ON THE VISUAL ACUITY OF THE PIGEON¹

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Several lines of evidence suggest that the pigeon is near-sighted for stimuli located in front of its beak and far-sighted for stimuli located to the sides of its head.

"The vision of the pigeon is of two types: for distant objects only one eye is used (monocular vision), while for grain or other close objects both eyes are used, looking forward (binocular vision)" (Levi, 1957, p. 378).

The effective use of an organism in behavioral research calls for a thorough understanding of its sensory systems. An examination of the pigeon's visual system, therefore, is prompted by the prominent role of visual stimuli in pigeon experiments (e.g., Ferster and Skinner, 1957). The present note reviews some literature on visual acuity in the pigeon, and attempts to characterize its visual system in a useful way. Several lines of evidence suggest that the pigeon's eye contains a hyperopic or far-sighted region, used in lateral or "panoramic" viewing, and a myopic or near-sighted region, used in anterior or "binocular-stereoscopic" viewing.

Evidence for a hyperopic lateral field. A large part of the evidence for a hyperopic lateral field in the eye of the pigeon comes from casual observation, as in Levi: "The pigeon breeder, no doubt, has many times seen his birds cock their heads to one side and view with alarm some object in the distant sky. Many times the object is beyond the vision of the fancier or is a hawk or some other bird in flight so far distant as to be barely seen" (Levi, 1957, p. 249). In fact, lateral viewing by the pigeon seems to have been as much taken

for granted by earlier investigators as anterior viewing is taken for granted by current investigators, who project stimuli on the response key at which the pigeon pecks. For example, lateral distance viewing is assumed rather than observed in this description: "When I observed the Pigeon as it squatted on the sill just in front of my window, about 40-50 feet above the ground, the eye facing me moved all the time, as probably also did the eye looking in the other direction toward the buildings opposite and the court below where people were moving about" (Polyak, 1957, p. 946). In some experiments, the assumption of distance viewing is stated in a fairly explicit way: "It was deemed necessary to have the fields removed from the point of choice sufficient to insure approximate distance accommodation" (Gundlach, 1933, p. 327), whereas the assumption of lateral viewing is implicit, if indicated at all. Accommodation for focus on the fovea, the effective region of the retina in lateral viewing, is implicit in Gundlach, Chard and Skahen's (1945) discussion of the mechanism of accommodation in the pigeon.

The available data on visual acuity in the pigeon come from experiments that probably involved only lateral distance viewing, and provide strong support for a hyperopic lateral field. Hamilton and Goldstein (1933) and Chard (1939), both using jumping stands, are in good agreement: "The near point of accommodation is between 31 and 66 cm." (Hamilton and Goldstein, 1933, p. 197); and, "... it seems likely that the near-point of accommodation has been approached or even passed at 40 cm." (Chard, 1939, p. 607). Hamilton and Goldstein supplemented their data with a skiascopic determination of the refraction of the eyes of their pigeons, which were between

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0.5 and 1.5 Diopters hyperopic. Chard showed that the decrease in the pigeon's visual acuity (minimum separable), when stimuli were brought closer than the near point, was rapid. More recently, Catania (1963a) found it impossible to establish discriminations of forms that were only 1 to 3 in. from the pigeon's eye, and concluded that "the pigeon cannot accommodate for lateral stimuli that are very close to its eye" (Catania, 1963a, p. 628).

Evidence for a myopic anterior field. One problem in the analysis of the pigeon's fields of view is the difficulty of seeing where the pigeon is looking. For example, Levine states: "... the experimenter was never able to detect by observation which eye the pigeon was using. The head movements were very rapid, and . . . [one] eye appeared to look at the stimuli as often as did the other" (Levine, 1945a, p. 123). Casual observation, in this case, provides conflicting evidence. An anterior myopic field has been noted by Levi, quoted above, by Chard and Gundlach, and by Polyak: "The pigeon undoubtedly possesses a visual field which affords binocular vision, although the bird appears to use monocular vision much of the time" (Chard and Gundlach, 1938, p. 256); "... it is evident from their behavior that they [pigeons] do possess a binocular field" (Chard and Gundlach, 1938, p. 271); "... the House Sparrow (*Passer domesticus*) and the Domestic Pigeon (*Columba livia*), with their laterally placed eyeballs, ordinarily use their eyes monocularly for observation. . . . In pecking grain or aiming at an angleworm just prior to seizing it, the final act that follows the critical examination, however, these birds use both eyes simultaneously in a binocular stereoscopic way" (Polyak, 1957, p. 946). Levine, on the other hand, would seem to rule out such a field: "When fixating an object, practically all birds, including the pigeon and chicken, do not look directly at it with both eyes but turn the head to one side. They thereby fixate the object with only one eye" (Levine, 1945a, p. 126).

The most convincing evidence for a myopic anterior field comes from the large body of operant research with the pigeon: stimuli projected on the response key at which the pigeon pecks are generally directly in front of its beak, and these stimuli have been shown to exert a powerful control over the pigeon's

key-pecking (e.g., Ferster and Skinner, 1957; Skinner, 1960).

The "visual trident." Casual observations of pigeons in operant experiments support the notion that the pigeon is laterally hyperopic and anteriorly myopic. Stimuli projected on the response key tend to exert more powerful control than stimuli located at some distance behind the key; on the other hand, nearby lateral stimuli do not seem to be as effective as more distant lateral stimuli (Catania, 1963a). As an example of the effectiveness of distant lateral stimuli, the author has obtained excellent discriminative control of the pigeon's pecking with a row of lamps, 5/8-in. apart center-to-center, projecting from the front of the panel and located 10 in. to one side of the pigeon's response key.

The general characteristics of the pigeon's visual system, inferred from the present account, are illustrated in Fig. 1. The two acute fields are shown for the pigeon's left eye: the anterior myopic field, for stimuli in the region of the beak, and the lateral hyperopic field, for stimuli located to one side of the head. The acute anterior and lateral regions are shown subtending a small visual angle, by analogy with the small visual angle of the central area of acute vision in the eye of man. It has been argued, however, that acute vision is characteristic of the pigeon's entire visual field: "One had here a good demonstration of the tremendous advantage of a wide field of view, as the Pigeon has. The same is true of other Vertebrates which have panoramic, or rather largely panoramic, vision, practically amounting to a complete circle. It permits them to see simultaneously most of the horizon and to see it with about the same high acuity as that possessed by Man, as other observations of the Pigeons and Sparrows indicate" (Polyak, 1957, p. 947). This sort of account seems to stem more from the fine grain of the peripheral retina of the bird eye than from behavioral evidence, as Walls suggests: "The proverbial resolving power of the bird eye is based partly upon . . . the dense concentration of the cones and the high ratio of optic nerve fibers to visual cells" (Walls, 1942, p. 661).

In any case, the main point of Fig. 1 is that the pigeon's visual field includes both myopic and hyperopic regions, whatever the extent of these regions. It will be convenient to assume

Fig. 1. A highly schematic diagram of the visual fields of the pigeon. Angles are not drawn to scale. The two acute fields, arbitrarily shown subtending a small visual angle, are represented for the pigeon's left eye: the anterior myopic field, for stimuli in the region of the beak, and the lateral hyperopic field, for stimuli to one side of the head. These two fields are separated by a large but acute angle. The anterior myopic fields of the two eyes intersect in the region of the binocular overlap, at a locus presumably modifiable by either accommodation or eye movements. According to an oculist's measurement of a live pigeon (Chard and Gundlach, 1938), the region of binocular overlap is about 24°, or 12° beyond the midline for each eye, with maximal eye movements taken into account; the total field for each eye is a little more than 180°, and the blind region at the rear is therefore 18-20°. The hyperopic lateral fields of the two eyes form an angle of considerably less than 180°. The pecten and optic disk, temporal and ventral of the central fovea, have not been shown. It is unlikely that they are involved in vision in either the anterior or the lateral field (cf. Walls, 1942, p. 651).

also that these are regions of high acuity relative to the rest of the visual field, although no evidence is available on this point. The acuity of the anterior field, however, does not have to be very great to account for the accurate discrimination of stimuli in front of the beak, because stimuli close to the eye necessarily subtend a relatively large visual angle. The region need be only somewhat more finely grained than other parts of the retina.

The visual system represented in Fig. 1 agrees well with Polyak's general characterization of the visual system of birds: "The avian

visual apparatus represents a three-pronged mechanism with three visual axes—a common binocular axis directed forward and two monocular axes on the sides, the 'visual trident' of Rochon-Duvigneaud" (Polyak, 1957, p. 283).

Acuity, anatomy, and physiological optics. The validity of the present account depends in part on the structure of the pigeon's eye. Both its retina and its optical apparatus should be capable of resolving visual stimuli in the ways that have been discussed.

Polyak has commented on the diversity of the locally differentiated structures of bird's eyes: "Frequently two foveae are found in each eye: a central, nasal or anterior, and a lateral, temporal or posterior, area and fovea. . . . the two lateral foveae of both eyes apparently serve as an instrument in binocular stereoscopic vision, while the central foveae function independently" (Polyak, 1957, p. 283).² The pigeon, however, possesses only a single fovea in each eye, the central fovea (see Fig. 1). Probably the absence of a posterior fovea, to subserve acute vision in the binocular region, has been an important determinant of the assumption that the pigeon is a bird of predominantly "panoramic" rather than "binocular-stereoscopic" vision.

The absence of an anatomically distinct fovea does not rule out the possibility of a functionally distinct region on the pigeon's retina. Thus, it may be relevant that Chard and Gundlach, in discussing the diversity of the layers of the pigeon's retina, state: "One possible explanation of the diversity of these layers is the fact that the bird cannot move the eye in its socket a great deal for foveal vision. This might result in a structural differentiation of various parts so that some would, in part, take over some of the functions of the fovea" (Chard and Gundlach, 1938, p. 270). Walls has observed that: "The imperative need for accurate distance judgment . . . has lead to specializations of the temporal

²It should be noted that "lateral" has a different referent in "lateral field" than in "lateral fovea." A "lateral field" is lateral with respect to the pigeon's head; it is the field viewed by the central fovea. A "lateral fovea" is lateral with respect to the pigeon's eyeball; it is the fovea that views the anterior field. Confusion may be avoided by restricting the terms "lateral" and "anterior" to fields, and labelling the corresponding foveae "central" and "posterior," or "nasal" and "temporal."

part of the retina. Some of these are slight, like the 'red field' of the hen; but in many different groups of birds, independently of each other, a second fovea has been differentiated in the temporal quadrant" (Walls, 1942, p. 307). It also may be significant that, in those birds with two foveae, the posterior fovea is usually less well-differentiated from the rest of the retina than the central fovea: "Except in the eagles and in *Apus apus*, the temporal foveae are inferior in construction to the central ones" (Walls, 1942, p. 308); "... the grain of its photoreceptors [the posterior fovea of the barn swallow] also seems to be rougher than that in the central fovea" (Polyak, 1957, p. 856). These various observations call for a more detailed examination of the retina of the pigeon than is available at present.

The eyes of many birds provide certain advantages for anterior stimuli. In the barn swallow, for example, "... binocular convergence and fixation are [assisted by] ... the position of the corneae, which face, as in the half-profile, in the antero-lateral direction ... [and] a slight distortion of the corneal curvature similar to the 'anterior bulge' of the Fishes, because of which the more sharply curved anterior segment of the cornea is more favorable to the passage of rays coming from the direction of the beak" (Polyak, 1957, p. 853). The pigeon also possesses the former advantage, though it is not clear whether it possesses the latter. In any case, there appears to be no anatomical reason to reject the notion that the pigeon's optical apparatus is adequate for acute near vision in the binocular region.

A final suggestive property of the pigeon's optical system is its range of accommodation: "... the cornea itself provides a range of accommodation of something of the order of 17 Diopters. This is a very large figure when it is recalled that the maximal human range of accommodation is around 10 to 12 Diopters" (Gundlach, Chard and Skahen, 1945, p. 41). As mentioned above, the pigeon's eye is 0.5 to 1.5 Diopters hyperopic. Given this ametropic error and the 17 Diopter range of accommodation, the predicted near point of accommodation is about 6 cm (*cf.* Davson, 1963, p. 421), which is not in agreement with the experimentally-obtained near point of roughly 40 cm. The large range of accommodation, there-

fore, may indicate the involvement of an additional factor (in the eye of the turtle, for example, the 40-50 Diopter range of accommodation permits adequate refraction in both air and water). It may be that, in the eye of the pigeon, accommodation serves not only the central fovea but also, in binocular viewing, a differentiated region of the posterior retina.

Acuity and evolution. The conclusion that the pigeon is anteriorly near-sighted and laterally far-sighted is also supported by evolutionary considerations. The pigeon must be near-sighted if it is to see, directly in front of its beak, the food that it eats, whereas it must be far-sighted if it is to see, in the lateral "panoramic" field, the approach of predators from the distance. An organism with such a visual system might have a distinct competitive advantage. For this reason, the visual systems of other organisms with "panoramic" vision (*e.g.*, deer, rabbits) might be expected to have similar characteristics.

A related argument has been made to account for the correlation between frontality and predacity: "... the hunters tend toward frontality so as to have the best vision of the prey they are pursuing, while the hunted tend to retain laterality of eye position so as to be able to detect an enemy coming from any direction" (Walls, 1942, p. 290). Such an argument, however, deals with the evolution of different degrees of frontality in different species, rather than with the evolution of different fields within a given species.

Horizon-fixation may also have been important in the evolution of the lateral field, but it has usually been cited to account for the extended or "troughlike" areas or foveae, primarily found in open plain or water birds (Pumphrey, 1961).

Acuity and attention. It is generally assumed that looking behavior is controlled in part by the location of objects in the field relative to the location of the acute regions on the retina: "... the presence of more than one small area of distinct vision suggests alternative regions of accurate fixation. The most reasonable determinant of the use of one of these regions would appear to be the location of the object fixated in the visual field of the bird" (Levine, 1945b, p. 141); "We infer that the shift in locus of the stimuli forced the bird to shift from one retinal fixation point to another" (Levine, 1952, p. 25). The present anal-

ysis indicates that both position in the field and distance may determine the "distinctiveness" of visual cues to the pigeon (*e.g.*, Jones, 1954).

Experiments on attention in the pigeon indicate that the extent to which a pigeon attends to one or another part of a stimulus complex is controlled by the relative locations of the parts of the complex. Reynolds (1961), for example, presented a stimulus complex made up of forms and colors projected on the response key, and lamps located to one side of the key. After an analysis of the control of the pigeon's pecking by various parts of this complex, Reynolds suggested that "the effective stimulus was the difference in the effects of the high and low side-lamp intensities upon the form and color combinations as they appeared on the response key" (Reynolds, 1961, p. 208). This implies that the pigeon attended to a nearby anterior stimulus, such as the glare of the lamps on the key, in preference to a nearby lateral stimulus, the lamps themselves.

Experiments on matching-to-sample behavior in the pigeon (Skinner, 1950) provide another relevant example. In these experiments, a stimulus is presented on the center key of three response keys. A peck on this key turns on stimuli on both side keys, one of which matches the center key stimulus. A peck on the matching key is then reinforced. The initial peck on the center key guarantees that the pigeon attends to the stimulus on that key; the present account suggests that this attention involves, at least to some extent, a simple kind of stimulus clarification, in that the peck guarantees that the stimulus is in focus for the pigeon.

Acuity and interocular transfer. Levine (1945a, 1945b, 1952), in a series of experiments on interocular transfer in the pigeon, distinguishes between views in front of or below the bird's head: "'Anterostral' will be used hereafter to refer to the position of stimuli when they are lying in front of the bird, and the line of regard between the stimulus and the eye forms an acute angle with the ground or is parallel to the ground. 'Subrostral' will be used to refer to the position of stimuli when they are lying directly below the head of the bird, so that the line of regard is approximately perpendicular to the ground" (Levine, 1945b, p. 138). This distinction was based on

the finding that discriminations among subrostral stimuli transferred from one eye to the other, but discriminations among anterostral stimuli did not. Levine also was not able to demonstrate subrostral to anterostral transfer in a single eye. With different procedures, Catania (1963b) demonstrated complete interocular transfer. The present account may bear on Levine's findings.

Levine distinguished between anterostral and subrostral fields on the basis of the placement of stimuli in a modified Lashley jumping stand (*cf.* Halstead and Yacorzynski, 1938). This specification did not necessarily correspond to stimulated regions of the pigeon's retinae, determined by where the bird looked. Anterostral discriminations involved stimuli mounted vertically at the backs of the platforms to which the pigeons jumped, whereas subrostral discriminations involved stimuli mounted horizontally on the floors of the platforms. In most cases, the subrostral stimuli "were much closer to the eyes of the bird [and] . . . extended to a position directly below the bird's eyes" (Levine, 1945b, p. 136). This suggests that the pigeon viewed the anterostral stimuli laterally and the subrostral stimuli anteriorly. Thus, the difference in distance could have made generalization between anterostral and subrostral stimuli in a given eye less likely, even without taking into account a possible difference in the grain of the two retinal regions. Also, some loss in transfer may have depended on time the pigeon spent in learning to fixate stimuli in their new locations in a test for transfer.

The present analysis also may account for the more complex case, in which subrostral discriminations transferred completely from one eye to the other but anterostral discriminations did not. To respond appropriately to the distant anterostral stimuli in the jumping stand, the pigeon had to cock its head to one side, however briefly, at the time of jumping, to land on the "safe" platform (if the pigeon jumped to the incorrect stimulus, on the other platform, the platform collapsed, dropping the pigeon into a net). Thus, the pigeon learned to look and jump with a particular head and body orientation. When the blindfold was shifted from one eye to the other, in a test for transfer, the pigeon probably cocked its head to the usual side, at least for the first few trials, before learning to look and jump

with the new eye. This might have confounded the test for transfer. With the subrostral stimuli, however, the pigeon probably looked at the stimuli, which were close by on the floor of the platforms, anteriorly and so binocularly. Consequently, it could look and jump with the same head and body orientation with either eye. Under these circumstances, the shift of the blindfold from one eye to the other could not have interfered with the test for transfer.

These interpretations may not account fully for Levine's findings, which were supplemented by a variety of control experiments. Nevertheless, the analysis suggests that the anterior-lateral distinction is more relevant to the proper interpretation of these experiments than the anterostral-subrostral distinction. Perhaps the results were determined more by the pigeon's looking behavior than by peculiarities of the hookups in its brain. It is interesting to note that, if the pigeon possessed two foveae in each eye, Levine's dichotomy between anterostral and subrostral fields would more likely have been a distinction between the anterior and lateral fields.

Conclusion. The present account has a practical bearing on ways to arrange apparatus for presenting visual stimuli to pigeons. Because the pigeon seems to be anteriorly near-sighted and laterally far-sighted, anterior stimuli should be located directly on the response key or, if behind it, not far from the pecking surface. Lateral stimuli, on the other hand, should be placed at a fair distance to one side of the key. The latter case provides some advantages over the usual presentation of stimuli on the key. For example, an effective stimulus continuum can be arranged simply by mounting a row of lamps to one side of the key. Other kinds of displays can be arranged laterally without the miniaturization, and its related optical problems, forced by the small area of the standard key.

These practical considerations drawn from the present account point up the importance of understanding an organism's sensory systems. Such an understanding depends on a knowledge of both the behavior of an organism and its anatomy and physiology, and may be crucial in an experiment at any point from the design of its apparatus to the interpretation of its results.

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