Bird Orientation: A Method of Study

Abstract. *A psychophysical technique has been applied to the study of bird orientation. The technique enables precise determinations of the accuracy with which a bird can orient itself. Data indicate that a pigeon can detect angular displacement as little as 3.4 degrees.*

Some of the mechanisms hypothesized to explain the homing behavior of birds would require a bird to make rather precise measurements of (i) the position of Sun or of other celestial bodies (that is, altitude and azimuth), (ii) the movement of Sun (for example, rate of change of altitude or azimuth, or both), and (iii) intervals of time (*1*). These problems have been studied (*2*), but the precision with which birds can make these measurements, and the role that each of these parameters plays in bird orientation, have not been satisfactorily determined.

As a first step toward answering of these questions, the accuracy with which a bird can orient itself, using only Sun (or another celestial body) as a reference point, needs to be determined. Once this is done, the extent to which each of the above parameters is used for orientation can be investigated by manipulation of each parameter independently and evaluation of the effect, if any, on the orientation of the bird.

I have begun to use a psychophysical method that may provide answers to some of these questions; it is a modification of one first used by Blough (*3*) to determine visual thresholds of birds. Now I am using the technique for investigation of the accuracy with which pigeons can orient themselves using an artificial sun as the only reference point.

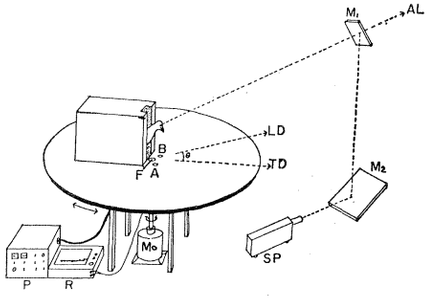

Fig. 1. Diagrammatic representation of the experimental arrangement: *A* and *B*, response keys; *F*, food-reward cup; *LD*, direction of the light; *TD*, training direction; θ, angle between training and light directions; *SP*, slide projector; M_1 and M_2, mirrors; *AL*, apparent light; *P*, programmer; *R*, position recorder; *Mo*, motor. Mirror M_1 can be moved manually, vertically or horizontally, around the platform; M_2, horizontally.

A pigeon is placed in a small box having an opening through which the bird places its head to gain access to two pecking keys and the food-reward cup (Fig. 1). The box sits on a rotatable platform. The entire apparatus is in a circular enclosure 4.6 m in diameter, with the light from a 500-watt slide projector serving as the artificial sun. The light is projected directly onto the bird through two movable mirrors so that the position of the light can be changed manually. The visual angle subtended by the light is about 0.5 degree, approximating Sun. An arbitrary direction, at a fixed horizontal angle from the direction of the light, is used as the training direction. (Since in this instance I was interested only in the ability of the bird to orient with reference to a light, and not in ability to compensate for daily or seasonal movement of Sun, I used a stationary light, making no attempt to simulate the movement of Sun.)

The bird is trained to peck key-B if it is oriented in any direction counterclockwise from the training direction (reinforced by a displacement to the exact training direction); key-A if it is oriented in the training direction (reinforced by food). A peck on key-A rotates the bird through a small angle (0.25 to 1.0 deg) away from the training direction, and a peck on key-B rotates the bird toward the training direction.

Since the bird pecks key-A whenever it cannot distinguish its position from the training direction and key-B whenever it detects that it is not oriented in the training direction, it oscillates about the minimum detectable angular displacement from the training direction.

At the end of a random interval, pecks on key-B not only rotate the bird but also accumulate to a randomly determined total number of pecks (between one and ten). When this total is reached, the bird is automatically rotated to exactly the training direction, where a randomly determined number of pecks on key-A is then required for food reward. During these pecks on key-A, the table is not rotated. While the bird is feeding, the table is automatically returned to its last position before it was rotated to the training direction.

Operation of the apparatus is fully automatic. The table position is recorded by a Bausch and Lomb V.O.M-5 laboratory recorder through a linear potentiometer connected to the table.

Training of two pigeons in pilot work during the fall of 1967 indicated that they could learn the task quite rapidly (1 hour daily for 10 to 15 days). Data collected from a well-trained pigeon show that the average minimum angular displacement it can detect is 3.4 deg, with a standard deviation of 0.5 deg (Table 1).

Figure 2 shows an example of the data: the bird began at 10 deg and soon moved to within 4 deg of the training direction; about 20 minutes after training began, the light was manually moved 14.5 deg counterclockwise, and the bird adjusted its orientation accordingly; the light was then returned to its original position, and the bird again readjusted.

The same technique can be used for investigation of pigeons' (and other birds') ability to detect and use for orientation the other above-mentioned parameters of Sun. For example, pecks may be used for controlling the position

Table 1. The performance of pigeon No. 6 on 7 different days of training. $\bar{X}$ and *sx* are means and standard deviations of the oscillations, about the minimum angular displacement from the training direction, that the pigeon can detect.

Trial (No.)	Degrees	
	$\bar{X}$	*sx*
1	3.7	0.9
2	3.5	1.1
3	2.8	1.0
4	4.0	0.9
5	3.7	1.1
6	3.1	1.0
7	2.8	1.0

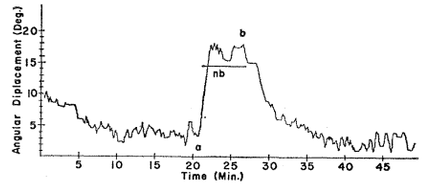

Fig. 2. Performance of bird No. 6 on 9 May 1968. The bird was initially placed at 10 deg. At point *a*, the light was moved 14.5 deg counterclockwise; *nb*, the new base line after movement of the light. At *b*, the light was returned to the original position.

of the artificial sun rather than the bird's position. The technique will be particularly useful for evaluating the bird's ability to compensate the daily and annual variations of Sun's movement, and in investigation of the accuracy of the bird's internal clock. Similar measurements are possible while the bird is in flight in a wind tunnel.

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References and Notes

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Rhodopsin Photoproducts: Effects on Electroretinogram Sensitivity in Isolated Perfused Rat Retina

Abstract. *Isolated perfused retinas of albino rats were exposed to brief saturating flashes of white light which bleached about 50 percent of the rhodopsin present. Transient photoproducts of the reaction could be detected for about 30 minutes. The b-wave threshold increased by some 3 logarithmic units immediately after the flash and remained stable at this level thereafter. This suggests that the longer-lived intermediate products of rhodopsin photolysis do not influence scotopic visual sensitivity.*

It is now well established from studies on the rat retina, which contains primarily rods (*1*), and cone-deficient retinas of humans (*2*) that the logarithm of the scotopic visual sensitivity is linearly related to the concentration of rhodopsin in the rods. In the isolated perfused retina of the frog—which contains both rods and cones—a similar result has been found under conditions in which electroretinogram b-wave thresholds are determined by the rod system alone (*3*). However, these studies were carried out under steady-state conditions, in which presumably only intact rhodopsin or free retinal (retinaldehyde) and opsin were present in the rods.

After a rhodopsin molecule absorbs a photon, it passes through a series of short-lived intermediate states before the carotenoid chromophore hydrolyzes from the opsin (*4–6*). Whether some or all of these photoproducts affect visual sensitivity is not clear. Recently, Donner and Reuter (*7*) have observed that the rate of thermal decay of one photoproduct, metarhodopsin II, parallels an early increase in the sensitivity of ganglion cells in the frog eye cup during dark-adaptation. These authors have suggested, therefore, that the concentration of metarhodopsin II may determine thresholds in the initial stage of rod adaptation.

To investigate directly such possible relationships, we have examined the effects of brief intense light flashes on the isolated retina of the albino rat. Retinas were mounted in a perfusion chamber inside a recording spectrophotometer, making it possible to measure both electroretinogram (ERG) thresholds and rhodopsin absorption spectra in rapid sequence with the same preparation. A previous report (*8*) describes the preparation in detail and shows that the rapid, "neural" phase of dark-adaptation occurs in the viable, isolated rat retina, but that slow, "photochemical" adaptation does not occur because rhodopsin does not regenerate under such conditions in vitro. Thus, after a partial bleach, the absolute sensitivity of the preparation is permanently decreased in proportion to the amount of rhodopsin bleached. There is a linear relation between rhodopsin concentration and the logarithm of ERG sensitivity in the isolated perfused rat retina, similar to the relation between rhodopsin and ERG sensitivity that exists in the intact rat eye (*1, 8*).

We exposed isolated perfused rat retinas to flashes from a xenon phototube (Ultrablitz Meteor SP-GH). This procedure bleaches about 50 percent of the rhodopsin in the retina (*9–11*), leaving it initially in the form of transient photoproducts whose decay we could measure for comparison with b-wave thresholds determined on the same preparation. Since no rhodopsin regenerates in the isolated rat retina under these conditions (*8*), any changes in sensitivity that occur after the neural component of adaptation is completed may be attributed to the decay of photoproducts.

In a typical experiment, threshold b-wave responses (20 μv criterion) and absorption spectra were first recorded from the dark-adapted preparation. After these base-line measurements were made, the retina was exposed to a single white flash from the xenon flash gun. Immediately thereafter, absorption spectra and b-wave thresholds were recorded in alternate succession until no further changes were observed. The retina was then exposed for 10 minutes to a bright white light from a tungsten source, which bleached nearly all the remaining rhodopsin. After this bleach, measurements of threshold and absorption spectra were continued for about 20 minutes.

Figure 1 shows the absorption curves for one experiment. Beginning 45 seconds after the flash, there is a sharp decrease in absorption above 430 nm and an increase in absorption at lower wavelengths. Five minutes after the flash, absorption decreases in the near-ultraviolet, maximally at about 380 nm, and there is a significant increase at longer wavelengths, maximal in the vicinity of 465 to 475 nm. Later there are progressive decreases in absorption at all wavelengths below about 550 nm. This fading continues for about 30 to 50 minutes, after which the tracings stabilize. After the final prolonged bleach, the spectra remain stable for at least 20 minutes, from about 420 to 650 nm. Below 420 nm, sequential spectra often reveal a slight decrease in absorption. This probably represents free retinal being reduced to retinol (vitamin A_1).

The difference spectra of the transient dark processes occurring after a flash (Fig. 1, inset) were obtained by subtracting the stabilized tracings recorded 40 to 60 minutes after the flash (curves 9 to 11) from the tracings recorded 45 seconds after the flash (curve 3), when the near-ultraviolet absorption was maximum, and the curve beginning 5 minutes after the flash (curve 4), when the longer wavelength absorption reached its peak. These spectra reveal the existence of two photoproducts, one absorbing maximally at about 380 nm and the other at about 470 nm. These probably correspond to metarhodopsin II and a later intermediate with maximum absorption, as determined in digi-