

## Localization of Noise, Use of Binaural Cues, and a Description of the Superior Olivary Complex in the Smallest Carnivore, the Least Weasel (*Mustela nivalis*)

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Cats and dogs have relatively good sound-localization acuity, and the question arises as to whether this trait is a characteristic of all carnivores or whether it is due to the fact that they have large heads and correspondingly large binaural localization cues available to them. The localization acuity of the least weasel, the smallest extant carnivore, was found to be less accurate than larger carnivores but more accurate than other small mammals. This suggests that carnivores may be under strong selective pressure to localize accurately but that interaural distance may be a limiting factor. The least weasel is capable of using both binaural phase differences and intensity differences to localize, but has a relatively broad mid-frequency range for which neither cue is optimal. Finally, the superior olivary complex of the least weasel is well developed and resembles that of larger carnivores more than that of small rodents.

Because of the obvious importance of sound localization to an animal's survival, it has seemed reasonable to assume that all mammals are under strong selective pressure to localize sound accurately (e.g., Masterton & Diamond, 1973). Although it has been recognized that some mammals can localize more accurately than others, this fact has usually been attributed to the availability of binaural sound-localization cues, which is determined largely by an animal's interaural distance (cf. Phillips & Brugge, 1985). That is, a large interaural distance generates large binaural localization cues both in the time of arrival ( $\Delta t$ ) and the frequency-intensity spectrum ( $\Delta I$ ) of a sound at the two ears. These physically larger cues, in turn, enable the nervous system to analyze more accurately the azimuth of a sound source.

Recently, however, it has become apparent that localization acuity is not simply determined by the availability of locus cues. In particular, it has been demonstrated that the horse is unable to localize as accurately as much smaller animals even though its interaural distance and available binaural cues are quite large. For example, whereas monkeys and cats can localize as accurately as  $4^\circ$  and  $5^\circ$ , respectively, the horse has a comparable threshold of  $22^\circ$  (H. E. Heffner & R. S. Heffner, 1984). Thus we have been forced to conclude that at least some of the variation in localization acuity is due not to the availability of adequate locus cues, but to variation in the degree of selective pressure for accurate localization.

If some mammals localize more accurately than others as a result of selective pressure, the question arises as to what those pressures may be. One possibility is that predators may be under more pressure to localize accurately than prey (H. E. Heffner & R. S. Heffner, 1984). To be successful, a predator may need to know exactly where its prey is, whereas the prey, in order to escape, may need only an approximate idea of where the predator is.

Although the good localization acuity of cats and dogs and the poor acuity of rodents and horses support this idea, it should be noted that most of the prey species tested so far have smaller interaural distances than the predators. Even though interaural distance may not be a determining factor in localization acuity, it may be a limiting factor that prevents small mammals from localizing more accurately than they do. The localization acuity of a carnivore with an interaural distance equal to that of small rodents could provide insight into the importance of interaural distance for sound localization.

To determine whether a small carnivore could localize sound more accurately than small rodents, we measured the localization acuity of the least weasel, the smallest extant member of the order Canivora. A member of the mustelid family, the least weasel is a strict carnivore that feeds on mice and voles (e.g., Nowak & Paradiso, 1983). In particular, the least weasel's weight and interaural distance are similar to those of mice, making it an ideal choice for comparison with small rodents. In addition to determining localization acuity, we also assessed the ability of the least weasel to localize low- and high-frequency tones at an angle of separation of  $60^\circ$ . This latter test provides an assessment of an animal's ability to use the binaural phase-difference cue ( $\Delta\phi$ ) and the binaural intensity-difference cue ( $\Delta I$ ). Because the superior olivary complex is the first auditory nucleus in the brain stem to receive binaural input and because the analysis of interaural phase and intensity differences has been linked to the medial and lateral superior olive, respectively (e.g., Masterton,

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Thompson, Bechtold, & RoBards, 1975), a description of these nuclei in the least weasel is also provided.

## Method

### Subjects

One male and 1 female least weasel (*Mustela nivalis*) approximately 2.5 years old and weighing 67 g and 54 g, respectively, were used in these experiments. They had been trapped in the vicinity of East Lansing, Michigan, and their audiograms had been determined in a previous experiment (R. S. Heffner & H. E. Heffner, 1985). They were housed in covered glass tanks in a quiet room and fed a meat paste composed of raw meat and liver, canned fish, crushed cat chow, and a vitamin supplement. This diet was supplemented with at least one mouse each week. Water was used as a reward and was available only in the test sessions. Sessions were conducted twice daily, and the animals were weighed each day to monitor their health and deprivational state. The weasels typically consumed 1.5–3.0 ml of water per session, which was sufficient to maintain them in good health. Their middle ears were later examined and found to be free of signs of disease.

### Behavioral Apparatus

The behavioral apparatus was the same as that used previously (for an illustration, see R. S. Heffner & H. E. Heffner, 1985). The weasels were tested in a cage constructed of ¼-in. (6.4-cm) hardware cloth on a wooden frame. The cage consisted of a larger section (50 × 25 × 25 cm) with a small compartment (8 × 6 × 9 cm) attached to the front of the cage. The top of the cage was removable to allow access. The cage was mounted on a table covered with egg crate foam and located in a double-walled sound chamber (IAC, 2.55 × 2.75 × 2.05 m).

A blunted 22-ga. hypodermic needle, which served as the waterspout, was mounted so that it protruded just inside the front of the small compartment. The waterspout was connected by plastic tubing to an electrically operated water valve and a 25-ml water reservoir, both of which were located outside the chamber in an adjacent control room. To detect when an animal was drinking from the spout, a contact circuit was connected between the waterspout and damp electrically conductive foam, which was placed on the cage floor to improve the electrical contact with the animal's feet. A constant current shock generator was also connected between the spout and the foam.

### Sound Production and Measurement

**Noise localization.** Sound-localization thresholds were determined for a single brief burst of white noise (100-ms duration, 0.1-ms rise-decay). The noise was generated by a noise generator (Grason Stadler 1285), shaped by a rise-fall gate (Grason Stadler 1287), and led through an impedance matching transformer to a pair of dual loudspeakers consisting of a 3-in. (7.6-cm) paper cone speaker mounted in a 500-cc enclosure and a piezoelectric tweeter with a 3-in. (7.6 mm) horn mounted directly above such that the center of the speakers were 3.5 in. (8.9 cm) apart. The loudspeakers were mounted on a perimeter bar (102-cm radius) which was centered on the middle of the animal's head when it was drinking. This arrangement produced noise with greatest intensity between 3 and 50 kHz and an overall intensity of 69.5 dB SPL at the location of the animal's ears. (For the spectrum of the noise, see H. E. Heffner & R. S. Heffner, 1985.)

**Tone localization.** The weasels were tested for their ability to localize a single tone pip from 200 Hz to 40 kHz at a fixed separation of 60°. The tones were produced by an oscillator (Hewlett Packard 209A), shaped with a rise-decay gate (Grason Stadler 1287), attenuated with a programmable attenuator (Coulbourn S85-08), filtered (Krohn Hite 3202), amplified (Crown D75), and finally led through an impedance matching transformer to a pair of matched speakers (12.7-cm wide range speakers or 7.6-cm speakers in 905-cm<sup>2</sup> enclosures for frequencies of 8 kHz and below, and 3-cm dome tweeters, or piezoelectric tweeters for frequencies of 8 kHz and higher).

The speakers were mounted on the perimeter bar at ear level at a fixed angle of 30° to the left and right of midline. The speaker pairs were equated for intensity with a sound level meter (Bruel & Kjaer 2203 or 2608 microphone amplifier, 4131 or 4135 microphone, and 1613 filter). The tones ranged in octave intervals from 250 Hz to 32 kHz with 200 Hz and 40 kHz also being used. The tone pips were 100 ms in duration with rise-decay times of 50 ms to avoid onset and offset transients. All tones were presented at an average intensity of 50 dB above threshold (see Figure 1) and were randomly attenuated ±2 dB to reduce the possibility that the animals might detect slight differences between speakers.

### Psychophysical Procedure

The avoidance procedure used here is similar to that described elsewhere (H. E. Heffner & R. S. Heffner, 1984). A thirsty animal was trained to make steady contact with the waterspout by providing a steady trickle of water (0.15 ml/min) as long as the animal maintained contact with the spout thereby centering the animal's head in the sound field. The weasels were initially trained to drink steadily while listening to "safe" trials (S) which consisted of 2-s trains of broadband noise bursts (5/s) presented once every 5 s from a loudspeaker located 90° to the right of the animal. After the animals had learned to maintain steady contact for 15 min or more, "warning" trials (W) were introduced in which the auditory stimulus was occasionally switched to a loudspeaker 90° to the animal's left side and its offset was followed by a mild electric shock delivered between the waterspout and the damp electrically conductive foam on which the weasel stood. After only a few pairings of the left sound with shock, the animals learned to avoid the shock by breaking contact with the spout whenever the noise burst was presented from the left side. In order to provide feedback for successful avoidance, the light in the

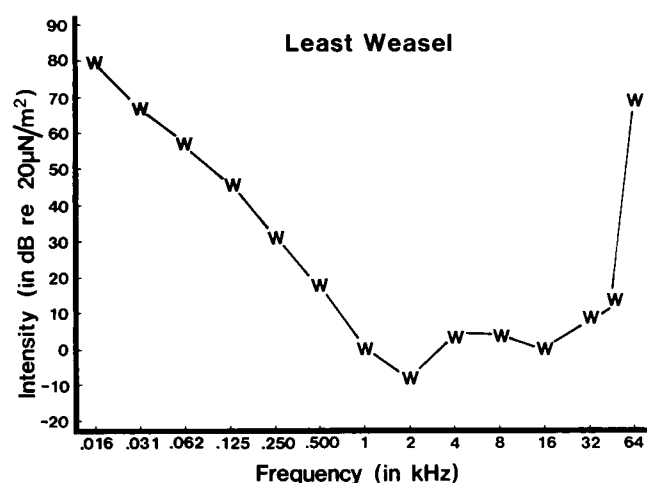


Figure 1. Audiogram of the least weasel (R. S. Heffner & H. E. Heffner, 1985. W = weasel.)

test room was momentarily turned off each time shock was delivered. Thus the light served to indicate that a warning trial was over and that the animal could return to the waterspout. Cessation of spout contact was used as an indication of an animal's ability to perceive a shift in locus.

The presentation of safe and warning trials was randomized, with a warning trial likely to occur anywhere from 1 to 10 trials after the previous warning trial. Occasionally no warning trial was given in a sequence of 10 trials in order to prevent an animal from using the time or number of safe trials since the last warning trial as a cue. The trial sequence was suspended during the 5 s immediately following a warning trial in order to allow the animal sufficient time to return to the waterspout.

For the purpose of quantifying an animal's response, the duration of spout contact was measured in 0.02-s increments beginning 1.8 s after stimulus onset until 0.2 s later at the end of the trial. This measured "time in contact" was then averaged separately for the safe trials and the warning trials for each angle of separation. A measure of discrimination could then be expressed in the form of the ratio  $(S-W)/S$  for each angle. In trained animals this measure varies from near zero (failure to discriminate) to unity (perfect discrimination). In order to reduce the effects of spurious pauses, the results of a trial were automatically discarded if the animal was not in contact with the spout at any time during the 1 s immediately preceding the trial, though the trial and shock were presented as usual. Because this criterion was applied equally to safe and warning trials, it did not bias the results.

In the final stage of training, the duration of the stimulus was reduced to a single 100-ms noise burst in order to prevent the animals from using scanning movements of the head and pinnae to localize the sound. Sound-localization thresholds were then estimated by gradually reducing the angular separation between the left and right loudspeakers until the animal's performance fell to chance. Once a preliminary threshold had been obtained, threshold testing was continued with trials given in blocks at angles both above and below threshold. Psychophysical functions were then plotted by taking the average of the scores from each animal's best three sessions (asymptotic performance) with a minimum of 30 warning trials per angle. Threshold was arbitrarily defined in both of two ways: (a) as the smallest angle yielding a performance ratio of 0.50 (i.e., 50% detection) and (b) as the smallest angle at which the animal could discriminate between the two stimuli at the .01 one-tailed level of statistical reliability (Mann-Whitney  $U$  test) which in this case was a performance ratio of .30.

Following completion of acuity tests with brief noise bursts, the same conditioned avoidance procedure was used to determine the weasels' ability to discriminate the source of tone pips separated by 60°. A total of 40 warning trials were given at each frequency over three to six sessions, and performance ratios were calculated at each frequency for blocks of 10 consecutive warning trials. The highest performance maintained over a block of 10 consecutive warning trials was recorded as asymptotic performance.

A typical session lasted as long as 30 min, during which an animal received from 50 to 120 trials (18% of which were warning trials).

### Anatomical Method

The brains of 2 adult *Mustela nivalis* were perfused with 10% formalin and prepared for frozen sectioning by immersion in a graded series of glycerin solutions ending in 25% glycerin. Both coronal and horizontal sections were cut at 25- $\mu$ m thickness. Two sets of sections with 75- $\mu$ m separation were prepared in each plane, one stained with thionin for cell bodies, and the other one stained with Protargol for neurons and neuropil. These sections were examined with a light

microscope and compared to similarly prepared sections from other carnivores and small rodents.

## Results

### Broad-Band Noise Localization

The ability of the 2 weasels to localize 100-ms bursts of noise is illustrated in Figure 2. The animals were able to maintain perfect performance at angles larger than 20°, which indicates that the task was an easy one for them to perform. Performance declined below 20°, with Weasel A unable to localize 6° and Weasel B unable to localize 10° above chance. The 50% discrimination thresholds were interpolated to be 11° and 13° for A and B, respectively; the .01 chance level thresholds were calculated to be 9° and 11°. The average false positive rate for both of the animals was 6%.

### Tone Localization

To further explore the ability of the weasels to discriminate differences in the direction of a sound source, the animals were tested for their ability to localize a brief tone pip at frequencies from 200 Hz to 40 kHz. This test is of significance because the ability to localize low-frequency tones indicates that an animal can use the binaural phase-difference cue for sound localization and the ability to localize high-frequency tones indicates the use of binaural spectrum- or intensity-difference cues (e.g., Brown, Beecher, Moody, & Stebbins, 1978; Masterton et al., 1975; Stevens & Newman, 1936).

The ability of the two weasels to localize the sources of tone pips separated by 60° is illustrated in Figure 3. At 60° separation, the calculated frequency above which the phase cue is ambiguous is 13.7 kHz (indicated by the arrow in Figure 3; see Kuhn, 1977, or Brown et al., 1978, for the formula for calculating the frequency of phase ambiguity). As shown in the figure, the weasels were able to localize frequencies above and below the frequency of ambiguity, which indicates that they could use both the phase- and intensity-difference cues. Indeed, both animals were capable of perfect performance on at least one low frequency (500 Hz) and one high frequency (32 kHz).

Two additional points are apparent from their tone-localization performance. First, there is a region around 8 kHz where neither cue is particularly effective. This region is relatively broad as a result of the gradual decrease in performance beginning above 1 kHz. Evidently, the weasel's ability to use the phase cue begins to decline well before the theoretical upper limit of its usefulness is reached. The second notable point concerning their tone-localization performance is the decrease in performance at the lowest frequencies tested. We will return to these two points in the Discussion.

### Superior Olivary Complex

The superior olivary complex (SOC) of the least weasel is illustrated in Figure 4. The SOC is large in relation to the brain stem, completely filling the region between the exits of

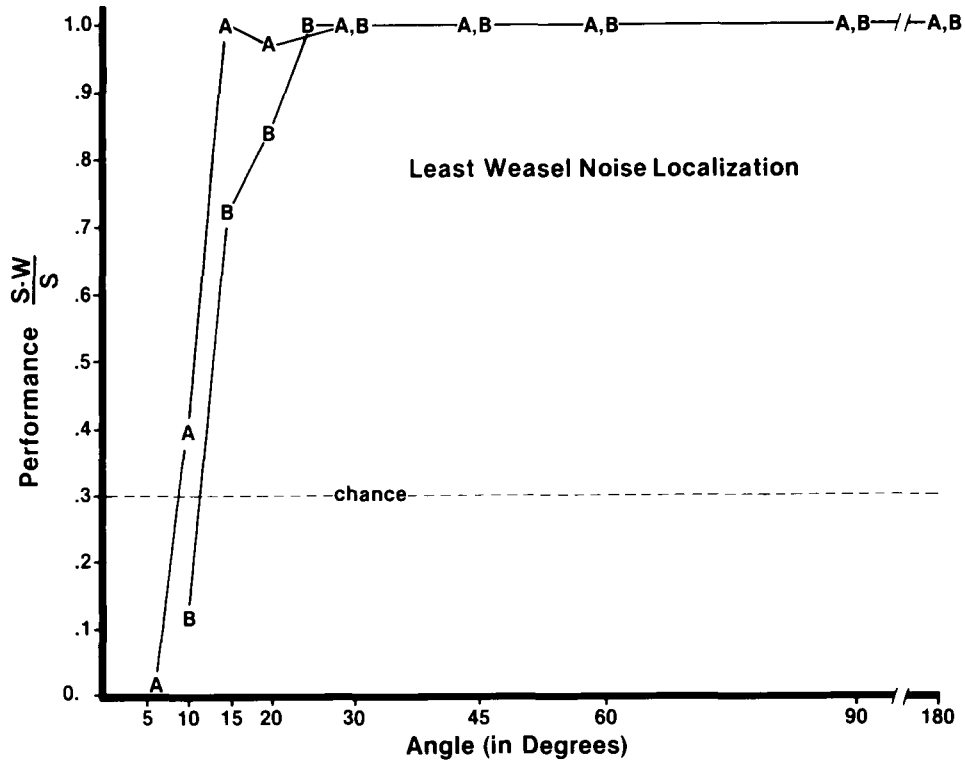


Figure 2. Sound-localization performance of two weasels for white noise (100-ms duration, 0.1-ms rise-decay). (A and B represent individual animals; dashed line represents the .01 statistical threshold.)

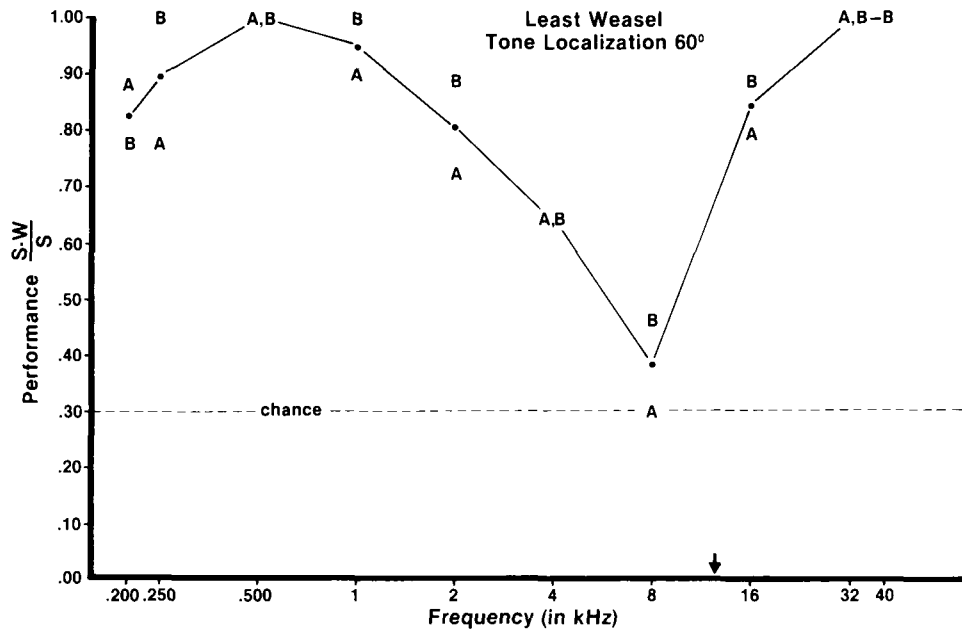


Figure 3. Ability of two weasels to localize pure-tone pips (100-ms duration, 50-ms rise-decay) separated by 60°. (Arrow indicates the calculated frequency above which the phase cue is ambiguous. Note that although the weasels can localize both low and high frequencies, there is a broad region of ambiguity in which neither the phase nor intensity cue is effectively used. A and B represent individual animals.)

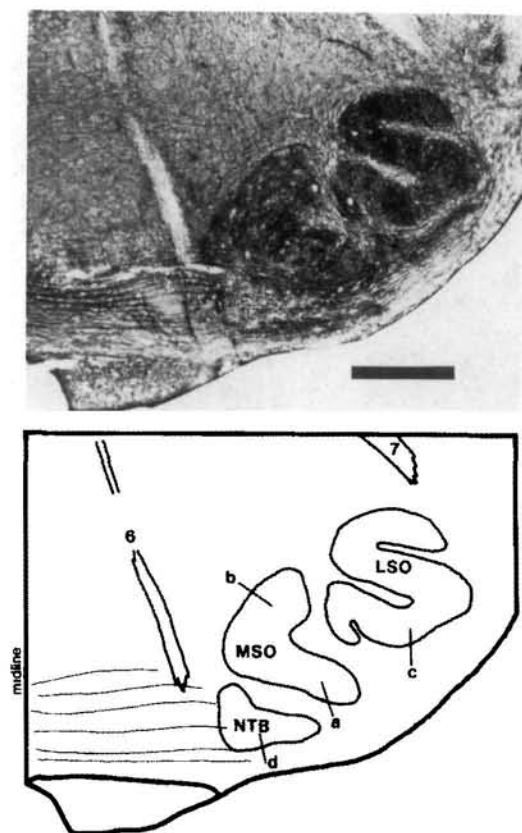


Figure 4 Superior olivary complex of the least weasel. (Note the dense neuropil and the large size of the nuclei in relation to the brain stem. Protargol stain; 6 = sixth nerve; 7 = seventh nerve; LSO = lateral superior olive; MSO = medial superior olive; NTB = nucleus of the trapezoid body; a-d indicate location of photomicrographs in Figure 5; scale bar equals 0.5 mm. See Plate C.)

the sixth and seventh nerves. Both the medial and lateral nuclei are well defined by their dense neuropil. The medial superior olivary nucleus (MSO) is large, and the dorsal portion bends laterally—a condition also seen in the dog (Goldberg & Brown, 1968). In transverse section the cells of the MSO have a typical fusiform shape and appear to be of two types similar to those described for the kangaroo rat (Webster, Ackermann, & Longa, 1968). One type of cell is narrow with a dark-staining nucleus, and the other type is broader with a light-staining nucleus (Figure 5A). The narrow cells are common ventrally (Figure 5A), becoming less common in the dorsal (bent) region (Figure 5B). The density of neurons is less in the dorsal region with the larger cells comprising the majority.

The lateral superior olivary nucleus (LSO) of the least weasel is large and convoluted (Figure 4). Although it is similar in appearance to the LSO in the dog and cat (Goldberg & Brown, 1968; Stotler, 1953), it contains four limbs rather than three. The individual neurons are spindle-shaped in transverse sections with their poles oriented perpendicular to the borders of the nucleus (Figure 5C). Most of the cells in the LSO stain lightly and contain large nuclei.

The medial nucleus of the trapezoid body (MNTB) lies within the fibers of the trapezoid body lateral to the sixth nerve. The neurons of the MNTB are round to oval in shape, stain darkly, and receive calyx-type synapses from large fibers in the trapezoid body (Figure 5D).

## Discussion

### Localization Acuity

A comparison of the localization acuity of weasels with that of other carnivores and rodents provides some insight into the relative influence of interaural distance and trophic level (i.e., whether an animal is a predator or prey). Table 1 lists sound-localization thresholds for the seven species of carnivores and rodents whose thresholds are available. In comparing animals, it is important to note the type of stimulus used to determine threshold. Noise bursts are usually localized more accurately than single clicks, perhaps owing to their longer duration and broader bandwidth (cf. H. E. Heffner & R. S. Heffner, 1984; R. S. Heffner & H. E. Heffner, 1982; Stevens & Newman, 1936). The comparison in Table 1 uses noise-localization thresholds wherever they are available. In the case of the dog, the noise burst-localization threshold would be expected to be slightly better than that for single clicks.

Among these animals, the 50% detection thresholds range from 5° in the domestic cat to 27° in the gerbil and kangaroo rat. It is interesting to note that there is no overlap between the thresholds of the carnivores and rodents even though one of the carnivores (the least weasel) has a smaller interaural distance than any of the rodents. Although the least weasel's interaural distance is smaller than that of even the smaller rodents, its threshold of 12° is far superior to that of the kangaroo rat and gerbil. Indeed, the threshold of the weasel is slightly better than that of the Norway rat, a rodent with nearly twice its interaural distance.

The relatively good localization acuity of the weasel illustrates that a very small animal can be more accurate than the performance of small rodents had indicated was possible. This in turn suggests that the poor acuity of some small species may not be due solely to the small magnitude of the binaural difference cues provided by their small head and close-set ears. On the other hand, the least weasel's threshold is obviously poorer than the 5° and 8° thresholds of the cat and dog. This difference raises the possibility that the small interaural distance of the weasel may be limiting its acuity.

Taken together these results lend support to the notion that Carnivores, and perhaps predatory species in general, are under strong selective pressure to localize sound accurately. However, the fact that weasels cannot localize as accurately as larger carnivores suggests that interaural distance may be a limiting factor in localization acuity.

### Localization of Tones and the Use of Binaural Locus Cues

The ability to localize low- and high-frequency tones has long been used to demonstrate the duplex theory of sound

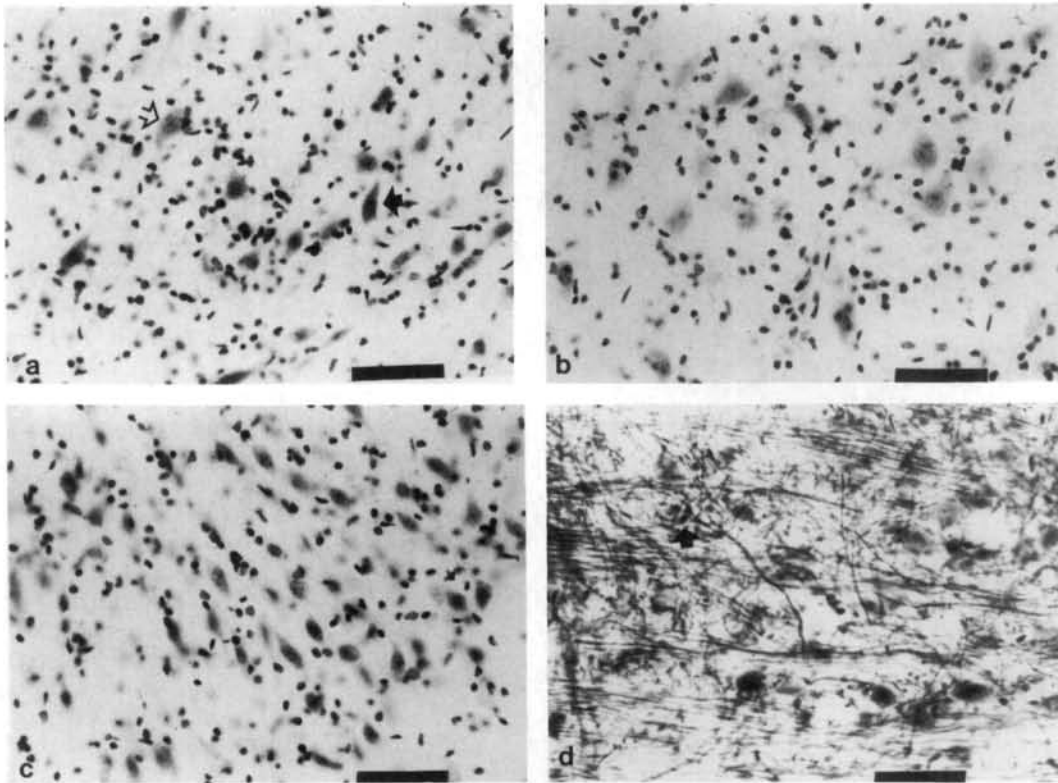


Figure 5. High-power photomicrographs of the three major nuclei in the superior olivary complex of the least weasel. (a, ventral region of the MSO, note difference between dark-staining [closed arrow] and light-staining [open arrow] cells, thionin stain; b, dorsal region of the MSO, note that there are only light staining cells, thionin stain; c, LSO, note spindle shape and orientation of neurons, thionin stain; d, cells and neuropil of the NTB, arrow indicates calyx-type ending, protargol stain; scale bars equal 50  $\mu\text{m}$ . See Plate D.)

localization (Stevens & Newman, 1936). Classically, the ability to localize low-frequency tones has been attributed to the use of binaural  $\Delta\phi$ , whereas the ability to localize high frequencies has been attributed to the use of binaural  $\Delta I$ . Furthermore, the occurrence of a region of reduced acuity in the midrange has been interpreted as indicating that neither cue is particularly effective in that region (Stevens & Newman, 1936).

In humans and some other animals such as cats and monkeys, the decrement in tone-localization acuity in the mid-range is relatively small (cf. Brown et al., 1978; Casseday & Neff, 1973; Masterton et al., 1975). However, for other mammals, particularly the smaller ones such as the least weasel, this decrement can be large. Indeed, in the case of the weasels, performance at 8 kHz at 60° separation fell almost to chance, which indicates that neither  $\Delta\phi$  nor  $\Delta I$  was very useful at this frequency (Figure 3).

In analyzing the weasel's performance in Figure 3, the usefulness of the  $\Delta\phi$  cue appears to decrease at frequencies above 1 kHz, and the animals' performances decline steadily to 8 kHz above which frequency the  $\Delta I$  cue becomes available. Theoretically, for an animal with an interaural distance of 76  $\mu\text{s}$ , the  $\Delta\phi$  cue should not become ambiguous at a 60° separation until 13.7 kHz. The fact that the weasel makes poor

use of binaural phase differences at 4 and 8 kHz suggests that there is a limit to the ability of an animal to use the binaural phase cue at these frequencies.

A physiological upper limit to the use of binaural  $\Delta\phi$  was first suggested by Stevens and Newman (1936), who noted that the auditory nerve was limited in its ability to synchronize with the phase of the stimulus. At that time the upper limit of phase locking was thought to be 2.8 kHz. More recently, it has been shown that the degree of synchronization in the auditory nerve of the squirrel monkey begins to decline with frequency above about 1 kHz and is no longer detectable above 5 kHz (Rose, Brugge, Anderson, & Hind, 1967). Similar results have been observed in the cat in which synchronization falls precipitously above 2 kHz and becomes difficult to detect above 4 kHz (Johnson, 1980). However, there is reason to believe that the vertebrate auditory system is capable of phase locking at even higher frequencies as phase locking up to 9.0 kHz has been observed in the cochlear nucleus of the barn owl (Sullivan & Konishi, 1984).

In large animals, a decrease in the ability to use phase is masked by the fact that  $\Delta\phi$  becomes physically ambiguous and binaural  $\Delta I$  becomes available before the upper limit of neural phase locking is reached. However, the weasel's head and pinnae are so small that  $\Delta I$  evidently does not become

Table 1  
*Sound-Localization Thresholds and Maximum Binaural Time Disparities for Carnivores and Rodents*

Species	Maximum $\Delta t^a$ (in $\mu s$ )	Threshold <sup>b</sup> (in degrees)	Stimulus	Source
Carnivores				
Cat	258	5	Noise burst	Casseday & Neff, 1973
Dog	435	8	Single click	H. E. Heffner, 1976
Least weasel	76	12	Noise burst	present paper
Rodents				
Norway rat (wild)	130	13	Noise burst	H. E. Heffner & R. S. Heffner, 1985
Wood rat	115	19	Noise burst	H. E. Heffner, 1987
Kangaroo rat	90	27	Single click	H. E. Heffner & Masterton, 1980
Gerbil	87	27	Noise burst	R. S. Heffner & H. E. Heffner, in press

<sup>a</sup> Maximum  $\Delta t$  is the maximum interaural distance divided by the speed of sound. <sup>b</sup> Threshold is defined as the 50% detection level (75% correct in two-choice procedures and 0.5 performance in conditioned avoidance procedures).

effective until approximately 13 kHz, with the result that the 4-kHz upper limit of usability of the phase cue is revealed. Thus, if the weasel's upper limit of phase locking is similar to the cat's, then the results of tone localization by the weasel are consistent with the idea that the limit of usefulness of the binaural phase cue at high frequencies is determined by the ability of auditory nerve fibers to synchronize with the phase of the stimulus.

It should be noted that the upper limit of usefulness of the binaural phase cue appears to vary between species. In humans, the upper limit for phase has been established at 1300 Hz (Klumpp & Eady, 1956), whereas many animals appear able to use phase at higher frequencies. For example, the upper limit in macaques and cats is around 2000 Hz (Houben & Gourevitch, 1979; Wakeford & Robinson, 1974). Smaller animals appear able to use phase at even higher frequencies, with the kangaroo rat using it up to about 4 kHz (H. E. Heffner & Masterton, 1980), whereas the Norway rat (Masterton et al., 1975) and least weasel have their upper limits between 4 kHz and 8 kHz. If the upper limit for the use of the phase cue is determined by the ability of the auditory system to encode phase, then a corresponding variation in this ability among different species would be expected.

The weasel's low-frequency tone-localization performance suggests another physiological limitation in the use of binaural phase. It has been suggested elsewhere (Houben & Gourevitch, 1979) that animals should have difficulty localizing very low frequencies because multiple discharges sometimes occur during a single cycle at these frequencies (Rose et al., 1967). Electrophysiological studies have also noted that the lower limit of phase locking (75–100 Hz) may be very close to the low-frequency limit of hearing at least in cat (Kuwada & Yin, 1983) and kangaroo rat (Stillman, 1971). As seen in Figure 3, the performance of the weasels decreases below 500 Hz even though all stimuli were presented 50 dB above threshold and the weasel's hearing range extends 3 octaves below 250 Hz.

This decline in performance by the weasel at frequencies well above the low-frequency hearing limit supports the notion that phase is not as precisely encoded at very long wavelengths, thus limiting the accuracy of that cue at very low frequencies independent of the animal's low-frequency hearing range.

### *Superior Olivary Complex*

The SOC comprises the principal binaural integration nuclei in the brain stem and provides the first opportunity for input from the two ears to interact. Although the functions of the two main components of the SOC, the MSO and the LSO, have not yet been precisely determined, it seems clear that they play different roles in the localization of sound. The majority of cells in the MSO are responsive to low frequencies, and their firing rates are strongly affected by the phase difference of stimuli at the two ears while remaining relatively insensitive to intensity differences (Goldberg, 1975; Goldberg & Brown, 1968). The LSO on the other hand is responsive primarily to high frequencies, and the firing rate of its neurons is strongly affected by transient intensity differences (onset) and ongoing intensity differences between the input at the two ears (Caird & Klinke, 1983; Goldberg, 1975; Yin & Kuwada, 1984). These differences suggest that the MSO is concerned with binaural time cues, whereas the LSO is concerned with binaural intensity cues, a conclusion supported by the fact that the hedgehog lacks both an MSO and the ability to use binaural phase (Masterton et al., 1975). Thus it is not surprising that both the MSO and LSO are well developed in the least weasel, a species capable of using both binaural phase- and intensity-difference cues that are of necessity small in magnitude owing to the animal's small interaural distance.

Among mammals as a whole, the SOC of the weasel resembles that of other small and medium carnivores—other Mustelids, small felines, and dogs. In these species the SOC is

large relative to the size of the brain stem; the MSO is large, columnar in form, and densely populated with fusiform-shaped neurons; the LSO is large, convoluted in form with three or more limbs, and also densely populated. Although less similar to rodents in general, when compared with rodents whose sound-localization ability is known, the SOC of the weasel most resembles that of the kangaroo rat. Both species have a hypertrophied MSO that impinges dorsally on the LSO, and the LSO of both species has a small medial hook and distinct limbs. However, the LSO of the weasel has a third limb laterally, whereas the kangaroo rat has two limbs forming a U shape. Although the auditory sensitivity of these two species is similar (H. E. Heffner & Masterton, 1980; R. S. Heffner & H. E. Heffner, 1985) and both are capable of using both phase and intensity cues to localize, the sound localization acuity of the weasel is much better than that of the kangaroo rat.

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