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2. E. Fermi, *Z. Phys.* **88**, 161 (1934).
3. B. Pontecorvo [*Inverse Beta Decay* (Division of Atomic Energy, National Research Council of Canada, Chalk River; declassified and issued by the Atomic Energy Commission in 1949)] and L. W. Alvarez [*Univ. Calif. Radiat. Lab. Rep. UCRL-328* (1949)] suggested a radiochemical method using a fission reactor based on the reaction $\nu + {}^{37}\mathrm{Cl} \rightarrow {}^{37}\mathrm{Ar} + \mathrm{e}^-$. They did not pursue the method. Alvarez was dissuaded by his estimates of the background to be anticipated from cosmic rays; these estimates later proved to be correct for the reactors then available. As we know now, the neutrino produced in fission is $\bar{\nu}_e$ and the neutrino required for the ^{37}Cl reaction is ν_e, so the reactor result would have been negative even though the neutrino exists.
4. It is, of course, not possible to know how the field would have developed if Cowan and I had not met and decided to work together on this "manifestly impossible" search, but in view of the general absence of activity in this direction at the time, I suspect that the observation would have been somewhat delayed. A popular account of these early days was written by Cowan in 1964 ["Anatomy of an experiment: An account of the discovery of the neutrino," *Smithson. Inst. Annu. Rep. 4626* (1964), p. 409]. The status of the neutrino in 1936 was reviewed by H. A. Bethe and R. F. Bacher [*Rev. Mod. Phys.* **8**, 82 (1936)]. Attempts to detect the neutrino up to 1948 were summarized by H. R. Crane [*ibid.* **20**, 278 (1948)].
5. N. Bohr, *J. Chem. Soc.* (1932), p. 349.
6. S. Drell [*Am. J. Phys.* **46**, 597 (1978)] suggested that in view of the fact that an isolated quark has not yet been detected, experimental criteria for the existence of elementary particles may require revision. However, he recalled that the neutrino was suggested to preserve conservation of energy, momentum, and spin, whereas no conservation laws require quarks.
7. However, I do remember one conversation regarding detection techniques. "Why not," suggested Cowan, "make a device analogous to a cloud chamber but of liquid to obtain the necessary target mass, and use it in our search." We discussed it at some length but discarded it because it could not be triggered by the event, and random triggers would give a small duty cycle. It was a good idea, as subsequent events have demonstrated, but it did not suit our purpose (to detect the neutrino) and we did not pursue it. (As we now know, the bubble chamber was invented around that time by D. Glaser, and in the hands of L. W. Alvarez and others turned out to be extremely useful for particle physics, eventually including neutrinos at accelerators.)
8. The technique of scintillation counting followed the discovery by W. Crookes and by J. Elster and H. Geitel [*Phys. Z.* **4**, 439 (1903)] of the scintillation properties of zinc sulfide exposed to alpha particles [described by E. Rutherford, J. Chadwick, and C. D. Ellis, *Radiations from Radioactive Substances* (Cambridge Univ. Press, Cambridge, England, 1930)]. It received great impetus from the development of the photomultiplier tube and the crucial observation [H. Kallmann, *Phys. Rev.* **78**, 62 (1950); M. Agena, M. Chiozotto, R. Querzoli, *Atti Acad. Naz. Lincei Cl. Sci. Fis. Mat. Nat. Rend.* **6**, 626 (1949); *Phys. Rev.* **79**, 720 (1950); G. T. Reynolds, F. B. Harrison, G. Salvini, *ibid.* **78**, 488 (1950)] that liquids could be made to scintillate with high efficiency when the scintillating compound was at low concentration. Our contribution was to recognize that with a sufficiently transparent scintillator and enough photocathode area, one should, in principle, be able to make a detector of almost arbitrarily great size—just what was needed for neutrino detection. Our first large detector, nicknamed El Monstro, was a 1-m^3 bipyramidal brass tank containing toluene and viewed on the top and bottom by four 2-inch photomultiplier tubes. Our subsequent detectors employed many more photomultipliers to increase light collection and so obtain the desired energy resolution.
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12. At that time R. Davis, Jr., reassessed the ^{37}Cl approach and decided to make an effort to observe the reactor neutrino by using that reaction. We called to his attention the existence of other well-shielded, powerful SRP reactors, and he placed 4000 liters of CCl_4 near one of them. He obtained a negative result (R. Davis, Jr., paper presented at the American Physical Society Meeting, Washington, D.C., 1956) which, taken together with our observation, proved that although the $\bar{\nu}_e$ existed it was incapable of inverting ^{37}Ar decay. This suggested that the neutrino emitted by neutron-rich fission fragments (e^- decay), $\bar{\nu}_e$, was different from the ν_e emitted in e^+ decay, which at that time was one of the two possibilities to be checked.
13. This prediction incorporated the then held belief that parity is conserved in the weak interaction. In view of the large experimental errors and the poorly known $\bar{\nu}_e$ spectrum, we considered this crude agreement consistent with the $\bar{\nu}_e$ origin of the signal and continued our program to make this comparison more precise. (Our initial analysis grossly overestimated the detection efficiency with the result that the measured cross section was at first thought to be in good agreement with prediction.) As commented on later in this account, the effect of parity nonconservation is to increase the predicted cross section by a factor of 2. In the two-component theory the electron neutrino has only two states—one, $\bar{\nu}_e$, with its spin angular momentum parallel, and one, ν_e, with its spin angular momentum antiparallel to its linear momentum. The old four-component theory allowed each neutrino to have two spin states.
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24. Supported in part by the Department of Energy. Clyde Cowan left a legacy that will live in the annals of physics. In the search for that polsearch for that poltergeist, the neutrino, he exhibited the courage to tackle a problem that had defied experimentalists for 20 years and the creative imagination to contribute in a fundamental way to its solution.

Echolocation and Pursuit of Prey by Bats

James A. Simmons, M. Brock Fenton, Michael J. O'Farrell

Of the 700 living species of echolocating bats in the mammalian order Chiroptera (*1*), about 600 actively pursue prey, probably with partial or complete guidance by sonar. The great majority of these bats are insectivorous and chase airborne insects or glean resting insects from surfaces when they forage for food. Some are carnivorous and presumably must often actively hunt other bats, small birds, or lizards. A few species have evolved active hunting procedures to the point where they can use echolocation for detecting fish (*2*). In species that have been observed hunting, echolocation serves as an important perceptual modality for finding prey (*3*, *4*). In laboratory studies on their pursuit of airborne targets, bats use echolocation for detecting, locating, identifying, and tracking prey to a successful capture (*5*).

Modern portable electronic equipment for recording and analyzing the ultrasonic orientation signals used by bats (*4*, *6*) has broadened the range of species of bats that have been studied while they hunt. The number of species about which something is known is now large enough for a comparative analysis of some aspects of hunting strategies as they are related to echolocation. In this article we discuss the relationships found among feeding behavior, echolocation, and the acoustic environment within which bats seek their prey.

Summary. Echolocating bats use different information-gathering strategies for hunting prey in open, uncluttered environments, in relatively open environments with some obstacles, and in densely cluttered environments. These situations differ in the extent to which individual targets such as flying insects can be detected as isolated objects or must be separated perceptually from backgrounds. Echolocating bats also differ in whether they use high-resolution, multidimensional images of targets or concentrate specifically on one particular target dimension, such as movement, to detect prey.

Echolocation of Prey

An echolocating bat interrogates its surroundings to perceive salient features of neighboring objects (*3*, *4*, *7–9*). The various acoustic dimensions of orientation sounds serve as vehicles for conveying information about particular targets to bats. There seems to be no simple one-to-one relationship between the physical features of targets as objects (size, shape, distance, direction, velocity) and the acoustic features of echoes (intensity, frequency, spectrum, time of occurrence) that represent target features. The perceptual image of a target built up in the bat's central nervous system must contain elements compounded of several acoustic features of echoes (*8–10*).

Many different species of bats feed on insects that they capture in flight. Other species can capture prey resting on surfaces as well. The structure of the orientation sounds used for hunting provides valuable data on the kinds of information sought by the bat (*7–9*, *11*). Figures 1 and 2 show sound spectrograms drawn from data representing orientation sounds of six species of bats in six different families. The basic features of bat orientation signals are conveyed by this type of graph (*3*, *4*, *7*, *9*, *11*). The data illustrate the acoustic emissions of these bats as they search for prey, approach prey for identification, and close in for the final capture (*3*, *5*).

In Fig. 1 the hunting orientation sounds of *Tadarida brasiliensis* (Mexican free-tailed bat, Molossidae) (*12*), *Eptesicus fuscus* (big brown bat, Vespertilionidae) (*3*, *13*), *Pteronotus personatus* (= *psilotis*, Mormoopidae) (*14*), and *Rhinolophus ferrumequinum* (greater horseshoe bat) (*15*) are illustrated. Figure 2 shows the feeding sounds of *Phyllostomus hastatus* (greater spearnose bat, Phyllostomatidae) (*16*), the sounds of *Plecotus phyllotis* (long-eared bat, Vespertilionidae (*17*), a target-ranging sound of *T. brasiliensis* (*12*), and the hunting sounds of *Noctilio leporinus* (a fishing bat, Noctilionidae) (*18*).

Pursuit of flying insects in open spaces. Tadarida brasiliensis hunts for flying insects in very open areas devoid of substantial obstacles to flight (*12*). The echolocation signals used by *T. brasiliensis* when hunting (Fig. 1a) show a systematic progression from constant-frequency (CF) or slightly frequency-modulated (FM) signals around 50 kilohertz, which are used for searching, to increasingly broad FM sweeps beginning above 50 kilohertz and becoming progressively lower and lower, covering 50 to 25 kilohertz toward the end of the pursuit sequence. The signals also become progressively shorter, from as much as 10 milliseconds in the search to about 1/2 millisecond in the terminal stage. These search, approach, and terminal signals are intense, being roughly 2 to 10 newtons per square meter near the bat's mouth (*19*). The repetition rate of the sonar sounds increases fairly smoothly during pursuit from roughly 10 to about 100 to 150 sounds per second. Only one harmonic is present in the orientation sounds used by *T. brasiliensis* for hunting prey.

The information contained in the echo of a sonar sound depends first of all on signal bandwidth; broadband signals carry more information with which to construct an acoustic image of a target (*7*, *8*). Short (less than 10 msec) narrowband signals carry little precise information besides their presence or absence. Long (more than 10 msec) CF or narrowband signals contribute little to a high-resolution acoustic image, but their long duration enables precise specification of their frequency, providing good resolution of target velocities from echo Doppler shifts. The high duty cycle (percentage of time a sound is being emitted) inherent in the use of long-CF transmissions provides an opportunity to monitor fluttering motion of targets from small amplitude or frequency modulations in echoes (*11*).

The sonar sounds of *T. brasiliensis* represent a pursuit strategy in which nearly all echo information during the search process is devoted to finding a prey target. Only a single frequency or a slight FM sweep is emitted, and such a narrowband signal can carry little information about the features of the target beyond the target's mere presence. *Tadarida brasiliensis* uses sounds for searching that are short CF signals in a sense defined previously (*7*). These sounds are 5 to 10 msec long, and their durations are never observed to extend into the 10- to 100-msec range of the long-CF signals used by horseshoe bats for Doppler velocity resolution and to detect target fluttering from echo modulations.

When *T. brasiliensis* responds to the presence of a target by shortening its emitted sounds and increasing the repetition rate of the emissions, the bat also begins to change the signals from essentially short-CF to FM, gradually increasing the breadth of the sweeps as it approaches the insect (Fig. 1a). The increasing bandwidth of the signals provides for greater acuity in perceiving target features and locating the target's position (*7*). The FM signals become broadest in bandwidth at the point in the pursuit sequence when the bat may be judging whether the target is suitable for capture (*5*). The terminal "buzz" of sounds is similar in pattern to those of other bat species that feed on flying insects or to the sounds of bats coming up to an obstacle. Such rapidly emitted sequences of sonar sounds are made by *T. brasiliensis* in the laboratory when orienting toward objects that are near and getting nearer, such as a mealworm held in forceps. This terminal stage of pursuit echolocation guides the final maneuvering to seize prey, a general perceptual problem for nearly all bats. The duty cycle of the emissions during hunting varies from 5 to 20 percent. The same kind of short-CF search signal is used by *Tadarida macrotis* (*12*). The occurrence of CF signals without FM components has been observed in a number of other species (*18*, *20*).

In environments where obstacles to flight are present, *Tadarida* uses FM signals with three harmonics (Fig. 2c) that are similar to the FM signals of most other species of insectivorous bats, which usually forage in more obstacle-plagued situations than *Tadarida*. The type of pursuit echolocation used by *Tadarida* appears to be specifically adapted to open, uncluttered spaces.

In that only the prey target is of apparent concern to the bat, this is a *basic pur-*

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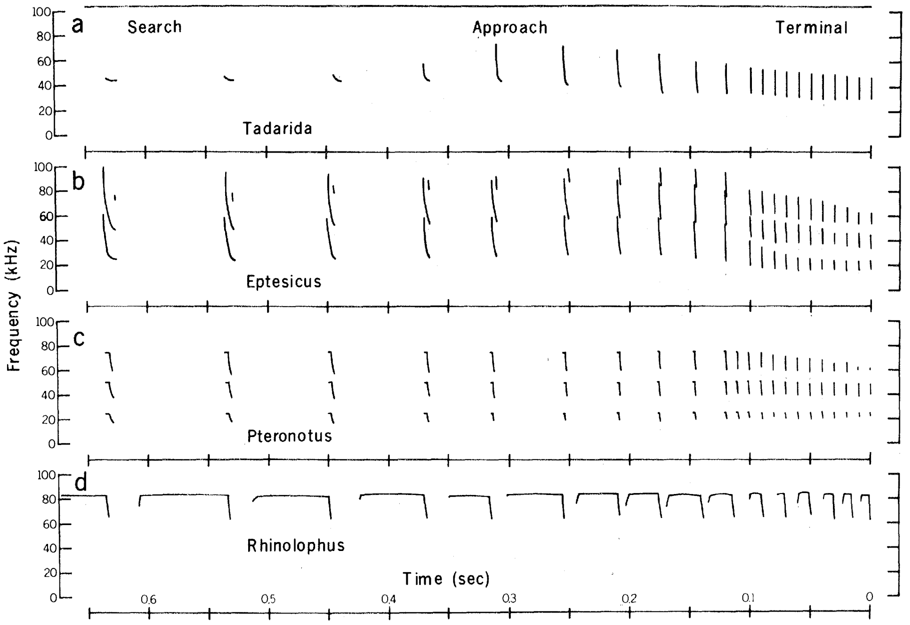

Fig. 1. Sound spectrograms representing sonar signals of (a) *Tadarida brasiliensis*, (b) *Eptesicus fuscus*, (c) *Pteronotus personatus*, and (d) *Rhinolophus ferrumequinum* during search, approach, and terminal stages of pursuit of prey. The entire detection, identification, and tracking process usually takes place in less than 1 second. The time scale is reversed and counts down to the time of capture. These spectrograms illustrate four distinct patterns of orientation sounds for hunting and reveal differences in the information-gathering strategies of the bats correlated with differences in the acoustic environments.

suit strategy. Elements of such a basic strategy, which incorporates a purely detection-oriented search stage and resolution-oriented approach and terminal stages (*3, 5*), are also present in other, more sophisticated strategies used to deal with more complex perceptual situations in which the prey are embedded.

Pursuit of prey in the presence of obstacles. Most species of bats that have been studied do their hunting in moderately open environments through which obstacles to flight such as trees or buildings are scattered. Although pursuing prey, these species must be aware of obstacles to their flight that are hazards to navigation. *Eptesicus fuscus* is representative of species that often forage in the general vicinity of obstacles, but not usually very close to them. The orientation sounds of this bat progress from multiple-harmonic FM plus short-CF search signals to multiple-harmonic FM signals in the approach and terminal stages of pursuit (Fig. 1b). The search signals contain broadband FM sweeps several milliseconds long and narrowband short-CF signals up to 5 to 10 msec in duration. After detection has occurred, the bat drops out the short-CF component as it closes in on the target, shortening the FM sweeps to less than 1/2 msec at the time of capture. These orientation sounds are intense. The repetition rate of the sounds varies from about 10 to as much as 200 sounds per second. The duty cycle of the emissions varies from 5 to 20 percent during the various stages of pursuit.

The short-CF component, which, like the search signal of *Tadarida*, may actually sweep through a narrow range, is associated with detection of targets. It is a short-CF component in that it is narrowband. The FM component during search and at other times probably gives the bat a good acoustic image of objects in the immediate area as well as of the prey once it is detected. The bat "keeps an ear out" for potential dangers to its flight. When *E. fuscus* is performing an echo detection or other task in the laboratory, and echo signal-to-noise ratios are degraded through addition of noise interference, the bat adds a short-CF component to the end of each FM sound (Fig. 2d) (*7*). The pattern of sonar emissions exhibited by *E. fuscus* while hunting is also used by a variety of other species, including bats in the widely distributed genera *Myotis* and *Pipistrellus* (*4*). It is this kind of acoustic behavior during feeding that characterizes bats to most people.

A number of different species of bats, found particularly but not exclusively in the tropics, may use a variation of this echolocation strategy in which the short-CF component precedes the FM sweep rather than follows it. Figure 1c shows the insect-pursuit sonar behavior of *P. personatus*. Several harmonics appear in all of the sounds. The sounds used for searching are short-CF-FM waveforms, and the leading CF component decreases from 5 to less than 1 msec during the course of the entire pursuit sequence. The repetition rate of the sounds again changes from roughly 10 to 100 sounds per second, and the duty cycle varies between 10 and 20 percent. Observations of *Pteronotus* in Panama indicate that these sounds are intense. This short-CF-FM pattern is observed in most bats of the family Mormoopidae, in many Hipposideridae, and in various species from other families such as Emballonuridae and Noctilionidae (*9, 14, 18, 20, 21*). Even *T. brasiliensis* uses short-CF-FM signals with multiple harmonics when scanning the environment for obstacles as it takes flight from its roost (Fig. 2c) (*12*).

Bats using FM-short-CF and short-CF-FM sonar sounds while hunting flying prey maintain the broadband, image-forming capability of FM signals even while searching for prey at least partly with narrowband short-CF signals (Fig. 1, b and c). One can see the transition of the basic hunting strategy from short-CF to FM even while the bat is also working near obstacles. The constant presence of FM components reflects the increased complexity of the perceptual situation, the obstacle-filled acoustic environment that also contains prey in flight. The short-CF component must certainly yield echoes from obstacles, but probably not of sufficient perceptual resolution to locate and identify the obstacles for navigation. Bats often swoop quite close to these obstacles in pursuit of prey (*3, 5*), and they must surely keep close contact with the whereabouts of each part of an obstacle (tree branches, for example) while still pursuing the insect. This *obstacle-monitoring pursuit strategy* with its two variations is an increase in sophistication in a perceptual sense over the basic strategy. The simple detection problem is beginning to seem more like separation of the image of the prey from the background (see below). This increased sophistication in no way implies advancement in an evolutionary sense. Hunting in open spaces may well be more "advanced" in its evolutionary status than hunting in clutter.

Pursuit of prey in dense clutter. Although bats such as *E. fuscus* sometimes pursue prey in the neighborhood of clutter, they do not appear to routinely enter densely cluttered areas to pursue flying prey or pick prey from vegetation. Some species of bats have been observed to forage quite frequently not just in the presence of some obstacles to flight but within a complex sonar-target environment composed of many objects forming a background matrix for the prey. In such situations many objects are intimately associated with the prey, and detection versus nondetection of echoes is not an important element of pursuit. Simply making louder sounds will not pick out prey. The perceptual problem is discrimination of prey from the background, which can be accomplished either by forming multidimensional, high-resolution acoustic images of prey on the background or by exploiting some salient acoustic feature of prey, concentrating on that feature as a strategy.

Bats that have been seen to hunt in or on vegetation or along surfaces are gleaners, taking prey largely from the surfaces of leaves, branches, or walls. Bats such as *Antrozous*, *Macrotus*, *Plecotus*, and *Megaderma* are generally included in this category. Bats that glean prey from clutter seem not to have been studied in the act of feeding in natural situations as much as in laboratory situations. Artifacts introduced into the perceptual situation indoors may lead bats to behave quite differently than in nature (*12, 17, 22*), and it would be desirable to obtain high-quality recordings of gleaner bats foraging. It does appear, however, that *Antrozous* and *Macrotus* and other spearnose bats (Phyllostomatidae) can be characterized by the data illustrated next.

Figure 2a shows orientation sounds used by the omnivorous *P. hastatus* to locate individual mealworms on a rough concrete floor under and near the legs of a table. The bat, which was blinded, landed on the worm and picked it up in its mouth. These signals were not recorded in the bat's natural environment, but these data do correspond to field observations of *Macrotus* and *Antrozous* made with bat detectors providing visual and audible outputs. These FM signals were emitted at a fairly constant repetition rate of 20 to 30 sounds per second, with increases to about 50 sounds per second as the bat dropped about 30 centimeters out of slow or hovering flight to capture the mealworm. The signals are 0.5 to 1 msec long, and they contain three strong harmonics and one weaker harmonic (the first). They are of low intensity (0.5 to 2 N/m^2). The duty cycle is about 5 percent. They are similar to the terminal buzz sounds of many bats (Fig. 1, b and c), except that they are less intense.

The orientation sounds used by *P. hastatus* for catching mealworms are broad in bandwidth not so much because they sweep extensively as because they combine several FM harmonics that together cover a wide span of frequencies. Their bandwidth ensures good resolution of target and background features, including a mealworm against an irregular floor. These signals represent a *high-resolution, clutter-rejecting pursuit strategy*. In perceptual terms it is an extremely sophisticated strategy in that large amounts of information must be processed to distinguish prey from clutter. Many bats use multiple-harmonic, broadband signals in the terminal stage of insect pursuit (Fig. 1, b and c). Multiple-harmonic FM orientation sounds seem to be used rather commonly for targets at close ranges or in clutter. *Tadarida brasiliensis* uses a three-harmonic FM signal in small spaces or in a room (Fig. 2c) (*12*).

The next category of pursuit behavior is introduced here in the context of clutter rejection because it has been observed to function for that purpose. Bats using signals representing this strategy have, however, also been observed feeding in more open situations. (None of the behavior patterns described here should be viewed as rigid. *Eptesicus fuscus* readily feeds on insects caught on the ground or the floor, for example, but its principal activity probably is pursuit of flying insects.)

An alternative to forming multidimensional, high-resolution acoustic images of prey against a complex clutter background is to concentrate the sonar system on some acoustic feature of the prey that is particularly likely to distinguish it from the background, while still gathering enough information to monitor obstacles and maintain a minimum image of the situation. One such distinctive feature of prey derives from its being alive; it is motion.

Bats that emit long-CF signals use the frequency of the returning echo CF component to determine Doppler shifts and

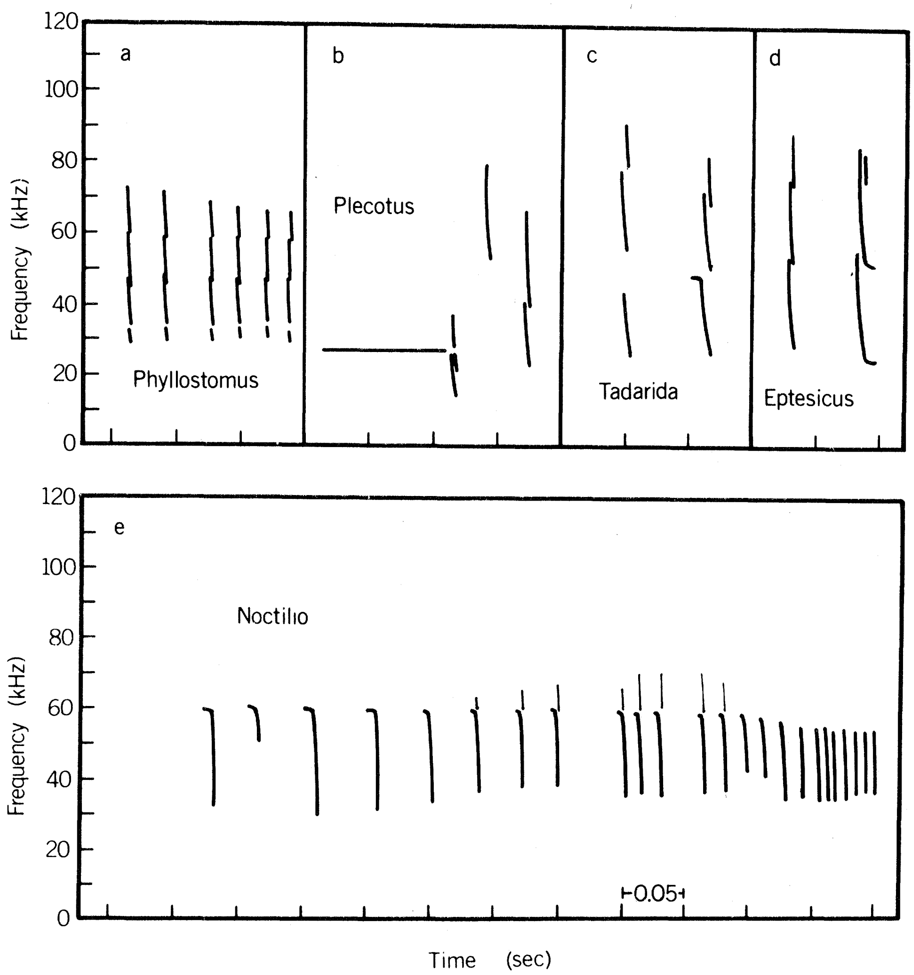

Fig. 2. Sound spectrograms representing sonar signals of (a) *Phyllostomus hastatus* while feeding, (b) *Plecotus phyllotis* in a variety of situations, (c) *Tadarida brasiliensis* performing target-range discriminations (left) or flying from its roost (right), (d) *Eptesicus fuscus* detecting targets in quiet (left) or in jamming noise (right), and (e) *Noctilio leporinus* hunting for fish. A fifth pattern of sound emission for hunting is revealed by *Phyllostomus*, and the other spectrograms at the top indicate the flexibility of orientation sounds emitted by bats. When hunting, *Noctilio* appears acoustically similar to *P. personatus* in the use of CF-FM sounds and to *T. brasiliensis* in using only one strong harmonic.

hence relative target velocity (*23*). In fact, these bats actually adjust the frequency of their emissions to maintain CF echoes at a species- and individual-specific frequency, thus compensating for Doppler shifts. In bats using reasonably long-duration CF components (more than 10 msec), the magnitude of the Doppler shift is known with sufficient accuracy to readily distinguish small changes in the bat's approach velocity or to pick out prey in motion against a fixed background.

Some species of bats using short-CF signals also compensate for echo Doppler shifts (*24*), but their frequency resolution may not be acute enough for true velocity measurement. They may compensate to bring the echo into a region of maximum auditory sensitivity for detection. It seems probable that Doppler compensation for acute velocity perception evolved as a refinement of the use of short-CF components and rough Doppler compensation to facilitate detection (*7*).

Figure 1d shows a sequence of orientation sounds used by *R. ferrumequinum* for detecting, approaching, and capturing an insect fluttering at the end of a tether. These signals reveal two important points about the bat's echolocation of prey. First, the FM components exhibit a pattern similar to those shown in Fig. 1, a, b, and c. They occur at repetition rates varying from about 10 sounds per second during searching to almost 100 sounds per second as capture takes place. Second, most of the time intervals between FM signals are filled with long-CF signals. The FM duty cycle is less than 10 percent, whereas the CF duty cycle ranges from perhaps 50 to 80 percent. The sounds are intense. The long-CF emissions provide accurate echo information about target velocity with respect to the background and about the fluttering of prey. The FM signals provide multidimensional acoustic images for other aspects of the perception of prey against background and for tracking of prey after CF echoes have demonstrated the presence of an interesting target, just as they do for other types of pursuit. Both the CF and the FM signals appear to provide information about the direction of prey (*25*), but only the FM signals provide good information about distance and most other target features. This is a *velocity-sensing clutter-rejection pursuit strategy* in which the specialized activity of observing target motion comes to dominate the bat's echolocation behavior. The peripheral auditory system is greatly modified through evolution to accommodate fine frequency resolution around the CF frequency (*26*). Sometimes, but not always, the FM target-imaging sonar system evolves to a condition of reduced acuity (*7*).

The foraging behavior of *R. ferrumequinum* is such that perception of target fluttering motions and target movement may be important for initiating the pursuit behavior by identifying a target as potential prey (*4, 15, 23*). The bat may pay less attention to unmoving objects, which would be an efficient specialization of behavior.

Pursuit of prey by fishing bats. Noctilio leporinus uses sonar to detect and locate small fish at the surface of water (*18*). This behavior requires the detection of ripples caused by the fish or the detection of a small part of the fish (a fin) projecting above the surface; it might appear to be a special instance of target detection and identification in the presence of clutter.

Figure 2e shows the sequence of orientation sounds used by *Noctilio* as it detects, approaches, and attacks prey in water. The sequence of signals progresses from short-CF–FM to FM waveforms during the pursuit. The signal patterns resemble the echolocation behavior of *P. personatus* (Fig. 1c), except that only one harmonic is used by *Noctilio*.

It is apparent from many observations that multiple-harmonic signals are associated with the presence of clutter or even the proximity of individual as opposed to complex obstacles. *Noctilio* can use multiple-harmonic signals in some circumstances (*18*), so it is somewhat surprising that it does not do so routinely when pursuing fish. The single-harmonic signals used by *Noctilio* suggest that detection and localization of ripples or small objects on a smooth water surface may not, in fact, be an instance of echolocation in clutter. It may be that the reflective properties of an object on water are such that the object appears as an isolated acoustic event, a discontinuity in the surface. *Noctilio* behaves more like *Tadarida* than like *Pteronotus* when examined from this viewpoint. Research is needed to answer this question.

Adaptive Changes in Echolocation

The data presented in the previous sections illustrate the ways in which different species of bats have evolved with differences in their sonar systems to more closely meet the requirements of their particular acoustic environments. Some of these species differences appear to be features of echolocation as part of each bat's genotype and not strictly situation-based adaptations of a single generalized form of echolocation possessed by all bats. When such diverse species as *Eptesicus*, *Phyllostomus*, *Pteronotus*, and *Rhinolophus* are placed in the same situation, a target-range discrimination task, they still use different sonar signals and perform differently (*7*). However, when *Tadarida* is placed in this situation it abandons its characteristic single-harmonic FM sounds (Fig. 1a) and uses multiple-harmonic FM sounds quite similar to those of *Eptesicus* (Fig. 2c).

The changes observed in the signals of all bats in the search, approach, and terminal stages of the pursuit of prey are illustrations of adaptive changes within individuals to different acoustic tasks: detection versus identification and localization. The range of adaptations that can occur is limited by the genotype, however. Some species are extremely adaptable (*Tadarida*), some are moderately adaptable (*Eptesicus* and *Pteronotus*), and some are relatively inflexible (*Rhinolophus*) in terms of their orientation sounds. Recent studies of the species *P. phyllotis* suggest that it may be particularly flexible in its use of sonar sounds (*17*). Figure 2b shows spectrograms of several different kinds of orientation sounds recorded from *P. phyllotis* in different situations. These signals encompass the range of signal types used by nearly all bat species. *Tadarida* exhibits a comparable breadth of adaptability. It remains to be seen whether many more species will prove to be more flexible than we know at present.

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Australian Prehistory: New Aspects of Antiquity

Recent discoveries make the prehistory of Australia's Aborigines longer and emphasize local developments.

J. Peter White and James F. O'Connell

Interpretations of Australian prehistory have generally emphasized the foreign origin of many aspects of Aboriginal culture, as of Aborigines themselves. While excavations from 1790 onward showed that economic and technological changes occurred in Australian prehistory, full appreciation of the import of these changes is recent. Since the 1960's, the development of anthropologically oriented archeology has led to the discovery of a prehistoric record dating back into late Pleistocene times. We review evidence that defines more precisely the antiquity and probable mode of arrival of the first Australians and shows that their impact on the local fauna and the evolution of their economy and technology possess distinctive characteristics.

Earliest Arrivals

The earliest indisputable date for human occupation of Greater Australia (including New Guinea, Tasmania, and other islands on the Sahul Shelf) is 32,750 ± 1,250 years before present (B.P.; sample ANU-331) on man-transported unioid shells at Lake Mungo in western New South Wales (Fig. 1) (*1, 2*). This site, on the shores of a now extinct lake, lies within the Mungo depositional unit, one of a series of layers of wind-blown sand and clay that document fluctuating water levels during the late Pleistocene. Other dates on charred plant remains and unioid shells from the same unit are older (34,000 to 38,000 years B.P.), but less certainly associated with human activity (*3, 4*). Slightly more recent human occupation (24,000 to 30,000 years B.P.) is well documented both from these deposits and their stratigraphic equivalents in nearby lake basins (*1, 5*). Extensive searches have so far failed to produce any evidence for man in the underlying Golgol unit, which has an estimated age of 70,000 to 120,000 years B.P. (*2*).

At Keilor, southern Victoria, long-term investigations of a complex depositional sequence in the Maribrynong Valley have led to the discovery of quartzite artifacts from throughout a unit (the "D Clay") with an age conservatively estimated at 26,000 to 36,000 years, and possibly as great as 45,000 years (*2, 6*). Stone tools are claimed from earlier horizons (*7, 7a*), but their human origin has not been clearly demonstrated (*8; 9*, p. 146).

Other claims for greater antiquity are based on indirect evidence. Singh reports (*10*) evidence from studies of pollen of an increasing proportion of myrtaceous herbs and shrubs in forests around Lake George, eastern New South Wales, beginning at about 50,000 years B.P. He suggests that this could result from an increased frequency of fire, reflecting a drier climate, or the presence of man, or both. There is at present no direct archeological evidence for man in the area before 4000 years B.P. (*11*).

The most controversial claims for occupation prior to 50,000 years B.P. are made on the basis of human skeletal remains from several terminal Pleistocene (about 10,000 years B.P.) sites in northwest Victoria and adjacent parts of New South Wales. These remains are definitely from *Homo sapiens*, but bear a strong resemblance to mid-Pleistocene *Homo erectus* in certain features of cranial morphology, notably overall cranial size, vault bone thickness, and form of face and mandible (*12*). Thorne (*13*) has offered several possible explanations for this resemblance, one being that greater Australia was initially occupied by a morphologically archaic population. This would require a date much older than any mentioned above. The only other indication of similarly early movement toward Australia comes from reported occurrences of Patjitanian or Patjitanian-like stone tools on several islands within

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