which training occurred. Learning was fastest during March and slowest during September (Spring in the Southern hemisphere). This variation may be related to hormonal changes.

The results indicate that pigeons can discriminate depth from nondepth in the Frisby stimuli, and the discrimination appears to have been learned with ease; responses on S+ increased in approximately linear fashion, requiring a mean number of approximately 1,000 trials to reach criterion.

We also found that performances of birds trained on the SDT immediately transferred to a discrimination in which the glass medium of the Frisby stimuli was replaced by air (McFadden, 1984). This was achieved by mounting the photographic images on a frame, the edges of which were concealed from view. It is clear that differential refraction or reflection from the front or back surfaces of the optically clear glass does not provide the cue for the standard depth discrimination. In addition, criterion was also achieved on a discrimination in which the depth stimulus was used as S- and the nondepth stimulus was reinforced as S+ (McFadden, 1984).

Transfer to the Relative Depth Task

The percentage-correct scores obtained on the transfer test from the standard depth task to the relative depth task are shown in Figure 3. Transfer was immediate in two of the four cases. Performance of Bird 40 was slightly disrupted by the change in the negative stim-

ulus (S-) for three sessions, after which criterion performance was reinstated. Performance of Bird 35 was disrupted for only one session. In contrast, all subjects' performances fell to chance levels of responding (45.8% to 54.2%) when the standard control was introduced for a single session. The easy transfer from the SDT to the RDT indicates quite clearly that the two stimuli that differed in the direction of the displaced circle were discriminable.

Interposition Simulation

The 4 subjects to be exposed to the simulation of interposition cues attained a mean score of 56% ($SD = 5.7$) on the standard control. Their criterion performance was immediately reestablished in the SDT session that followed. However, when tested on the monocular cue simulation of overlay, performances again fell to chance. The mean score attained by the 4 birds was 55% ($SD = 6.3$). Thus, when S+ simulated two types of monocular cues to depth—object overlay and a static image produced during motion parallax—it was not functionally equivalent to the depth stimulus in the SDT in which binocular cues to depth were present.

EXPERIMENT 2: MONOCULAR PERFORMANCE

The depth stimulus contains strong binocular cues to depth, and only binocular cues are present in the depth stimulus if it is viewed from a direct stationary position. The ease with which criterion performance was attained on the standard depth task provides some evidence that subjects discriminated between the depth and nondepth stimulus on the basis of these binocular cues. We have seen that monocular cues of the sort that would arise from indirect viewing did not support the depth discrimination. However, inasmuch as the birds are free to move, monocular cues could arise from flow in the optic array as the pigeon moves its head towards the stimulus. Furthermore, motion parallax occurs if the head moves sideways. On this point it is interesting to note that frame-by-frame photographic analysis of birds performing the discrimination revealed that subjects did not move their heads sideways (McFadden, 1984). Rather,

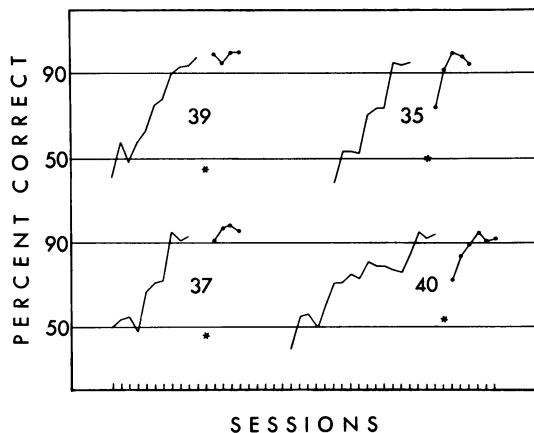


Fig. 3. Initial acquisitions of discrimination on the standard depth task and subsequent transfer to the relative depth task (connected dots) for 4 pigeons. Performances on the standard control procedure are indicated by asterisks.

head movements were always directed towards the stimulus with fast saccadic movements separated by brief fixation periods, a pattern that was also reported by Goodale (1983) for birds pecking in an operant pattern discrimination. In addition to the monocular cues introduced by motion, the possibility also exists that accommodation could provide a cue to depth.

All of these monocular cues would still be available with one eye covered. The hypothesis that binocular cues were the main basis of the depth discrimination predicts that performance should be inferior under monocular conditions. This was tested in Experiment 2, in which it was reasoned that if the discriminations were based purely on monocular cues, no deficit in performance should be evident after one eye is occluded. This assumes, of course, that covering one eye has no nonspecific effects on discrimination performance due, perhaps, to blocking half the visual field or wearing the goggle per se. Hence, monocular performance was examined not only on the depth task but also on a pattern discrimination composed of the components of the depth stimulus. If binocular cues were the basis of the depth discrimination, a deficit should be seen in monocular performance on the depth-discrimination task but not on the pattern-discrimination task.

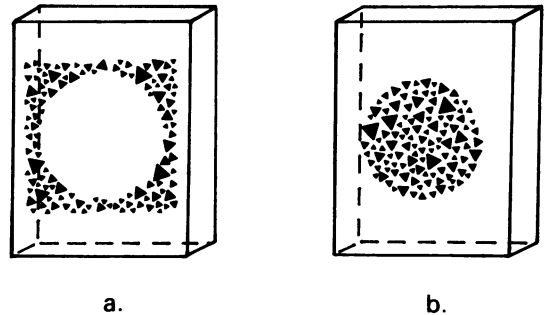


Fig. 4. Stimulus configurations for the pattern discrimination in Experiment 2. Panel a: the negative stimulus (S-); Panel b: the positive stimulus (S+).

METHOD

Subjects

Ten feral pigeons were used for monocular testing. Seven of the birds (8, 9, 10, 11, 37, 40, & 50) had already been trained on the standard depth task in Experiment 1. The remaining 3 pigeons (17, 19, & 24) were naive. All were maintained at 80% of their normal body weights.

Apparatus

The same apparatus was used as in Experiment 1.

Stimuli

The stimuli used for the standard depth task have already been described. The stimuli for the pattern discrimination, shown in Figure 4, were based upon the same array of randomized triangles used in the SDT. The array was divided into two components of equal area. The pattern discrimination consisted of a positive stimulus (S+) that was composed of a center circular component of the array and a negative stimulus (S-) that consisted of the remaining surround (Figure 4). Each was mounted onto the front face of separate pieces of optically clear glass 10 mm thick.

Procedure

After completion of training to criterion on the pattern or the depth task, all birds were tested monocularly on their respective discriminations. Subjects 37 and 40 were tested for transfer to the RDT in Experiment 1 before monocular sessions were introduced. Cri-

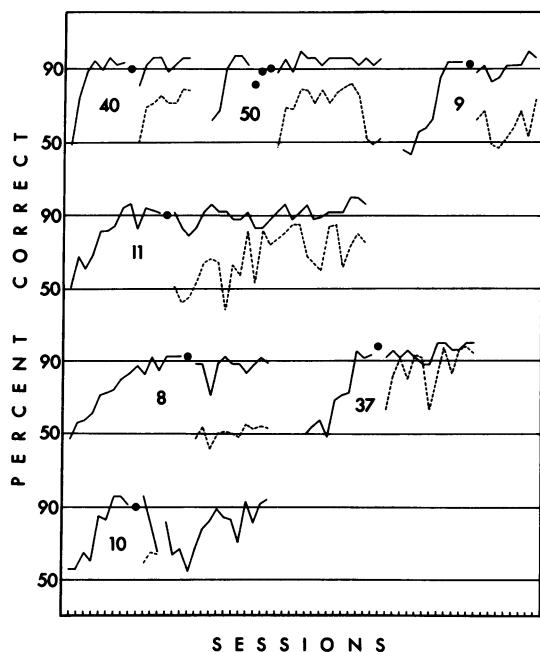


Fig. 5. The performance curves for individual birds before and during monocular testing on the standard depth task. Subject identification is indicated by the numbers beside each graph. Shown for each subject is the initial acquisition curve followed by performance after application of the Velcro ring alone (see dot) and subsequent binocular performance (solid line) and monocular performance within the same sessions (dashed line). Each division on the x axis indicates one session.

terion performance on the depth task was re-established (1 to 2 sessions) before monocular testing was begun.

Monocular occlusion was achieved by the application of a small light-tight, felt-lined rubber goggle that fitted neatly over either eye without contacting the eye or lid. The goggle was attached by the use of Velcro tape. A ring of the hooked side of the tape was glued onto the feathers around each eye with a mild contact adhesive. The other side of the Velcro tape was fitted around the base of the goggle. The goggle could then be attached to either Velcro ring simply by contact of the Velcro tape. Once attached, it could be removed by holding the base ring firmly and gently peeling the Velcro apart. Occlusion of the eye in this fashion had a number of advantages. First, the goggle was light and appeared comfortable as evidenced by the bird's rapid adaptation to its presence. Second, it was secure and could

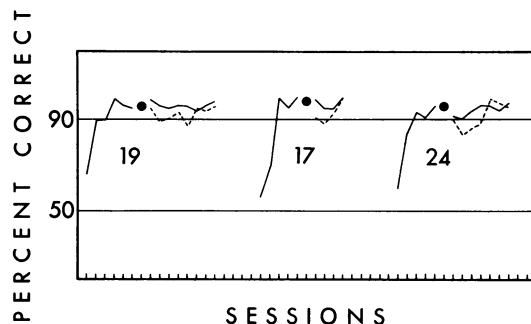


Fig. 6. The performance curves before and during monocular testing on the pattern task in Experiment 2 (cf. Figure 5).

not be removed by the subject. Finally, the method allowed easy transfer of the goggle from one eye to the other.

Each subject was initially tested with the rings glued in position. Monocular testing was then implemented with each eye alternately occluded from session to session. The choice for which eye was occluded for the first session of monocular testing was random. Within each session, each subject was given, in addition to four blocks of monocular trials, one block of binocular trials. Each block consisted of 24 trials, and the order of monocular and binocular blocks was randomized from session to session. Monocular testing was continued for at least the same number of sessions that had been required by an individual subject to reach criterion performance under the initial, binocular conditions.

RESULTS AND DISCUSSION

The performance curves both before and during monocular testing for subjects trained on the depth and pattern tasks are shown in Figures 5 and 6, respectively. For all subjects, application of the Velcro rings did not affect criterion performance and the percentage-correct score typically remained above 90%.

Qualitatively, Figure 5 shows that performance on the depth task was severely affected by the occlusion of one eye. With training, monocular performance improved for 5 of the 7 subjects to levels better than chance, but except for Subject 37, all birds did not reach criterion even after extended training (including 27 monocular sessions shown for Subject 11). Monocular performance was highly vari-

able from session to session. In contrast, performances during binocular blocks of trials (one block per session) remained relatively constant for all subjects except Subject 10. For this bird, three monocular sessions disrupted binocular performance and resulted in extinction of the original discrimination. This subject had to relearn the task binocularly.

Quantitatively, the mean binocular percentage-correct score was compared with the corresponding mean monocular score for the first eight sessions that included the one-eye testing procedure. Subject 10 was excluded from the analysis. A highly significant difference was found between monocular and binocular performance [$F(1, 75) = 239, p < .001$; randomized block factorial design] and this difference was constant over the eight sessions.

The monocular deficit on the SDT may reflect interference with viewing by the goggle and may not be related to the nature of the discrimination. However, in striking contrast to subjects tested monocularly on the depth task, all subjects tested monocularly on the pattern discrimination were generally unaffected by the presence of the goggle (Figure 6). Each monocular mean score was compared independently with binocular performance on the pattern discrimination. There was no statistically significant difference for Sessions 1 ($t = 2.09$), 2 ($t = 1.74$), or 4 ($t = 1.57$). On Session 3 there was a small significant difference ($t = 4.5, .01 < p < .05, n = 3$).

The effect of occlusion of one eye on the pattern task was compared with the performance decrements seen on the depth task during the first four monocular sessions. For each bird, a difference score was obtained in each session by subtracting the mean score achieved during monocular occlusion from the corresponding binocular performance score. This difference score measures the size of the performance decrement for any particular monocular session. The difference scores in the first four sessions of the one-eye testing procedure were compared in the depth and pattern task groups using an unweighted means solution for a split-plot factorial design. There was a highly significant difference between the effect of monocular occlusion in the pattern and SDT groups, and this difference remained constant over the four sessions compared [$F(1, 7) = 23.7, p < .005$].

It should also be noted from the initial bin-

ocular acquisition curves that the depth task required more sessions on average, and had a slower rate constant than seen for the pattern task. The difference in the number of sessions taken to learn the two tasks binocularly was statistically significant [$t(7) = 2.46, p < .025$]. One might consider that the monocular deficit seen only on the depth task and not on the pattern discrimination may be a function of task difficulty or amount of binocular experience. If this were true, there should be a correlation between variation in task difficulty and the size of the monocular deficit within the birds trained on the depth task. One way to assess this is to measure the correlation ratio (r) between either the number of sessions taken to reach criterion (SN) or the slope of the fitted regression line (SL), and the mean difference between binocular and monocular performance scores for the first four or eight sessions of the one-eye testing procedure.

It was found that there was no correlation between SN and the mean difference score for the first four ($r = .21, n = 6$) or eight ($r = .16, n = 6$) monocular sessions. Nor was there any relationship between SL and the mean difference score for the first eight sessions of the one-eye testing procedure ($r = -.17, n = 6$). Thus, within the SDT group, there was no correlation of the size of the initial monocular deficit with parameters of the initial acquisition curves that indicate task difficulty. It is unlikely that the lack of a monocular deficit in the pattern task was simply a function of the difference in the initial acquisition curve rates. The most plausible conclusion is that the performance decrement observed with monocular occlusion was a function of the specific nature of the depth discrimination. It occurred because the initial discrimination had been based upon binocular cues that became unavailable under monocular conditions.

EXPERIMENT 3: THE NATURE OF THE BINOCULAR CUE

There are two binocular cues that may be considered effective in the discrimination of the displaced circle in the Frisby stimuli. The binocular cue is not the oculomotor movement accompanying a change in the convergence angle of the eyes, as such a cue would not be effective in the relative depth task (RDT). However, if the angle of convergence is com-

puted (thus allowing egocentric absolute distance information to be derived), then convergence could be the basis of the binocular cue in both the RDT and the standard depth task (SDT), as illustrated in Figure 7a. However, absolute convergence angles would not be a sufficient cue unless fixation was approximately in the center of one of the stimuli. If this occurred, the positive stimulus would be directly correlated with the smallest angle of convergence (α_1) for both the SDT and the RDT. However, if fixation occurred off-center, convergence would not provide the appropriate key to the discrimination unless it was combined with pattern recognition. A more effective binocular cue is horizontal retinal disparity, the basis of stereoscopic vision. It provides a cue to depth over a much greater range of stimulus area. The discrimination of the SDT would consist of crossed diplopia versus no disparity (Figure 7b), whereas the RDT would consist of a discrimination of crossed versus uncrossed disparity. Thus, the positive stimulus would be correlated not simply with the disparity present, but with the direction of the displacement in depth.

If retinal disparity rather than convergence is the effective binocular cue in the depth discrimination, then performance should not be affected if the absolute convergence angle is changed. Another variation of the Frisby stimuli was made to examine this hypothesis.

METHOD

Subjects

The 3 pigeons used were numbered 55, 57, and 59. Bird 55 had been used in Experiment 1.

Apparatus

The apparatus was the same as that used in Experiments 1 and 2.

Stimuli

The new stimulus set differed from that used for the SDT in three ways. First, the depth difference was reduced to 6 mm. Second, the density of the array was halved. Third, the elements of the array were displaced over the entire stimulus and no circular form was present. Thus the negative stimulus (S-) consisted of an array of random-sized triangles all lying in a single plane and at-

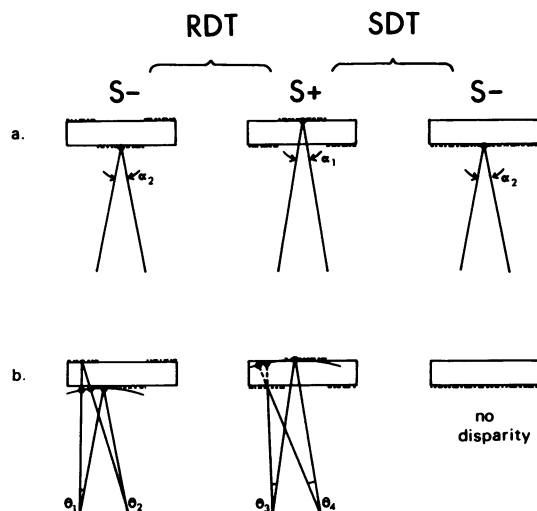


Fig. 7. Panel a: absolute convergence angle (α_1) could serve as a cue for the positive stimulus (S+) in both the standard depth task (SDT) and the relative depth task (RDT), provided fixation occurs near the center of the stimulus. Panel b: retinal disparity could also serve as a cue to depth. Fixation is shown as on the circle, thus making S+ a function of crossed disparity and S- a function of either uncrossed (RDT) or no disparity (SDT). Retinal disparity would also serve as a cue to depth if fixation occurred on the surround.

tached to the front face of a piece of optically clear glass 6 mm thick (Figure 8a). The positive stimulus (S+) consisted of an identical array but divided such that alternating triangles over the entire array were displaced onto the back of a second piece of optically clear glass 6 mm thick. The remaining half of the array was on the front face of this piece of glass (Figure 8b). The positive stimulus looked like two lacy planes separated in depth by 6 mm. These two stimuli served in the local depth discrimination.

Procedure

All pigeons were trained until they reached criterion, as described for Experiment 1. At the completion of criterion, one session was given in which both stimuli were presented back to front. Reversing the stimuli in this manner had a differential effect on the positive and negative stimuli. Reversing S- had the effect of transposing the triangle array onto the back rather than the front of the optically clear glass. The positive stimulus was unaffected and still contained two lacy planes separated in depth.

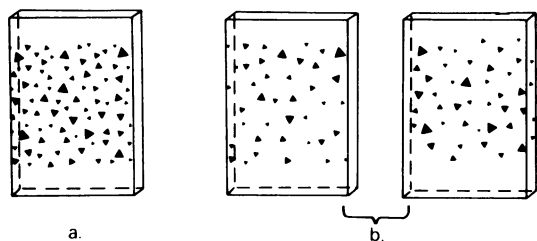


Fig. 8. Stimulus configurations for the local depth discrimination. Panel a: the negative stimulus (S-); Panel b: the front and back faces of S+.

RESULTS AND DISCUSSION

All pigeons learned the local depth discrimination despite the absence of a global shape displaced in depth. The numbers of sessions required to reach criterion (SN) were 22, 19, and 30 for Subjects 55, 57, and 59, respectively. The mean slope of the fitted regression line was 2.1 ($SD = 0.5$, $n = 3$) and the mean correlation coefficient was 0.88 ($SD = 0.02$, $n = 3$). We have subsequently trained additional birds on the local depth task and the mean SN was 22.6 ($SD = 3.3$, $n = 8$) (McFadden, 1984).

The local depth discrimination required a greater SN than did the SDT and was accompanied by lower values for the slope of the fitted regression line. The difference between the two tasks was too extreme to be attributable to seasonal variation. It would appear that the local depth discrimination was more difficult to learn than the standard depth discrimination. This could be due to the absence of a salient form produced by the displaced elements of the array, or to the reduction in the density of the elements.

All birds attained mean scores greater than 90% correct during the session in which the stimuli were reversed. Thus, changing the absolute convergence angle (or the egocentric distance of the fixation plane) in the negative stimulus did not affect discrimination performance. Figure 9 shows that the absolute angle of convergence, α_1 , cannot be the appropriate cue to distinguish S+. Although reversing the S+ did not change the stimulus (two random arrays of triangles still appeared in two planes), reversing S- effectively decreased the absolute convergence angle (Figure 9b). Yet performance was not perturbed by this change, indicating that in the local depth task the binocular cue to depth involves the difference be-

tween α_1 and α_2 . This is equivalent to the binocular disparity of a fixated point in one plane with respect to another point in the second plane.

GENERAL DISCUSSION

The pigeon's panoramic field of view is supplemented by a region of binocular overlap in the frontal field. The results of the present study suggest that this overlap mediates a functional binocular mechanism. It has been found that pigeons can easily discriminate between a three-dimensional object and black and white photographs of the same object (Cabe, 1976). In that discrimination, all primary cues to depth present in the real object are absent in the two-dimensional photograph. The present experiments show that the pigeon is capable of discriminating between a two- and a three-dimensional stimulus, or indeed between two depth stimuli that differ only in the direction of a displaced circle with respect to the background (relative depth task). The detection of depth was not dependent upon a displaced global configuration, such as the circle, but occurred when no form was present (local depth task). Thus, the birds appeared to be attending to local depth cues.

The Frisby depth stimuli contain strong binocular cues to depth. The rapid and almost linear rate of acquisition of the standard depth task is suggestive in itself than binocular cues contributed to the discrimination. When one eye was occluded, performance on the standard depth task was severely disrupted. This inability to reliably discriminate depth from nondepth under monocular conditions was not a reflection of some nonspecific effect of occlusion of one eye, as no comparable decrements in performance were seen on a pattern discrimination. The monocular deficit did not vary as a function of task difficulty, but was peculiar to the depth discrimination. Thus, the detection of depth in the Frisby stimuli was dependent upon binocular viewing conditions.

The traditional view of binocular depth perception describes the two primary cues as convergence and stereopsis (see Graham, 1965). In the human visual system, no study has conclusively shown that convergence acting alone (without accommodation or other monocular cues) is effective in predicting the

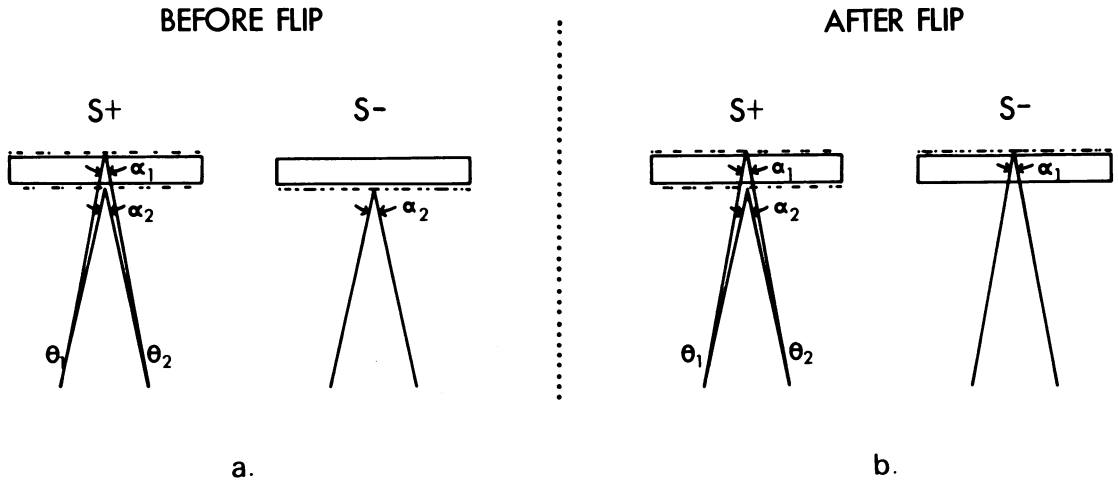


Fig. 9. Effects of changing the angle of convergence by inverting both stimuli that constitute the local depth discrimination. Panel a: Before the session in which the stimuli were reversed, it can be seen that in terms of absolute convergence angles, α_1 will predict S+. Panel b: After reversing both stimuli, it can be seen that α_1 will no longer predict the presence of S+, because the absolute angle of S- has been changed to α_1 . Inasmuch as subjects still respond to S+ appropriately, $\alpha_1 = S+$ cannot be the binocular cue. Thus, only the difference between the angles of convergence to the front and back faces of the depth stimulus ($\alpha_1 - \alpha_2 = \theta_2 - \theta_1$), which is the retinal disparity of the two planes in depth, can serve as a binocular cue in the local depth discrimination.

discrimination of depth between two objects. However, there is some evidence that limited changes in the absolute distance of an object may be detected by convergence alone (Foley, 1978; Gogel, 1961). In the animal world, it has been shown that both the toad (Collett, 1977) and the praying mantis (Rossel, 1983) are guided to the position of a prey object by the angle of convergence of the target. We have shown that in the Frisby depth test, the pigeon was insensitive to a change in the angle of convergence of one of the stimuli with respect to the bird. Rather, it was found that the binocular cue that consistently accounted for the behavior observed was the discrimination of a difference between the angles of convergence to some point in one plane with respect to another point in the second plane of the depth stimulus. Theoretically, this is equivalent to the detection of the horizontal retinal disparity between a fixated point or feature and some other point on the stimulus. It requires the matching of corresponding points or features in the images of each eye. The local elements of the array are triangles that vary in orientation and size. Thus, there is likely to be a unique set of local features that match in each image. This local matching process forms the basis of local stereopsis (see

Bishop, 1984). Local stereopsis is distinct from global stereopsis. The latter involves solving the ambiguity inherent in complex stimuli in which many false local matches of corresponding points may occur. Dynamic random dot stereograms provide an almost pure stimulus for global stereopsis (see Julesz, 1971). As yet, there exists no evidence that pigeons can decode the ambiguity of global stereopsis, and it is possible that their binocular system is limited to local stereopsis.

Local stereopsis would enable discrimination of the spatial position of an object with respect to the background, as in the detecting, locating, and pecking at grain. It is known that the terminal position of such pecking varies as a function of the location of the target (Zeigler et al., 1980). Precision and efficiency in pecking are reduced when the binocular component of the frontal field is removed either by occluding the frontal field of one eye (Martinoya et al., 1984) or by anatomically separating the two half brains (McFadden, 1984). In addition, the position of the binocular visual field is correlated with the position components of the peck response (McFadden & Reymond, in press). Taken together, the results show that the pigeon's discrimination of depth is based upon binocular cues. In partic-

ular, it is probable that the pigeon has a local stereoscopic mechanism for viewing near targets in the frontal binocular field.

REFERENCES

- Binggeli, R. L., & Paule, W. J. (1969). The pigeon retina: Quantitative aspects of the optic nerve and ganglion cell layer. *Journal of Comparative Neurology*, **137**, 1-18.
- Bishop, P. O. (1984). Binocular vision. In R. A. Moses (Ed.), *Alder's physiology of the eye, clinical application* (8th ed., pp. 575-649). St. Louis, MO: Mosby.
- Bloch, S., & Martinoya, C. (1982). Comparing frontal and lateral viewing in the pigeon: I. Tachistoscopic visual acuity as a function of distance. *Behavioural Brain Research*, **5**, 231-244.
- Blough, P. M. (1973). Visual acuity in the pigeon. II: Effects of target distance and retinal lesions. *Journal of the Experimental Analysis of Behavior*, **20**, 333-343.
- Cabe, P. A. (1976). Transfer of discrimination from solid objects to pictures by pigeons: A test of theoretical models of pictorial perception. *Perception and Psychophysics*, **19**, 545-550.
- Catania, A. C. (1964). On the visual acuity of the pigeon. *Journal of the Experimental Analysis of Behavior*, **7**, 361-366.
- Collett, T. (1977). Stereopsis in toads. *Nature*, **267**, 349-351.
- Cowey, A., Parkinson, A. M., & Warnick, L. (1975). Global stereopsis in rhesus monkeys. *Quarterly Journal of Experimental Psychology*, **27**, 93-109.
- Emmerton, J. (1983). Vision. In M. Abs (Ed.), *Physiology and behaviour of the pigeon* (pp. 245-266). London: Academic Press.
- Foley, J. M. (1978). Primary distance perception. In R. Held, H. W. Leibowitz, & H. L. Teuber (Eds.), *Handbook of sensory physiology: Vol. 8. Perception* (pp. 181-213). Berlin: Springer-Verlag.
- Galifret, Y. (1968). Les diverses aires fonctionelles de la rétine du pigeon. *Zeitschrift für Zellforschung und Mikroskopische Anatomie*, **86**, 535-545.
- Gogel, W. C. (1961). Convergence as a cue to absolute distance. *Journal of Psychology*, **52**, 287-301.
- Goodale, M. A. (1983). Visually guided pecking in the pigeon (*Columba livia*). *Brain, Behavior and Evolution*, **22**, 22-41.
- Graham, C. H. (1965). Visual space perception. In C. H. Graham (Ed.), *Vision and visual perception* (pp. 504-547). New York: Wiley.
- Hinchliffe, H. A. (1978). Clinical evaluation of stereopsis. *British Orthoptic Journal*, **35**, 46-57.
- Hodos, W., Leibowitz, R. W., & Bonbright, J. C., Jr. (1976). Near-field visual acuity of pigeons: Effects of head location and stimulus luminance. *Journal of the Experimental Analysis of Behavior*, **25**, 129-141.
- Julesz, B. (1971). *Foundations of cyclopean perception*. Chicago: University of Chicago Press.
- Martinoya, C., & Bloch, S. (1981). Depth perception in the pigeon: Looking for the participation of binocular cues. In E. Grastyán & P. Molnar (Eds.), *Advances in physiological sciences: Vol. 16. Sensory functions* (pp. 477-482). Oxford: Pergamon Press.
- Martinoya, C., Le Houezec, J., & Bloch, S. (1984). Pigeon's eyes converge during feeding: Evidence for frontal binocular fixation in a lateral-eyed bird. *Neuroscience Letters*, **45**, 335-339.
- Martinoya, C., Rey, J., & Bloch, S. (1981). Limits of the pigeon's binocular field and direction for best binocular viewing. *Vision Research*, **21**, 1197-1200.
- McFadden, S. A. (1984). *Depth perception in the pigeon*. Unpublished doctoral dissertation, Australian National University.
- McFadden, S. A., & Reymond, E. (in press). A further note on the binocular visual field of the pigeon. *Vision Research*.
- Millodot, M., & Blough, P. (1971). The refractive state of the pigeon eye. *Vision Research*, **11**, 1019-1022.
- Nye, P. W. (1973). On the functional differences between frontal and lateral visual fields of the pigeon. *Vision Research*, **13**, 559-574.
- Rossel, S. (1983). Binocular stereopsis in an insect. *Nature*, **302**, 821-822.
- Walls, G. L. (1967). *The vertebrate eye and its adaptive radiation*. New York: Hafner. (Original edition published 1942 by Cranbrook Institute of Science, Bloomfield Hills, MI)
- Yazulla, S. (1974). Intraretinal differentiation in the synaptic organization of the inner plexiform layer of the pigeon retina. *Journal of Comparative Neurology*, **153**, 309-323.
- Zeigler, H. P., Levitt, P. W., & Levine, R. R. (1980). Eating in the pigeon (*Columba livia*): Movement patterns, stereotypy, and stimulus control. *Journal of Comparative and Physiological Psychology*, **94**, 783-794.

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