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THE SENSORY PHYSIOLOGY OF ANIMAL ORIENTATION*

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I. INTRODUCTION

A number of animals maintain orientation with respect to their surroundings under conditions where it has been difficult to understand what sort of information from the animals' environment is employed, or what sensory "window" conveys such information into the central nervous system. In some cases we remain ignorant about both aspects of the matter. Because of the surprises that have resulted from discoveries about animal orientation, this field has become a significant area of comparative neurobiology. Again and again it has turned out that the previous thinking of scientists had been constrained by what might figuratively be called "simplicity filters." Puzzling phenomena have tended to be neglected in efforts to restrict scientific consideration to relatively simple explanations. When certain of these have eventually been studied with adequate methods, the animals have turned out to be doing things that had scarcely been thinkable. The theoretical framework previously taken for granted has then required modification. Simplicity filters are an important part of scientific thinking, inasmuch as it is impracticable to bear constantly in mind all conceivable complexities. But their use involves the danger that they will cause us to rule out in advance hypotheses that may in fact be correct.

Another limitation of perspective results from an understandable concentration on problems and phenomena of importance in our own bodies, or those of a few convenient animal surrogates such as cats or rats. But when an experimental biologist limits his thinking in this way he misses a great deal of significant interest. Furthermore, as stressed by many physiologists from August Krogh to T. H. Bullock, important advances have come from the strategic use of species in which a particu-

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lar function is especially well developed or for other reasons especially accessible for investigation (Krebs, 1975).

This paper will concentrate on five examples of orientation behavior the investigation of which has revealed unexpected sensory processes. They have been chosen largely because enough is known to permit a fairly complete discussion in physiological terms. Many other examples could serve the same purpose, and full explanations are by no means complete in these five cases. It is encouraging to realize that so much has been learned since I prepared a comparable review in the early 1950s (Griffin, 1953).

II. NEW SENSORY WINDOWS

Not many years ago it was generally believed that fish do not hear, and that aquatic animals are silent. Today it is difficult to understand how such an ill-informed belief could have lingered well into the 1950s. For example, in the 1920s and early 1930s von Frisch and his students had conducted a meticulous series of experiments demonstrating excellent hearing in several species of fish (reviewed by von Frisch, 1936). By modern standards, the transducers available at this time were crude and uncalibrated, but the experiments were so thorough that sensitivity to a broad frequency range could scarcely be doubted. Furthermore, comparative anatomists had described in detail the elaborate morphological specializations of the Weberian apparatus that mechanically links the inner ear labyrinth to the swim bladder in fishes of the order Ostariophysi (including catfish, carp, and the common goldfish). This reluctance to recognize a well documented fact of comparative physiology exemplifies the effectiveness of simplicity filters, especially when they are combined with an "anthropocentric" bias that tends to underrate the scientific significance of any structure or function not clearly related to human physiology (Griffin, 1955; Popper and Fay, 1973; Fay and Popper, 1975; Tavolga, 1976).

Not only fishes but marine mammals have excellent hearing, and their cochleas are efficiently coupled to water rather than to air. Both dominant groups of aquatic vertebrates are also well equipped with apparatus for generating sounds, and these are sometimes used for communication over long distances. Underwater hearing is also an es-

sential component of a highly specialized type of orientation behavior discussed below in Section V.

In a somewhat parallel fashion comparative sensory physiologists have found that insects and certain other animals can see the plane of polarization of light, although for a long time this capability was not recognized or considered to be a serious possibility (von Frisch, 1967). It is thus important to keep an open mind concerning the sensory channels available to animals, without of course jumping to the conclusion that all forms of energy are detectable by animals even though we can think of uses that they might make of such information if they could perceive it.

III. INFRARED DETECTION BY SNAKES

Behavioral studies of the detection of prey by two groups of snakes, the pit vipers (Crotalidae) and the boas (Boidae), indicated that thermal radiation from a warmblooded animal such as a mouse was at least one source of information guiding the striking motion of the snake (Noble and Schmidt, 1937). Snakes can aim accurately at warm targets under conditions where vision is impossible, but not at those having the same temperature as the surroundings. Experimental impairment of the facial pits of the pit vipers and smaller depressions above the lips of the boas suggested that the heat receptors were located in these structures, even though only simple undifferentiated nerve endings were present.

Careful experiments by Bullock and Diecke (1956) showed that long-wavelength infrared radiation would indeed excite these nerve endings in pit vipers, and further anatomical and physiological studies by Bullock and Fox (1957), Bullock and Barrett (1968), and others have added substantially to our understanding of a specialized radiation detecting system. The whole subject has been recently reviewed by Barrett *et al.* (1970) and Hartline (1974). Hartline's experiments have shown that directional localization is possible with an accuracy on the order of 10° even though the pit itself is only crudely directional and admits radiation over a cone of approximately 75° - 90° . Thus even so simple a structure as this biological radiometer involves integration of sensory information in the central nervous system to improve significantly upon the directional capabilities of the peripheral sense organs.

IV. ELECTRORECEPTION

Charles Darwin remained seriously perplexed by a few attributes of animals that seemed to defy a reasonable explanation in evolutionary terms. Among these were the electric organs of fish, such as the electric eel, which as far as was then known served only as weapons. Large electric organs can administer severe shocks to predators or prey, but Darwin was at a loss to understand how such an elaborate organ could have evolved through intermediate stages, because it seemed that a weak electric organ would have no survival value at all. Nor were weak electric organs merely hypothetical stages postulated in the evolutionary history of electric eels. Several species of fish were discovered with small electric organs capable of producing only feeble discharges. Modern measurements have shown that many of these fishes produce only a few millivolts when their electric organs discharge maximally. Even the inspired imagination of Charles Darwin could not find a plausible function for such trivial discharges.

This paradox was solved by Hans Lissmann (1958), who demonstrated that weakly electric fish could detect objects in their immediate vicinity by sensing changes in the electric fields produced by their own electric organs. Most of these fish are nocturnal and many live in turbid waters where vision is of limited usefulness, but electroreception suffices for finding their way about and for avoiding obstacles. It probably also helps them to locate appropriate cavities for shelter during the day. Receptors of the lateral-line system allow these fish to detect voltage gradients at least as small as $0.1 \mu\text{V}/\text{cm}$. The sensory and neurophysiology of electroreception have been intensively studied since Lissmann's original discovery, and the resulting knowledge of this unanticipated sensory window has been thoroughly reviewed by Bennett (1971), Bullock (1973), Fessard (1974), and Heiligenberg (1975, 1976).

Not only can sensory neurons of the lateral-line system respond to artificially applied electric fields, their activity is coordinated with the nervous control of electric organ discharges and the patterns of afferent impulses show clear changes when objects of varying dielectric constant are moved in the vicinity of the fish. A greatly enlarged cerebellum is active in analyzing the patterns of afferent electrosensory input.

Further studies by Black-Cleworth (1970), Bell *et al.* (1974), Hop-

kins (1974), Russell *et al.* (1974), and Westby (1974a,b) have shown that weakly electric fish also use their electric organs for social communication. Relatively simple patterns of change in the electric organ discharge serve to signal aggressiveness, submission, and probably courtship. In certain species the frequency of electric organ discharge varies inversely with body length, so that frequency is an indication of the size of a conspecific individual. Females tend to have higher frequencies for a given size than males. Hopkins reported the intriguing observation, limited unfortunately to two cases, that mated pairs may have frequencies an octave apart.

Another unexpected development in the electrosensory world of fish was the discovery by Dijkgraaf (1968), Kalmijn (1971), and Peters and van Wijland (1974) that many fishes not equipped with electric organs of any kind nevertheless have electrical sensitivities equalling or even exceeding those of species specialized for electrical orientation. Sharks and rays, catfish, and other species have low enough electrical thresholds to detect electrical potentials from other aquatic animals, and certain sharks find their prey by this means. A smaller fish buried in the mud is located and seized even when it is invisible and not detectable by the chemical senses. This remarkable discovery was supported in part by experiments in which electrodes replaced the buried prey, and potentials simulating those of a live fish of appropriate size would consistently elicit attack behavior from a hungry shark. Many species of fish can also detect a variety of naturally occurring electric fields of both animate and inanimate origin (Peters and Bretschneider, 1972; Kalmijn, 1974, and Akoev *et al.*, 1976).

One important physiological feature of electroreceptor systems in many fishes are elongated canals having walls with high electrical resistance and interior lumens filled with jellylike material of low resistance. Such structures serve to concentrate the environmental gradient of electrical potential across relatively thin membranes where electrosensitive cells are located. This anatomical device produces local potential gradients that greatly exceed the overall environmental gradient, and this seems to account in large measure for the remarkably low thresholds measured from some species (in extreme cases as low as $0.01 \mu\text{V}/\text{cm}$).

The information available to Darwin thus involved only the tip of the

proverbial iceberg. In the final section of this paper I will return briefly to the subject of electrical sensitivity in fishes because it throws significant light on another unsolved problem of animal navigation.

V. ECHOLOCATION

The ability of bats to orient their flight in darkness by emitting specialized sounds and locating objects through echoes of these orientation sounds has been one of the more thoroughly analyzed examples of animal orientation behavior that falls into the general "eye-opening" category selected for discussion in this paper. The history of this problem has been reviewed by Griffin (1958), and it is merely appropriate to point out that in the 1790s Cuvier appealed to a sort of simplicity filter when he argued that bats must simply *feel* the proximity of obstacles, and on this basis dismissed the experiments of Jurine and Spallanzani in which bats were drastically disoriented when their ears were blocked.

The fact that most bats use orientation sounds lying above the frequency range of human hearing delayed the discovery of echolocation until twentieth century electronic apparatus became available. Even now many scientists feel that there is something suspect about experiments with sounds above roughly 20 kHz (see, for example, the discussion following Suga, 1973). Yet echolocation is not a behavior pattern limited to the bats or to ultrasonic frequencies. One of the two suborders of the Chiroptera, the Old World fruit bats, have large eyes and lack echolocation altogether, except for one genus (*Rousettus*), which has secondarily acquired this mode of perception. On the other hand, two genera of cave-dwelling birds (*Steatornis* and *Collocalia*) use echolocation to guide their flight into dark caves. *Rousettus*, *Steatornis*, and *Collocalia* all use clicks that are clearly audible to human ears. Aside from the bats of the suborder Microchiroptera, the most advanced development of echolocation occurs in the marine mammals, which of course use underwater sounds. While both orientation sounds and communication signals overlap with the frequency range of human hearing, many of them also have strong ultrasonic components extending to well above 100 kHz. Certain terrestrial mammals, especially the shrews, employ a limited form of echolocation (Buchler, 1976). Furthermore, as will be discussed in more detail below, it also occurs in our own species.

The orientation sounds of echolocating bats and cetaceans appear to be well adapted for this purpose, although the relative advantages of the different types are only beginning to be worked out. The marine mammals use very brief clicks containing only a few individual waves, which, as transients, generate a very broad band of frequencies approximating the entire range audible to the animals involved. Echolocating bats, on the other hand, usually employ signals that contain many sound waves with well defined frequency structure. By far the commonest pattern is a rapid downward frequency sweep, usually an octave or more within a single brief pulse containing roughly 10 to several hundred waves. In many cases there are two or more harmonically related components that sweep together. The recent experiments of Simmons and his colleagues (reviewed by Simmons *et al.*, 1975, and Simmons, 1977) have shown that these FM pulses are well adapted for determining the distance of a target through the time interval between its emission and its return to the bat's ears. Range discrimination capabilities and detection of faint signals in noise approach very close to the limits set by the mathematical theory of signal detection (Griffin *et al.*, 1963; Simmons, 1977).

The FM pulses also provide information about the nature of the echoing target through spectral differences in the echoes. Within the octave or more of frequency sweep a given target may return a varying fraction of the incident acoustic energy, and this pattern of echo spectrum seems to provide the bat with qualitative information about the nature of the target (Griffin *et al.*, 1965). Recent experiments by Simmons and others (1974) have confirmed, under more precisely controlled conditions, that bats are capable of distinguishing between echoes having very nearly the same overall intensity but different frequency spectra.

When bats are faced with difficult orientational problems, such as avoiding small obstacles, drinking by skimming a water surface, landing, or catching flying insects, the duration of the orientation sounds and the rate of frequency sweep vary widely. In extreme cases the frequency may remain almost constant for a substantial fraction of the pulse duration. Constant frequency components are apparently used for two general purposes: (1) to concentrate most of the emitted energy into a narrow frequency band and thus detect faint echoes with improved signal-to-noise ratio, including those from small or distant targets; (2) to

detect relative motion of the target through Doppler shifts in the echo frequency. The first type of echolocation is being found more and more frequently as detailed studies of the orientation sounds are carried out under a variety of natural conditions. The same species of bat may employ a wide range of signal patterns under different conditions. These may include very brief purely FM sweeps, such sweeping frequencies followed by a relatively long period of nearly constant frequency, or a number of intermediate patterns. The nearly constant frequencies tend to be used when flying relatively high above the ground and searching for insect prey.

Certain groups of bats have become highly specialized for echolocation that relies on precisely controlled constant-frequency signals, and these are often called for convenience the CF bats. The highly specialized CF bats include one large family found in warmer regions of Africa, Eurasia, and Australia (the Rhinolophidae) and a single species from one genus of neotropical bats (*Pteronotus parnellii*). The CF signals always contain at least a brief terminal portion with a downward frequency sweep, and the constant-frequency portion seems to be employed primarily when searching for insects. When active pursuit and interception are underway, the constant frequencies are reduced in duration and the FM sweep becomes more prominent. Simmons and his colleagues have recently demonstrated that the same bat may adjust the duration and other properties of its orientation sounds according to the specific problem presented by a given experimental situation, for example, range discrimination or detection of faint echoes partially masked by interfering noise (Simmons, 1977).

A. Neurophysiological Adaptations for Echolocation in Bats

For a considerable period after the convincing demonstration that echolocation was used by bats, the only available information concerning their hearing was the demonstration by Galambos (1942) that cochlear microphonics were measurable at frequencies up to about 100 kHz. The fact that orientation sounds well above the human range were emitted and utilized by bats provided strong general evidence that they could be heard. As might be expected from their heavy reliance on echolocation, the brains of insectivorous bats have a strong emphasis on the auditory system at the expense of other sensory systems. Grinnell

(1963) opened up the neurophysiological analysis of the auditory areas of bat brains, and his experiments have been followed by the substantial and increasingly detailed investigations of Suga, Henson, Neuweiler, Schnitzler, and others. Since most of these have been reviewed by Suga (1973) and by Simmons *et al.* (1975), no general summary of this extensive work is appropriate here. But it is important to consider the degree to which these experiments have disclosed auditory mechanisms that differ from those of other mammals in ways that adapt the nervous systems of bats for extracting useful information from echoes.

Initially it seemed that one important element in such specialization was a simple matter of frequency. Bats were the first animals definitely demonstrated to use frequencies well above the range of human hearing. But later investigations have clearly established that all small mammals share with bats the ability to hear at ultrasonic frequencies. While only a few of the many groups of mammals have been adequately studied, the available data support the rough generalization that the smaller the mammal, the higher the frequencies it can hear (von Bekesy, 1960; Sales and Pye, 1974). This approximate scaling of auditory frequency range to body size should not be taken as a rigid formula, at least until a wider range of species have been adequately studied. But it is clear that the smaller rodents have excellent sensitivity up to roughly 80 kHz and useful hearing extending above 100 kHz. The shrews and other small members of the order Insectivora are logical candidates for high-frequency sensitivity. Although they have not yet been studied with adequate methods, they may well prove to have ultrasonic sensitivity matching or even exceeding that of the smaller bats.

The simple question of frequency range of auditory sensitivity can be studied in two general ways, by behavioral experiments in which the animal is induced to give consistent responses to sounds of various frequencies and its auditory threshold determined at enough frequencies to plot the type of curve generally called an audiogram. Such experiments are tedious, and variability is often great. Spontaneous responses such as the Preyer pinna reflex suffer from rapid habituation, and such spontaneous behavioral responses usually begin only at levels well above the absolute threshold. Electrophysiological methods are appealing in that conditions can be controlled and much more reproducible results obtained. Cochlear microphonic potentials have been measured in great detail by E. G. Wever and his colleagues from a number of

animals including bats (Wever and Vernon, 1961). While these potentials arise at, or very close to, the hair cells of the basilar membrane, and hence appear to monitor the earliest processes in auditory response, they are ordinarily discernible only at levels considerably above the absolute threshold determined by behavioral experiments.

Since the orientation sounds and their echoes are brief stimuli lasting at most for several milliseconds, they excite nearly simultaneously large numbers of afferent neurons of the bat's VIIIth nerve. Grinnell (1963) found that even gross electrodes on the dorsal surface of the inferior colliculus pick up a series of positive potentials, the earliest of which have a latency of 1 msec or slightly less and hence must be the primary afferent input to the medullary nuclei of the auditory system. A bat, such as *Myotis lucifugus* under barbiturate anesthesia, yields prominent evoked potentials whenever the orientation sounds of other bats, or indeed almost any impulsive sound, impinges on the animal's ears. The dorsal surface of the inferior colliculus typically yields the lowest thresholds for such evoked potentials. Subsequent experiments by Suga have shown that the most prominent component is the synchronized firing of axons of the lateral lemniscus, so that this wave is now called LL. It is the fourth wave evident after arrival of a brief pulse of sound and is therefore also designated as N₄. Comparable recordings from small rodents give similar results and have provided a major portion of the evidence that they too can hear well at a broad range of ultrasonic frequencies.

Neurophysiologists are seldom satisfied with field potentials recorded by large electrodes, since they comprise an unknown mixture of axonal or synaptic responses. Microelectrodes recording from single cells are far preferable in providing specific information about the responses of one neuron at a time. Such recordings were first made by Grinnell (1963) and, later, more extensively, by Suga and his colleagues (reviewed by Suga, 1973). A relatively recent development, fraught with many difficulties but nevertheless yielding important results, has been the use of implanted electrodes capable of monitoring neurophysiological potentials in unanesthetized bats (Suga *et al.*, 1974).

An unexpected result of the measurement of many audiograms from bats and other small mammals has been the common, but not universal, tendency for the higher ultrasonic frequencies (above roughly 50 kHz) to show a second minimum. That is, the threshold in the vicinity of 55–60 kHz is often lower than at 20–40 kHz. Other evidence suggests

that this higher ultrasonic frequency range is differentially more sensitive to physiological factors that depress sensitivity in general, such as reduced body temperature or lowered oxygen tension (Harrison, 1965). This hints at a specialized mechanism more vulnerable than the responses to lower frequencies, but definitive evidence is not yet available.

Because downward FM sweeps are so prominent in the orientation sounds of bats, Suga has made a special effort to search for "feature detectors" in bat brains that might show selective sensitivity to signals of this type. FM-sensitive neurons have indeed been found, and Suga has explained the mechanism by which they operate. As in most other mammalian auditory systems, sounds over a certain range of frequencies and intensities have an excitatory effect on particular central neurons. When these data are plotted on a graph of auditory threshold versus frequency, these stimuli with excitatory properties fall into what can conveniently be described as an excitatory area. This is of course the area above the conventional threshold curve for the cell in question. By presenting stimuli in pairs, however, it can also be demonstrated an inhibitory effect of sounds falling in other areas on this graph of intensity versus frequency. Individual neurons in the midbrain and more anterior auditory areas show a wide variety of such excitatory and inhibitory response areas. In the inferior colliculus and auditory cortex of bats Suga found numerous units whose inhibitory areas were asymmetrical, with a larger inhibitory area lying at either higher or lower frequency than the minimum of the excitatory area. Such units are differentially responsive to sweeping frequencies. A stimulus is quite effective if it begins at a frequency that lies in the excitatory area, and only later enters an inhibitory area. But the reverse situation produces sufficient inhibition to eliminate any response to a similar stimulus sweeping in the opposite direction. Units with similar behavior have been recorded from cats and other non-echolocating mammals, and it is not clear whether their abundance in bats as described by Suga has resulted from a special effort to search for them or whether, on the other hand, an adaptation for echolocation is to have a relatively large proportion of central auditory neurons selectively sensitive to sweeping frequencies.

All the CF bats so far studied have a narrow frequency band of auditory sensitivity close, but not absolutely equal to, the constant frequency in the orientation sounds (Schnitzler, 1968, 1970; Pollak *et al.*,

1972). A large part (but probably not all) of their central auditory system seems to be concerned with this sharply tuned "window" (Suga and Jen, 1976). Under many conditions these bats control the emitted frequency with a precision on the order of 0.1%. When their attention is directed at a particular target, they adjust this emitted frequency so that its echo, which may be Doppler shifted owing to relative motion, falls in this narrow frequency band where their auditory sensitivity is maximum (Schuller and Suga, 1976a,b; Suga *et al.*, 1976; Schnitzler *et al.*, 1976; Bruns, 1976a,b).

Another type of auditory mechanism that appears to be at least quantitatively specialized as an adaptation for echolocation is what might be called transmit-receive switching. The auditory system of an echolocating animal, like a radar or sonar system, faces the problem of protecting its sensitive receiver from severe overloading during the emission of an intense probing signal. All mammals have small muscles attached to the middle ear ossicles which have a protective function in that their contraction reduces auditory sensitivity—at least to certain frequencies. These muscles are greatly hypertrophied in echolocating bats, being enormously larger relative to the size of the animal than in nonecholocating mammals. It was therefore reasonable to speculate that these muscles might serve as a transmit-receive switching system; but before direct evidence was available, this speculation faced the difficulty that very rapid recovery of sensitivity would be necessary so that echoes returning within a few milliseconds could be heard.

Henson (1965) provided such evidence by showing that in certain echolocating bats the middle ear muscles do reduce the sensitivity of hearing by an appreciable amount (on the order of 20–30 dB) and furthermore that they can also relax very rapidly, so that within a very few milliseconds full auditory sensitivity has been restored. Suga and Jen (1975) have recently shown that these muscles contract in approximate synchrony with the emission of orientation sounds, and there is little doubt that they function as transmit-receive switches. Contraction of the laryngeal muscles is appropriately coordinated (Jen and Suga, 1976).

Suga and Jen (1975) also analyzed an additional, central, mechanism which augments the transmit-receive switching function of the middle ear muscles. They found that the orientation sounds of FM bats are less effective in stimulating the auditory system central to the lateral lemnis-

cus if they are emitted by the bat itself than if they are played back from an appropriate tape recorder. Control stimuli consisting of tape-recorded orientation sounds from the same bat were adjusted to elicit approximately equal response as the bat's own vocalizations at the VIIIth nerve and the medullary auditory nuclei. But the tape-recorded signal produced a considerably larger response at the lateral lemniscus and more anterior auditory areas. If the intensity of the tape-recorded signal was adjusted to produce equal amplitude of response, or equal thresholds, at the lateral lemniscus, the tape-recorded signal had to be roughly 12 dB lower than the bat's emitted sound. These experiments demonstrate that some process of neural attenuation occurs in approximate synchrony with the emission of orientation sounds and that this renders the more anterior portions of the auditory system less sensitive to the emitted signal than otherwise would be the case. Suga and Jen concluded that the combined action of this process of neural attenuation and the middle ear muscles together achieve something on the order of 30–35 dB of reduction in auditory sensitivity at the time the orientation sounds are being generated.

While these transmit–receive switching mechanisms may well be especially prominent in echolocating animals, somewhat similar processes are apparently at work in other mammals including men. The human and feline middle ear muscles are also known to contract in at least approximate synchrony with vocalization, but no experimental evidence is yet available to indicate how closely their action resembles the situation in echolocating bats.

B. Human Echolocation

Echolocation may appear at this point to be an esoteric zoological specialization found only in animals remote from practical or human concerns. But in fact it has a direct relevance to one of the most distressing of human afflictions. It has long been known that blind persons have some residual ability to detect obstacles before colliding with them. Subjective, introspective reports from even the most skillful blind people strongly suggest that some tactile mechanism is involved. The blind say simply that they feel something is there before bumping into it, and hence the customary term for such obstacle detection is "facial vision." The history of investigation of nonvisual orientation by the

blind and by bats has followed a curiously parallel course, although the published record suggests very slight interaction between the scientists studying these two questions. But at about the same time when Pierce, Galambos, and I were able to demonstrate the existence of echolocation in bats, Supa, Cotzin, and Dallenbach (1944) carried out the first clearly definitive experiments showing that blind people also rely heavily on echolocation. Blind subjects or sighted subjects wearing tight blindfolds lost most of the ability to detect objects when their ears were tightly plugged. Furthermore the entire process could be carried out by means of a loudspeaker and microphone carried by one subject while a second person listened from a remote room to the sounds picked up by the microphone. Rice (1967) has shown that under favorable conditions the most proficient subjects can detect objects as small as quarter inch rods at a distance of roughly two meters, and can discriminate between objects located in different directions or having different acoustic reflectivities. Differential judgments of acoustic size or target strength are also possible with practice.

Despite the surprising capabilities of experienced subjects in laboratory experiments, human echolocation has obviously not been perfected to a level remotely approaching that achieved by bats. Since the brain of a typical insectivorous bat weighs approximately 1 g, and since 1500 g of human brain are proficient at analyzing complex such sounds as speech and music, it is appropriate to ask what explains this enormous gap in ability to obtain pertinent information from echoes. Since bats catch flying insects on the wing, it is not altogether outrageous to inquire why a blind man could not fly an airplane and catch birds.

There are several possibilities to explain this unfortunate performance gap. The use of ultrasonic frequencies by bats does not appear to be the crucial factor. A few species of bats and the two species of cave-dwelling birds achieve reasonably proficient echolocation using sounds that overlap the human frequency range (roughly from 6 to 15 kHz). Furthermore the most specialized echolocating bats can detect such small obstacles as fruit flies or wires 0.2 mm in diameter. If a simple scaling of wavelengths were all that separated the capabilities of bats and blind people, one might suppose that what a bat can do with 80 kHz a blind man should be able to do with a 10-fold larger object returning echoes of 8 kHz. Another less obvious advantage of ultrasonic frequencies will be mentioned below.

A potential limitation to human echolocation is suggested by many experiments on human hearing which demonstrate a temporary loss of sensitivity for a substantial fraction of a second after a loud sound impinges on the ear. This is usually called the temporary threshold shift (TTS), and can be quite large for many tens of milliseconds after the end of a moderately intense sound. This of course is the time period within which echoes important to a blind man return. (A convenient constant to bear in mind in this connection is that sound travels 34.4 cm/msec. Hence most objects close enough to a blind man to be of crucial importance for him to detect will return echoes within roughly 10–30 msec.)

The importance of this phenomenon of temporary threshold shift is easily demonstrated when a sharp click lasting only a few milliseconds is tape-recorded both in a typical indoor room and also out-of-doors or in an anechoic chamber where only weak echoes return to the microphone after the end of the click itself. If such tape recordings are played back in the normal fashion, they do not sound very different under the two conditions, except that the "indoor" click will sound louder. If the amplitudes are adjusted so that the perceived loudness is approximately equal, there are only very slight qualitative differences in the sound of the two recordings. If another simple experiment is now performed by reversing the direction of motion of the tape over the playback heads, a striking qualitative difference is immediately apparent. The click recorded out-of-doors is relatively little changed, but the indoor click now sounds like "shhhiCK." Part of this difference is probably due to the gradual onset of the reversed signal. But the hissing component preceding the major portion of the click consists of the complex of echoes which return to the original microphone after reflection from the walls, floor, and other objects in the room. It is this complex of echoes which contains information that would be extremely helpful to a blind man if his auditory system could put it to use.

One way to get around the difficulty of the temporary threshold shift would be to protect the ear of a person attempting to echolocate objects in his environment from the outgoing signals. This might be done by simple mechanical baffles, or conceivably in other ways. In some preliminary experiments I have used electronic switching to "dissect" the echo complex from the original signal. Since in a typical room the echo complex may last for 50 msec or more after an emitted signal of 10 msec duration, the isolated echoes sound more or less like the original, com-

bined sound. Much more extensive additional investigations will be necessary to examine whether, with practice, a human listener could extract helpful information from these echo complexes even when they are experimentally separated from the original, outgoing signals.

It seems quite likely that a major limitation to human echolocation is not so much that the echoes are inaudible as that they are masked by what students of sonar and radar call clutter. If a blind man is looking for a chair, he needs to obtain information about its location and to separate such information from that provided by echoes from the floor, ceiling, or other furniture not directly in his line or approach to the chair. The optimal conditions under which human echolocation has been analyzed involve test targets isolated from other echoing surfaces by 2 or 3 meters. This is of course a highly unnatural situation, far removed from the real world faced by the blind. Bats too face severe problems of clutter, especially those that catch insects in the midst of relatively dense forests. Much louder echoes must return from the vegetation, the ground, and all sorts of clutter other than the minute moving insect prey. The superiority of bat brains may lie in the realm of neurophysiological clutter rejection.

The atmosphere becomes increasingly murky or absorptive as frequencies increase through the higher parts of the human range and into the ultrasonic frequencies employed by bats. The reduction in sound due to its absorption and conversion to heat is completely negligible over a few meters at all but the highest frequencies audible to our ears. But under certain conditions of humidity, the higher frequencies used by some bats may suffer absorption at rates up to 10 dB per meter. Bats using such high frequencies can almost certainly detect nothing at all by echolocation at more than a few meters. Indeed even their emitted orientation sounds are often undetectable by the best available equipment when they are flying 10 meters overhead, although they become readily apparent if the same apparatus is carried to the treetops where the bats are flying. It may be that this acoustic murkiness of the air is a distinct advantage in overcoming the clutter problem, and that one serious limitation to human echolocation is that we are forced to use frequencies so well transmitted by the air that innumerable multiple echoes from all objects within many meters contribute to a hopeless clutter. Yet in typical indoor situations the recognition of speech, in-

cluding individual identification of the speaker, involves an impressive discrimination between important and unimportant components of a chaotic mixture of direct signal coming straight from the speaker and a complex of overlapping echoes from other surfaces nearby. It may be that our auditory system has become specialized for this type of fine analysis and that such specialization interferes with the discriminatory responses required for understanding what can be called, figuratively, the language of echoes.

Pursuing this speculative approach a little further, let us suppose tentatively that speech recognition and echo recognition are to some degree competing processes. It would then become relevant to inquire whether the neural mechanisms for such pattern recognition are inherently different in bat and human brains. Or are such patterns largely learned in childhood, as we learn to recognize speech? In this case appropriate experiments might disclose significant differences between young children and adults. Furthermore if such patterns are the result of individual experience and learning, it is not unthinkable that they could be modified in the case of blind persons to help them understand the language of echoes. Persons who are totally blind but otherwise in good health differ widely in their abilities at echolocation. But no one has succeeded in correlating these differences with other factors such as age at which vision was lost, type of subsequent experience, auditory skills of other sorts, such as musical ability or linguistic competence. Perhaps in this area of obvious human concern our progress has also been held back by simplicity filters that have hindered us from thinking adequately about the questions that most deserve to be asked.

VI. BIRD NAVIGATION

The challenging problems posed by the long-distance migrations and homing flights of birds are well known in a general way, almost too well known in some respects for balanced scientific appraisal. Many observations and experiments provide tantalizing but inconclusive evidence which has very recently been reviewed in detail in the proceedings of a symposium edited by Schmidt-Koenig (1977). Not only are major questions still unanswered, in certain important areas we do not even know what are the important questions to ask. The available evidence can

conveniently be classified into two interrelated categories, directional orientation and goal-directed homing.

A. Directional Orientation

1. Sun-Compass Orientation

For a long time it seemed unrealistic, and even foolishly speculative, to postulate that birds might compensate for the apparent motion of the sun across the skies and maintain a constant direction of flight by heading at a gradually changing angle to the sun's azimuth. But in the early 1950s Matthews and Kramer demonstrated experimentally that birds are quite capable of doing just this. These developments have been well reviewed by Matthews (1968), Schmidt-Koenig (1965), and Emlen (1975).

Kramer (1959) developed a type of apparatus that, with minor modifications, has been widely used for many significant experiments on the orientation of birds. This "orientation cage" is a cylindrical enclosure roughly 1 meter in diameter, screened by an opaque barrier to conceal local landmarks but allow the bird inside a clear view of the sky. The direction in which a small bird orients itself is recorded by visual observation, or by one of several types of automatic devices. Under suitably controlled conditions Kramer showed that when birds were in the physiological state appropriate for migration they would flutter back and forth as though attempting to go roughly north in spring or south in fall.

Having, so to speak, brought bird navigation under experimental control, Kramer was able to show that the sun was one important cue. If the bird's view of the sky was manipulated appropriately with plane mirrors, the direction of its attempted migratory flights was deflected more or less as would be expected. In order to obtain more extensive data under better-controlled conditions, Kramer soon turned from spontaneous migration to directional choices motivated by hunger. Starlings, homing pigeons, and other species of birds learned to seek food in a symmetrically constructed, cylindrical orientation cage by going to one of several identical feeders located at the periphery. The food could not be seen until the bird pushed its bill into the feeder, and for critical tests all the feeders were empty. By making everything as uniform as possi-

ble, and by randomly rotating the cage at frequent intervals, all cues except compass direction were eliminated. Provided the sun was visible the birds chose the correct direction with an accuracy of roughly $\pm 30^\circ$, regardless of the time of day and the resulting azimuth direction of the sun. In certain experiments the sun was replaced by an artificial light which remained in one position throughout the day, and the birds then changed their directional choices in a pattern that would have compensated for the normal motion of the sun across the sky. McDonald (1973, 1975) has shown that reactions to shadows may complicate such experiments.

Experiments of this type were then extended by resetting the endogenous biological clocks of the birds by keeping them for several days on a shifted light-dark cycle. The orientation of such clock-shifted birds was deflected in approximately the predicted fashion (Schmidt-Koenig, 1965).

2. *Star-Compass Orientation*

Most species of birds migrate at night, for reasons that we can only guess. Thus the sun is directly available only to diurnal migrants, which tend in general to be waterfowl and other relatively large birds. Although Kramer performed a few preliminary experiments under the night sky, it was Franz Sauer who perfected the technique of using orientation cages to study the reactions of migratory birds to the stars. He found, like Kramer, that seasonally appropriate orientation occurred under the natural sky, and he was able to demonstrate comparable orientation under the artificial light patterns of a planetarium. Similar experiments were later perfected by Emlen (1967) with the addition of important improvements and controls not feasible with the planetarium originally available to Sauer. The net result of these experiments has been to show that directional orientation by means of the stars is quite within the capabilities of migratory birds. In the northern hemisphere the area of sky within roughly 30° of Polaris seems to be of primary importance, although the limited data available suggest that no one star, including Polaris itself, is essential.

Emlen has also carried out ingenious developmental experiments indicating that, while young birds can orient to the stars with very limited prior experience, the genetic information with which they come to this problem is not a detailed star map. Instead, Emlen's birds paid attention

to the apparent rotation of the stars, and in fall they tended to orient in a direction roughly opposite from that part of the sky that did not rotate (Emlen, 1970, 1975).

3. *The Problem of Overcast Skies*

For a few years after the discovery of time-compensated sun-and star-compass orientation, it seemed that the problem of directional orientation was largely solved, and it was easy to overlook the fact that much migration occurs under cloudy skies. But radar observations disposed of this simplicity filter. Some of the earliest observations of extensive migration, with the airport surveillance radar at Zurich, suggested that birds were disoriented when flying below clouds and yet on the same night were migrating in appropriate directions above the overcast. But most later observations with many types of radar in several parts of the world showed that there was little correlation between the accuracy of migratory orientation and the presence or absence of opaque clouds (reviewed by Eastwood, 1967; Griffin, 1969; Emlen, 1975). By concentrating on nights with low clouds, I have observed that some migrants maintain accurate orientation even when flying in or between layers of opaque cloud (Griffin, 1973).

It is important to point out that the volume of nocturnal migration is strongly influenced by weather conditions. The majority of migrants fly on nights when the temperature has changed in the characteristic direction for the season, that is, has turned warmer in spring and colder in fall than the previous day or so. In many areas there is also a strong tendency for the more abundant and smaller birds to fly primarily downwind. In those areas where the most extensive radar data are available these two meteorological patterns tend to coincide, and as a result a considerable proportion of the smaller migrants are able to take advantage of tail winds. Nights with low cloud do not, in general, produce nearly as abundant migration, and usually there are many more birds above or below the clouds than in or between them.

When migrants fly below opaque layers of cloud they can probably see something of the surface of the earth even on moonless nights. But many migrants fly above clouds, over relatively homogeneous terrain, or over the open ocean, where it seems unlikely that sight of the ground or water would provide useful information concerning the direction appropriate for migratory flight.

4. *Other Potential Sources of Directional Information*

It is appropriate at this point to digress briefly to certain other sources of information that might be important to migratory birds even though none of them seems likely to provide as generally helpful guidance as the sun or stars.

Wind direction, while highly changeable over long periods of time or large distances, does tend to remain roughly constant at the altitudes where birds migrate during considerable fractions of any one day or night through the distances covered by most migrants. It has been suggested that a migration initiated on the basis of other information, such as the position of the sun, might be continued for several hours by orientation with respect to the wind. There is, however, a troublesome problem for the majority of migrants that fly at night and at altitudes of many hundreds of meters. If the entire air mass is moving uniformly, as is approximately the case under most conditions, no direct effect of the wind would be felt by a flying bird. Only with the aid of information from some outside source can a pilot, or presumably a migrating bird, determine whether he is flying upwind, crosswind, or downwind in a homogeneously moving air mass (Able, 1977).

There are, however, some second-order possibilities that might help a bird determine wind direction even when the ground provides no visible patterns that could be used to estimate wind drift. Sounds reaching a migrant from the surface might substitute for visible landmarks and provide indication of wind drift (D'Arms and Griffin, 1972; Griffin, 1976). The air itself may not in fact always move as a homogeneous mass. Especially near the surface, turbulence is known to involve a wide range of changing velocities which locally differ from, although in aggregate they add up to, the net motion of the wind. It used to be generally believed that atmospheric turbulence is isotropic and hence lacking any consistent patterns that might enable a flying bird to determine the net direction of the wind. But recent studies of micrometeorology have weakened this particular simplicity filter, and it now seems possible that under many conditions patterns of small-scale atmospheric flow might convey to a flying bird information about the net wind through which it is flying (Griffin, 1969; Lenschow, 1970; Hines, 1972; Hooke *et al.*, 1972).

A final possibility, which remains almost entirely at the level of attractive speculation, is that a group of birds might greatly improve the

accuracy of their orientation by communicating with one another and pooling whatever information they may have individually concerning the appropriate direction of flight. Some, but as far as we know not all, migrating birds emit characteristic flight calls. Radar observations strongly indicate that nocturnal migrants are aggregated, but not into tight flocks. Spacings of a few tens of meters between individuals seem to be the rule, with these groups separated by relatively large distances. Some reports suggest that flight calls are more abundant on nights with low clouds, but it remains to be ascertained whether this is because birds fly lower, and hence are more easily heard by observers on the ground, or whether those that are present emit more calls. My colleague Dr. Ronald Larkin has demonstrated through computer simulations that a hypothetical group of migrants individually provided only with very crude means of orientation could greatly reduce their errors and deviations from the appropriate direction by relatively simple communication strategies. But at present we lack the necessary data to judge whether migrants actually employ such strategies.

B. Goal-Directed Homing

Many birds return to an area where they have been captured even after artificial transportation to distances of hundreds of kilometers. While such homing behavior has been demonstrated in several species of wild birds, in only a few of these, and in the most proficient homing pigeons, do the percentage and speed of returns suffice to demonstrate approximately direct flights from release point to the home. Simple homing experiments of this type often fail to provide data adequate to distinguish between two possibilities: (1) relatively slow progress in approximately the correct homeward direction, with long pauses for rest or feeding, and (2) rapid and prolonged flights that deviate from the correct direction but eventually reach the home area by a process of random wandering or systematic exploration. The appeal of parsimony and related simplicity filters made the second explanation appealing at one time (Griffin, 1952). But improved experiments by Matthews (1968) and Kramer (1959) demonstrated that homing pigeons and at least one species of wild bird (the Manx shearwater) may head roughly toward home within the first few minutes after release. The best homing pigeons do this so consistently as to rule out any explanation based on wandering or exploration (reviewed by Keeton, 1974).

Thus a very challenging problem is posed by the ability of pigeons to select approximately the homeward direction when transported to an arbitrarily selected release point. In the best of such experiments there is adequate evidence that the release point is in unfamiliar territory, far from any point the bird has ever visited previously. The birds are transported in opaque containers providing no visual information concerning the route of transportation, and a variety of methods ranging from simple visual observation through binoculars, to following from aircraft, or tracking by means of miniature radio transmitters carried by the birds, have all shown that by one or a few minutes after release the best strains of homing pigeons select the homeward direction within $\pm 30^\circ$ - 45° .

For several years after consistent homeward initial headings had been demonstrated it seemed that clear skies were necessary, because in most (but not quite all) homing experiments when the sky was overcast the initial headings were randomly oriented. More recently, however, Keeton (1974) found that pigeons accustomed to fly on cloudy days also showed accurate homeward headings when the sky was completely overcast. Doubts concerning the possibility that the birds could detect the sun's position through the clouds were dispelled by experiments in which endogenous biological clocks of the pigeons were reset. Schmidt-Koenig (1965) had previously reported that birds with a 6-hour clock shift deviated approximately 90° in the expected direction. Keeton's pigeons showed this same result when released under clear skies after a 6-hour clock shift. But if the skies were overcast, clock-shifted birds did not differ significantly from untreated controls; both headed toward home with reasonable accuracy. This elegant experiment demonstrated at one stroke that goal-directed homing involved some other source of information than the position of the sun.

It is of course evident that no simple directional system of orientation, whether based on the sun or any other source of environmental information, can by itself account for homeward orientation after displacement in an arbitrarily chosen direction into unfamiliar territory. Gustav Kramer expressed this problem in terms of the need for the equivalent of a map as well as the equivalent of a compass. What has thus come to be called the "map component" of homeward orientation remains the central mystery of animal navigation.

One approach to the problem of goal-directed homing is to inquire whether birds capable of this impressive type of orientation acquire the

information on which it is based during transportation to the release point or only after release. A variety of experiments appear to provide an unequivocal answer in favor of the latter alternative by Walcott and Schmidt-Koenig (1973). But more recently, some experiments, though not all, have indicated that information obtained on the way to the release point may, after all, play a role in goal-directed homing (Schmidt-Koenig, 1977). Birds transported under deep anesthesia, or in containers subjected to irregular and complex mechanical oscillations, show just as accurate initial headings and as rapid homing flights as controls subjected to identical procedures before or after the actual outbound journey. Most of the information on which goal-directed homeward orientation seems to be based is obtained between the moment a bird is released from its opaque cage and the time when it has made its directional choice. In most experiments with the best homing pigeons this is on the order of a minute, or in some experiments as little as 10 or 15 seconds. In almost all cases a better than random homeward orientation is demonstrated within 5 minutes at the very most.

It would obviously be a large step forward if goal-directed homing could be elicited in some type of cage or under any other circumstances that would permit experimental control of the situation and the environmental cues available to the bird. But numerous attempts by almost every student of the problem to discover such a procedure have so far failed. No one has yet accomplished for goal-directed homing what Kramer achieved when he perfected his orientation cage.

C. The Question of Magnetic Sensitivity

It has been repeatedly suggested that birds and other animals that migrate over long distances might have some physiological equivalent of a magnetic compass. The earth's magnetic field is universally available over the surface of the earth, and it would obviously be of great advantage to animals if they could utilize its horizontal component as a basis for directional orientation.

Until the last few years the evidence in favor of sensitivity to the earth's magnetic field was limited to experiments that were difficult to replicate. The situation has now changed, and a considerable amount of positive evidence has been presented. Yet none of those who are convinced by this evidence would consider the present situation a satisfac-

tory one, for several gaps and difficulties are evident. We are thus faced with a perplexing situation in which a new sensory channel may be in process of being adequately demonstrated. I shall therefore attempt to present both the strong and weak points of the available evidence.

Frank Brown has reported many experiments which he interprets as evidence that a variety of animals can respond to a variety of geophysical energy fluxes that are not ordinarily considered within the range of sensitivity of physiological receptors. These include cosmic rays, atmospheric tides, and the earth's magnetic field. In reviewing this work, Brown (1971) emphasized experiments in which the directional choices made by planarians and marine snails showed *average* deviations of about 1° to 5° in their direction of locomotion correlated with experimental changes in the earth's magnetic field. As pointed out in the published discussion of this paper, the raw data consisted of estimates of the directions that were ordinarily recorded in units of about 5° or 10° . Since these effects are so small and require such massive application of statistical averaging, they have not been widely accepted as adequate to demonstrate that animals can actually orient with respect to the earth's magnetic field.

Somewhat larger effects have been reported by Southern (1971, 1975) with ring-billed gulls. In most of Southern's experiments young gulls are released in relatively large circular cages, and their directional choices are recorded in terms of the portion of the cage periphery to which they move. While there is considerable variability, the data show a consistent tendency to orient in an approximately southeasterly direction. This statistical tendency weakened during some but not all periods when the earth's magnetic field fluctuated by an unusual amount, that is, during magnetic storms, (Schmidt-Koenig, 1977). Similar variations in directional orientation were reported when gulls were transported to the vicinity of a very large low-frequency radio antenna which generated alternating electromagnetic fields approximating, at the location of the orientation cage, the magnitude of the earth's field but fluctuating at about 70 Hz. Radar tracking of migrating birds flying within a few hundred meters of this antenna also showed a tendency to turn more often when the antenna was turned on or was changing its level of emission than when it was turned off (Larkin and Sutherland, 1977).

Wiltschko (1968) and Wiltschko and Wiltschko (1975, 1976) have reported in a series of papers growing out of earlier reports by Merkel

and others at Frankfurt that, even without any opportunity to see the sun or stars, migratory birds in cages similar to the orientation cage originally developed by Kramer show approximately correct seasonal orientation when in the physiological state appropriate for migration. The orientation is much weaker, however, with very much more variability than in the experiments described by Sauer and Emlen, which have convincingly demonstrated star-compass orientations. In typical experiments of the type described by the Wiltschkos, the number of directional choices registered in each of eight radially symmetrical directions differs by only about 1 or 2% from the proportion expected by chance. Nevertheless, statistically significant trends emerge from the averaging of hundreds or thousands of responses, and these are biologically appropriate in the sense that migrants tend to orient toward the north in the spring and toward the south in the fall. Furthermore the Wiltschkos have reported that these average directional tendencies can be experimentally shifted by means of artificially applied magnetic fields in a manner consistent with a compasslike sensitivity to the earth's magnetic field.

The results of these experiments appear quite sensitive to minor details of the experimental arrangements. The cage that the Wiltschkos have found to be most effective is actually a doughnut-shaped enclosure approximately 1 meter in diameter with a central cylinder blocked off to form a ring-shaped cage in which the birds can move freely. Eight radial bars provide resting places, and touching or landing on these bars is electrically recorded by microswitches. On nights when the birds are in the physiological state that produces migration restlessness, they tend to hop or fly round and round this enclosure activating the radial perches to a varying degree, but commonly at rates of several hundred times during an 8-hour night. Wiltschko (1968) described these procedures in full detail and presented the raw data in tabular form. Summing the perch activations shows slightly more landings or touches in certain sectors than others, but the variability in number of perch activations by a given bird during a particular night is very great. Only occasionally are the data from one bird averaged over one night significantly different from random. But when data from several bird nights are combined, statistically significant departures from randomness do emerge, and they appear consistently different according to the season, roughly north in the spring and south in the autumn.

The Wiltschkos ordinarily present their data in terms of radial graphs in which each point represents the weighted average direction from a

single bird night. While many of these individual points do not in themselves represent statistically significant departures from a random circular distribution, a significant trend emerges when a number of such points are plotted for a given set of conditions. Such trends show appropriate seasonal differences and appear to be altered by artificially applied magnetic fields. It should be emphasized that large numbers of experiments of this general type have been reported by the Wiltschkos and that similar results have been obtained by other investigators (Wallraff, 1972; Emlen, 1975).

Procedural details of these experiments have caused some concern. The doughnut-shaped cages are constructed with their parts as uniform as practicable, but it is known that birds are sensitive to small local differences in such cages. The cage is therefore rotated from time to time, and in the most recent replications reviewed by Emlen *et al.* (1976) great care was taken to randomize these rotations and to avoid statistical biases that might result from unequal numbers of bird nights under different experimental conditions. Nevertheless it is puzzling to find that if the cage is rotated at frequent intervals the birds become disturbed, and the results are reported to deteriorate. As a result the cages are ordinarily rotated only once each night. Another puzzling aspect of the behavior recorded in these cages is that the birds spend most of their time flying around the doughnut-shaped enclosure, and when activating the northern radial perch they are actually heading either east or west. In one unsuccessful attempt to replicate these experiments, tangential perches were used so that a bird whose body was actually pointing north would activate the north, rather than the east or west perch (Perdeck, 1963). It is also perplexing that even after many years of work with these doughnut-shaped orientation cages the directional preferences remain so very small, barely significant even when hundreds of perch activations are summed.

Keeton's extensive experiments with homing pigeons have included tests on the possibility that magnetic sensitivity plays a significant role in the orientation of these highly trained and selected birds. In the most clear-cut of these experiments, small bar magnets were cemented to the backs of pigeons just before they were released. While homing success (speed and percentage of return) were not significantly affected, there was a clear tendency for birds fitted with magnets to show less well oriented initial headings than control birds carrying brass bars of the same size. These differences were more pronounced under overcast

skies, and magnets had a somewhat greater effect on relatively inexperienced young pigeons. These results are consistent with the hypothesis that sensitivity to the earth's magnetic field provides an alternate source of directional information that is called in play under overcast skies. It is important to bear in mind that the effects of magnets were evident within a minute or two after release, but that the birds which initially headed away from home returned as soon as those which started in the homeward direction. In other words the effects of the magnets were relatively brief and did not prevent normally rapid homing.

In other experiments Keeton and his colleagues have reported that when pigeons are repeatedly released at the same place, so that the vicinity of the release point and the route home presumably become very familiar, nevertheless their initial headings show a slight statistical tendency to deviate from the actual home direction. Furthermore these deviations show statistically significant correlations with the fluctuations of the earth's magnetic field (Keeton, 1974; Larkin and Keeton, 1976).

Walcott and Green (1974) and Walcott (1977) reported tests with homing pigeons similar to Keeton's but employing miniature coils above and below the bird's head to generate a small local magnetic field. The initial headings of these pigeons released under overcast skies, while showing the usual amount of variation (roughly $\pm 30^\circ$), were significantly different when the coils were connected so that the current flowed in opposite directions. When the artificial magnetic field had its local magnetic north pole pointed upward the initial headings were less well oriented toward home, and indeed there was a tendency to fly in roughly the opposite direction. With the current reversed, however, there was no significant difference from the headings of control birds carrying identical apparatus but with the battery disconnected. These results add an important element to the others described above in that there appeared to be a change in the direction chosen by the birds during the first minute or two after release rather than a simple deterioration of orientation.

These experiments have been interpreted by the Wiltschkos and by Walcott and Green to be consistent with the hypothesis that pigeons detect the dip of the earth's magnetic field, which is more than 45° downward in the north temperate regions where these experiments have been carried out. For instance, the inclination of the earth's field where Walcott and Green's experiments were conducted is about 70° . If birds

can do this, they can presumably also detect the direction of the horizontal component, which is equivalent to having a conventional magnetic compass. In experiments where bar magnets or coils are carried by the birds, the resultant field at any point on the bird's body varies according to the bird's vertical and horizontal orientation with respect to the earth's field. Since pigeons do a great deal of turning shortly after release, it is difficult to evaluate all the complicated interactions between the earth's field and that carried by the bird. Nevertheless, the Walcott and Green experiments do indicate that a short-term effect on directional orientation can be produced experimentally by relatively small changes in the earth's magnetic field.

Very recently Bookman (1977) has reported that three pairs of homing pigeons showed a clear and consistent difference in behavior correlated with the presence or absence of a magnetic field having approximately the intensity of the normal earth's field. The apparatus employed was a wooden tunnel about 1 meter square and 4 meters long, closed at one end. The pigeons were placed by hand into the open end and trained to move along the length of the tunnel to the closed end, where two doors, symmetrically placed in the side walls, led to chambers, of which only one contained food located in a bin not visible from the main chamber. The tunnel was located in a room shielded with mu-metal, which reduced the earth's magnetic field to 0.02 ± 0.01 g or roughly 1/25th of its normal value. Three "Helmholtz coils" about 1 meter in diameter were located above and below the wooden tunnel, and when a direct current was turned on they produced a vertical magnetic field estimated at 0.5 g—or approximately the field near one of the earth's magnetic poles. One door led to food when a current of 0.1 amp flowed through these coils, the other when they were turned off. The vertical field produced by the three coils could not have been uniform along the length of the tunnel, especially since the diagram of the apparatus indicates that the coils were separated by approximately their diameters rather than by their radii, as in true Helmholtz coils.

Only the choice of the first member of the pair to enter one of the feeding chambers was recorded. Performance was above the chance level only if two conditions were met: (1) The two pigeons had to be a mated pair; single birds or a pair of nonmated birds were reported to be less active in the tunnel and apparently did not achieve any significant discrimination. (2) At least 3 seconds of "fluttering" had to occur before the bird entered a feeding chamber (Schmidt-Koenig, 1977).

When these two conditions were satisfied, correct choices were made in 68 out of 89 trials with one pair, 50 out of 61 with another, and 13 out of 16 with the third. The two-tailed binomial probability of these results occurring by chance is less than 0.0001 for the first two pairs and less than 0.025 for the third. It is not clear whether the fluttering birds jumped into the air and hovered in place or flew along the length of the tunnel. Since the experiments were apparently not conducted "blind," inadvertent cues could have been provided by the experimenter who placed the bird in the open end of the tunnel at the beginning of each trial.

Bookman's experiments may nevertheless have supplied the first clear-cut experimental demonstration of sensitivity to magnetic fields comparable in intensity to the normal earth's field. Since the experiment indicates only that the birds can distinguish between a field roughly equal to the normal earth's field and a field of very greatly reduced intensity, it could be argued that an ability to distinguish between the presence and the virtual absence of an environmental signal is not sufficient to demonstrate that it is used for directional orientation. But if Bookman's experiments can be confirmed, they will prove to be an exciting new development. They may even mark the beginning of a new stage in the experimental analysis of magnetic sensitivity, in which clear-cut and repeatable responses of individual organisms can be analyzed in detail.

When all this recent evidence in favor of sensitivity to the earth's magnetic field is reviewed, one may wonder why any doubt remains. Indeed almost all investigators of bird navigation seem convinced that the earth's magnetic field has some influence on bird orientation. Two significant uncertainties, however, must be seriously considered. The first is the fact that numerous attempts have been made to elicit unequivocal responses from pigeons or other birds to magnetic fields comparable in strength to the earth's, and in every case the results have been overwhelmingly negative. Negative results are viewed by scientists with justifiable suspicion, but in this case such a diversity of experiments have been attempted that their uniform failure cannot easily be overlooked. The most thorough of these experiments, and the only ones for which complete details have been published, are those of Kreithen and Keeton (1974) and Beaugrand (1976). A very effective method was developed for classical conditioning of pigeons to show a distinct change in heart rate when a stimulus that they could sense was followed

after a few seconds by an electric shock. This method worked well not only for stimuli known to be easily detected, such as lights and sounds, but also for two other classes of stimuli to which pigeons had not previously been shown to be sensitive. These were the plane of polarization of light, and relatively small fluctuations in atmospheric pressure down to roughly 1 millibar (equivalent to about 10 meters change in altitude). Thus the method was demonstrated to be effective not only for grossly obvious stimuli, but for relatively subtle ones. A determined experimental effort using the same individual pigeons which had showed inaccurate initial headings when carrying magnets yielded completely negative results.

A second problem is the very small magnitude of all the effects reported from these experiments to date except for those of Bookman discussed above. After many years of experimental work, the methods employed by the Wiltschkos achieve marginal statistical significance only by pooling the data recorded by several birds over several hours in the apparatus. Yet in the real world of a homing or migrating bird orientational choices must be made over short periods of time by individual birds. To be sure, under some conditions migrants might pool information by communicating, but individual homing pigeons released one at a time show as accurate initial headings as those flying in groups (Keeton, 1974). It has been suggested that sensitivity to the earth's magnetic field is such a marginal matter for birds that only by averaging information received over many hours can even an approximate orientation be achieved. The Wiltschkos have indeed postulated (Wiltschko and Wiltschko, 1975) that while magnetic orientation is in a sense primary, birds learn to "calibrate" other sources of information such as the stars, or possibly wind direction, and then base their immediate orientational responses on these nonmagnetic cues. These explanations postulate that the magnetic sense has a very long time constant. But this does not suffice to explain the effects on the initial headings of homing pigeons reported by Keeton and by Walcott and Green to occur within a few minutes after application of the bar magnet or activation of the coils, and within a minute or two after the bird begins to fly. Bookman's pigeons appear to have required only a few seconds to detect the presence or absence of a 0.5 g field.

Another possibility that has been discussed by Keeton (1974) and others is that the earth's magnetic field can be detected only by a bird in rapid motion through the earth's field. The physical basis for detecting

the earth's field might be the detection of induced voltage gradients or currents flowing through the bird's body as a result of its motion through the earth's field. But in many of the experiments in which responses to weak magnetic fields have been sought, including those of Kreithen and Keeton, changing magnetic field strengths have been employed. These should induce voltage gradients similar to those resulting from motion through the earth's field.

On balance then the whole question of avian sensitivity to the earth's magnetic field stands in a puzzling state. The positive evidence for a weak effect is far from trivial (Schmidt-Koenig, 1977), and yet the negative evidence is also relatively strong. It thus seems that the case might best be described as suggestive but not proved. It may be best to reserve judgment until more definitive evidence becomes available.

Evidence of Magnetic Sensitivity in Animals Other Than Birds

The experiments deriving from Lissmann's original demonstration that weakly electric fish orient themselves by sensing electric fields have led to the recent demonstration by Kalmijn and others that many fishes have sufficient electrical sensitivity that they should be able to detect the voltage gradients resulting from motion through the earth's magnetic field. Indeed Lissmann originally showed responses to moving magnets, and in recent experiments reviewed by Kalmijn (1974) fish have responded to weak magnetic fields, comparable to the earth's. Akoev *et al.* (1976) have reported thresholds for rate of change of a magnetic field in electrosensitive skates and found thresholds of about 0.8 g per second. Since the earth's field is about 0.5 g, these fish would have to execute very rapid turns or other maneuvers to reach this threshold level by swimming through the natural earth's field. One can therefore argue: If fish can do this, why not birds? But a serious physical difficulty remains to be explained away, and this is the fact that electrosensitive fish concentrate voltage gradients across their bodies so that local potential differences across receptor cells are much greater than the average gradient. An important part of the physical mechanism by which this is accomplished is the flow of current not only through the fish but through the surrounding water, which provides an electrical return path. A much more difficult problem is faced by a bird surrounded by air, which has an enormously lower electrical conductivity than even the purest fresh water. While the same voltage gradient would

be established, or perhaps a greater one owing to higher speeds of motion, the estimated difference in current flow remains very large.

Experiments by Lindauer and Martin (1972) on a wholly different kind of terrestrial animal, the honeybee, provide important support for the general conclusion that the earth's magnetic field can be sensed by animal nervous systems. As is well known from the pioneering experiments of von Frisch (1967), under conditions where the colony is in great need of food returning foragers execute a figure eight-shaped waggle dance, the straight portion of which indicates directions relative to the azimuth position of the sun. When bees are executing these dances with reference to a source of food at a fixed location, the actual angle of the dance relative to the vertical changes progressively during the day as the sun moves through the sky. Yet, as von Frisch noted many years ago, the dances do not precisely follow the change in the sun's azimuth, but rather show slight deviations of up to 10° - 15° from time to time during the day. Lindauer and Martin (1972) showed that these minor deviations disappeared in an artificial magnetic field of the appropriate strength and orientation to cancel the natural earth's field to within less than 5%. Under these conditions the dances shifted smoothly with the sun's azimuth and underwent only random variations of about 2° or 3° . Another important finding described in preliminary fashion by Lindauer and Martin (1972) is that when bees are induced to occupy a new cavity, the plane of the parallel layers of honeycomb which they build can be altered by suitable Helmholtz coils. In other experiments Lindauer (1976) reported effects on honeybee dances of daily fluctuations in the earth's field. Martin and Lindauer (in press) describe experiments on gravity orientation of bees that appear to provide additional evidence that honeybees can react consistently to the earth's magnetic field or to small changes in it. Thus a stronger line of argument than comparing birds to electrically sensitive fish would be: If bees can orient to the earth's magnetic field, why not birds?

Finally it is important to add to this long series of experiments on magnetic sensitivity the recent report by Blakemore (1975) that bacteria of a type living in marine sediments move toward the north magnetic pole under laboratory conditions. These magnetotactic bacteria are provided with cellular inclusions containing considerable amounts of iron. All a bird would seem to need is an appropriate infection of its inner ear with such bacteria!

From all this evidence it is clear that living cells have the capability of responding to the earth's magnetic field, but it still remains to be demonstrated in any satisfactory fashion that birds actually use the earth's magnetic field for their orientation. The evidence reviewed above has certainly stimulated many investigators to search by a variety of methods for clear physiological or behavioral evidence of the sort so conspicuously lacking to date; thus we may anticipate that unequivocal evidence will be forthcoming in the reasonably near future. Otherwise we may be forced to remain in the uncomfortable situation where animals that have less pressing need than birds for the equivalent of a magnetic compass are nevertheless the only ones in which this new sensory capability is unequivocally demonstrable.

D. The Problem of Kramer's Map Component

It is important to reiterate that the goal-directed homing after arbitrary displacement into unfamiliar territory requires more than directional orientation. Neither magnetic nor sun compass, nor both together, seem capable of furnishing the map component, as it was termed by Kramer. We are in the embarrassing position of lacking even a plausible hypothesis to account for goal-directed homing, and this, to put it mildly, hinders the design of adequate experiments. One natural reaction is simply to ignore the problem, to take refuge behind yet another simplicity filter, and hope the disturbing business will simply go away. But the history of this field provides little comfort for this attitude. Real animals persist in doing things with which our scientific *Zeitgeist* is not yet prepared to cope. This situation clearly presents a challenge and the opportunity for creative investigators to open new chapters in the history of this field which has already yielded so many significant surprises.

VII. SUMMARY

Investigations of comparative sensory physiology have disclosed several previously unsuspected "windows" by which information from an animal's environment reaches its central nervous system. The excellent underwater hearing of certain fishes and of marine mammals is one outstanding example. Another is the ability of insects and other animals to utilize the plane of polarization of light. In certain snakes (pit vipers

and boas) undifferentiated nerve endings located in specialized sense organs serve as effective radiometers. These are used to detect warmblooded prey, such as mice, with surface temperatures that differ from the background by a few degrees.

Many groups of fishes have lateral-line systems which are remarkably sensitive to small voltage gradients—down to well below $1 \mu\text{V}/\text{cm}$. By a previously unsuspected mode of perception, weakly electric fishes detect changes in the electric fields set up by their own relatively feeble electric organs. Further investigations of this electrical “window” showed that electric signals are also used for communication. Aggressive interactions and probably also courtship are mediated, at least in large part, by weak electric signals.

Still further investigations of electrosensitive fishes disclosed that many groups, such as the sharks and rays, that have no electric organs nevertheless have sufficiently sensitive electroreceptors that they can detect other fish, especially prey, by sensing direct current and low-frequency electric potentials of biological origin. Some fish can also detect naturally occurring electric fields originating from physical or chemical processes in the aquatic environment. Even the earth's magnetic field can be sensed through induced voltage gradients as fish swim or are carried by currents.

One of the best known examples of animal orientation based on an extension of previously appreciated sensory spectra is the echolocation of bats and marine mammals. Specialized orientation sounds yield echoes that convey important information via the auditory system. Although clicks audible to human ears are used by a few species of bats and two genera of cave-dwelling birds, the existence of echolocation was unsuspected until the late 1930s because the orientation sounds of most bats are above the frequency range of human hearing.

The underwater orientation sounds of marine mammals are very brief clicks with extremely broad frequency spectra, whereas echolocating bats usually employ orientation sounds with a definite frequency structure. Commonly this consists of a very rapid downward frequency sweep, typically an octave in roughly 50–100 waves. Usually each orientation sound is of short enough duration to avoid overlap between the emitted probing signal and returning echoes. Repetition rates almost always increase sharply when the animal is faced with a difficult problem of orientation, such as a bat pursuing flying insects.

Echolocating animals have developed auditory nervous systems exquisitely specialized for extracting pertinent information from echoes, including identification of targets and discrimination between them on the basis of frequency spectra of echoes. Discrimination between targets at slightly different distances and detection of faint echoes masked by interfering noise are both accomplished with a proficiency very close to the theoretical limits set by signal detection theory.

The auditory system of echolocating animals is basically similar to that of other mammals, but certain features are at least quantitatively accentuated. These include neural networks that achieve selective sensitivity to sweeping frequencies and "transmit-receive switches" of two sorts. The best known are the relatively hypertrophied middle ear muscles which contract synchronously with the emission of orientation sounds and yet relax within a very few milliseconds so that full auditory sensitivity is restored before echoes return. A second mechanism of this type, only recently discovered, is "neural attenuation" somewhere between the VIIIth nerve and lateral lemniscus also synchronized with the emission of orientation sounds. In the bats, where they have been best studied, these two mechanisms together reduce auditory sensitivity by about 30 decibels at the time when intense orientation sounds are being emitted.

Echolocation is not limited to specialized animals. In the human blind a simple sort of obstacle detection based on hearing echoes is well known. Unfortunately the proficiency achieved by bats and dolphins has not been matched even by the most skillful and experienced blind people. Since the physiological reasons underlying this regrettable performance gap are not known, it is unclear whether appreciable improvement in human echolocation is possible.

Major scientific challenges still confront us concerning the well known ability of birds to maintain correct orientation during migrations and homing flights. Birds and many other animals are capable of time-compensated sun- or star-compass orientation in which they head at an angle to the sun or to particular groups of stars which shifts progressively with time. But many migrants, and some of the most proficient homing pigeons, can orient almost as well under completely opaque clouds as when the sun or stars are visible.

A sensitivity to the earth's magnetic field is a possible alternate sensory window used by birds for directional orientation when the sky is

not visible. In several types of experiments, deterioration in orientation or a shift in the average direction of flight has been observed when the natural magnetic field is distorted. But most laboratory experiments designed to test unequivocally for sensitivity to the earth's magnetic field have yielded negative results. It therefore seems best to reserve judgment as to whether or not a new sensory window is in the process of being discovered. Yet investigations of animal orientation have led to so many extensions of our conceptual horizons that a continuation of this process would not be altogether surprising.

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