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Sound Localization by Monkeys: A Field Experiment

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Summary. Characteristic responses shown by free ranging mangabeys to playback of species-specific vocalizations allow field measurement of their sound-localizing abilities. The median error of localization of single 10 to 15 s calls heard through several hundred meters of tropical forest was only 6°.

Introduction

Groups of graycheeked mangabeys *Cercocebus albigena* respond to certain species-specific vocalizations with a constellation of behaviors including rapid approach by particular adult males (Waser, 1975a, 1976, 1977). These vocalizations, termed "whoopgobbles" (Chalmers, 1968), have long been suspected of playing roles in intergroup spacing and cohesion; recently, it has been possible to confirm these functions through experimental playback of recorded mangabey vocalizations (Waser, 1975a, 1977). Because males rapidly approach not only experimentally-broadcast but also naturally-occurring whoopgobbles, the abilities of these forest monkeys to detect and localize whoopgobble calls can also be investigated in the field.

Since Marler's observation of the convergent and apparently non-localizable structures of many avian alarm calls (Marler, 1957), the importance of sound localization in influencing the design of communicative signals (Konishi, 1970) and auditory systems (Beecher, 1975; Masterton, 1974) has become evident. Nevertheless, psychophysical data concerning sound localizing abilities are only beginning to be available for species other than *Homo sapiens* or for sounds other than tones, noise bands, or clicks (Brown et al., 1975; Casseday and Neff, 1973; Konishi, 1973; Erulkar, 1972; Gourevitch, in press). Since location and "monitoring" of neighboring groups' movements may be particularly important to mangabey males (Waser, 1976) an acute ability to localize whoopgobble calls would be expected.

Methods

Tn this study, examples of the whoopgobble call were recorded from individually recognizable males within a mangabey population in the Kibale Forest, western Uganda (See Struhsaker, 1975; Waser and Floody, 1974; Waser, 1975b). These recorded calls were subsequently played back to the same or neighboring mangabey groups. Each experiment involved two observers: one who remained with the test group and recorded movements, vocalizations, and other behaviors before and after the playback; and a second who controlled the playback equipment and observed any mangabey activity in its vicinity. Mangabey locations were plotted with reference to a mapped grid of trails that provided reference points at 50 m intervals or less. Playback tests reported here fell into two categories: "near," in which the location of the playback equipment was 100 to 150 m from the nearest mangabey at the time of the test; and "distant," in which that separation was 275 to 575 m (most commonly 400 to 500 m). In each test, only a single example of the whoopgobble call was broadcast, using a Uher Report 4000-L recorder and Kudelski DH external speaker, at approx. the call's normal intensity (See Waser, 1977, for further description of methods). In order to minimize the possibility that mangabeys would associate the rebroadcast calls with the playback equipment or observer, the tape recorder and speaker were immediately disconnected and concealed following each 10–15 s test. The second observer then left the playback equipment and observed any approaching mangabeys in the surrounding area. Tests were repeated only at intervals of two days or longer.

Results

In each mangabey group investigated, one male (Waser, 1976) repeatedly showed the following response characteristics: (a) at the initial "whoop," the male stopped its ongoing activity and oriented towards the call; (b) within 1 min of the completion of the call, he began an approach towards the playback site, leaving his group with a conspicious, stiff-legged bounding gait and gradually increasing his height in the trees as he ran; (c) if approach was not blocked by major gaps in the vegetation, he reached or passed the vicinity of the playback site within 5 to 20 min. This male then spent a period of 15 min to several hours in the forest beyond the playback site, remaining high in the canopy and commonly giving whoopgobble calls himself (Fig. 1).

Because whoopgobbles are normally stereotyped in form but are infrequent in occurrance, the pattern of testing approximated the natural situation as well as providing a standard test stimulus that allowed the monkeys only a single judgement of location per test. Even in "near" tests, it is extremely unlikely that the playback equipment itself was visible when in use, and once playback was completed no further auditory cues were available. Since males sometimes passed directly over the second observer or over the equipment without stopping or otherwise investigating, it seems likely that the track of a male passing the playback site provides a real estimate of his error in acoustic judgment of whoopgobble source azimuth. Moreover, since monkeys were to some extent limited to specific "routes" in the canopy by the forest structure, these are conservative measures of *auditory* localization ability (Fig. 1). In addition to the gross inattention of approaching males to the observers, several factors argue that their presence provided no subsidiary cues to playback location that a mangabey might learn: (a) the presence of two observers was an event of daily familiarity to these animals, and these observers' locations

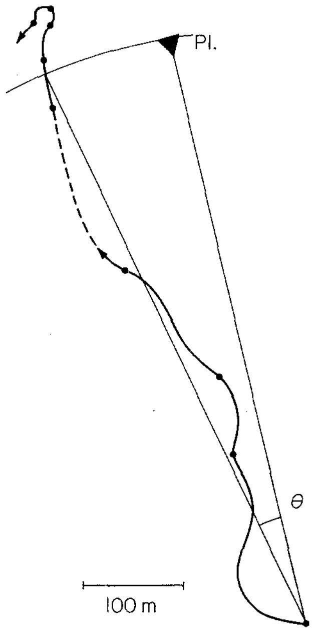

Fig. 1. Track of "rapidly approaching" male following playback of neighboring group's whoopgobble, illustrating method used to measure the angular error of localization θ. In this test, the mangabey was kept in sight through nearly his entire approach (solid line; locations at 5-min intervals are indicated by dots). His angular error was taken as that exhibited when crossing the arc drawn through the playback site and centered on his location at the time of playback. In this experiment, the male's location was 575 m from the playback site at the time of the playback, and his angular error was 14°

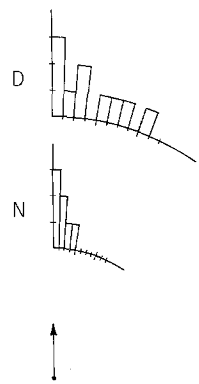

Fig. 2. Distribution of angular errors θ for near (N: $n=7$) and distant (D: $n=10$) tests; arrow indicates "correct" direction. Ordinate = number of tests; abscissa = error in degrees. Class limits for histograms are 2.5° apart. In one additional test, the approaching male was lost before passing the playback site; its angular error is thus unknown

were nearly always unrelated to those of naturally occurring whoopgobbles; (b) sympatric primate species, for which some of these tests served as controls to playbacks of their own species-specific calls, showed no measureable responses and thus, even when present, provided no indirect cues to playback location; (c) an improvement in localization ability with time, which would be expected if mangabeys were learning to use cues associated with the observer's presence, did not occur.

Tracks of males passing playback sites were recorded and their angular errors while passing the playback site calculated during 17 tests (Fig. 2). In 7 "near" tests, the median error of whoopgobble localization was 3° (range 0–9°). In 10 "distant" tests, during which mangabeys were required not only to make an initial azimuth estimate but also to maintain their bearing through several hundred meters of forest, their median angular error was 6° (range 0° to 21°). As impressive as these statistics was the observation that several of the most accurate approaches were to playbacks so far away as to be nearly or completely inaudible to the observer under the responding group.

The physical structure of the whoopgobble—a rapid, stereotyped series of stacatto pulses, preceded by a tonal, alerting whoop (cf. Waser, 1975a)—provides an admirable variety of potential cues to location. Of these, the repeated sharp pulse onsets in the gobble are the most obvious, but the concentration of energy at relatively low frequencies (100 to 1500 Hz, a range within which interaural phase differences can readily be used to determine azimuth) as well as the broad bandwidth of gobble pulse (harmonics above 3kHz occur, potentially allowing the use of differential intensity cues) may also be important (Gulick, 1971; Mills, 1972). Within the forest canopy, however, differential attenuation of high frequencies and "softening" of sharp onsets by scattering probably remove many of these cues rapidly (Waser and Waser, 1977). Nevertheless, the localization errors reported here compare very favorably with those of other nonhuman primates in psychophysical tests. For instance, Brown et al. (1975) found minimum audible angle for pure 8kHz tones to range from 7 to 14° for 3 individual macaques; increase of stimulus bandwith to 4kHz was necessary to allow these individuals to detect changes in sound source azimuth in the range of 3 to 6°. Determination of those specializations of the mangabey whoopgobble, or of the mangabey auditory system, that are responsible for their ability to localize these sounds, will require further experimental study.

For humans, the minimum audible angle for pure tones presented near the median plane—where accuracy is maximal—is on the order of 1° between 250–1000 Hz (Mills, 1958; Sandel et al., 1955). However, these mangabey tests appear more comparable in design to those of Stevens and Newman (1936) who asked human subjects to report the positions of sound broadcast nearby. These authors report average differences between real and reported azimuth of 12° for pure tones at 250 Hz, 8° for single clicks, and 5.6° for broad-band noise. I am aware of anly one attempt to measure the ability of humans to localize distant species-specific sounds in tropical forest: soldiers in Panamanian forests misjudge the azimuth of gunshots 300 to 600 feet away by an average of 16.5° (Eyring, 1946).

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