Brain, Behavior and Evolution
Editor-in-Chief: R. Glenn Northcutt, La Jolla, Calif.

Reprint
Publisher: S. Karger AG, Basel
Printed in Switzerland

Brain Behav Evol 1989;33:248-258

Sound Localization, Use of Binaural Cues and the Superior Olivary Complex in Pigs

Rickye S. Heffner, Henry E. Heffner
Laboratory of Comparative Hearing, University of Kansas, Parsons, Kans., USA

Key Words. Evolution · Auditory brainstem · Artiodactyla · *Sus scrofa*

Abstract. Noise localization thresholds and the ability to localize pure tones at 60° separation were determined for three domestic pigs using a conditioned avoidance procedure. The average threshold for localizing a brief noise burst was 4.5° which is much more accurate than the thresholds of other hoofed mammals, such as horses, cattle and goats. The ability of pigs to localize low-frequency tones indicates that they can use the binaural phase-difference cue. However, they were unable to localize tones of 4 kHz and higher, indicating that, like other hoofed mammals, their ability to use binaural intensity cues is greatly restricted if not completely absent. An examination of the superior olivary complex of pigs revealed that in relative size, shape and cell density it is more like that of cats than that of other hoofed mammals.

In our survey of sound localization among mammals of varying sizes, lifestyles and phyletic histories, we have found that localization acuity varies widely, from approximately 1° in humans and elephants to 20° and greater in horses and some small rodents [for recent reviews, see ref. 7, 13]. In attempting to analyze this variation, the first factor considered was the variation in the magnitude of the binaural cues for locus. That is, the large heads and widely spaced ears of some species result in larger interaural differences in time and intensity than do the small heads and narrowly spaced ears of smaller species. However, the correlation between interaural distance and localization acuity is not strong ($r = -0.50$, $n = 19$, $p < 0.01$) and indicates that interaural distance accounts for much less of the variance in acuity than originally expected.

In examining the relation between interaural distance and localization acuity, one group of mammals was found to be particularly exceptional in that its member species have much poorer acuity than expected based on their interaural distances. This group consists of hoofed mammals [7, 9]. Besides having poor localization acuity, these mammals are also exceptional in that each species seems to have lost, either partially or completely, the ability to use the binaural intensity-difference cue to localize sound [11, 12, 16]. Accompanying this inability is an atypical appearance of the superior olivary complex (SOC) [11, 12], the first nuclear complex in the auditory pathway to respond to binaural differences in intensity [18]. Thus, an understanding of the extent of variation in localization abilities, along with an appreciation of the selective pressures that produce the variation and the neural substrates that permit it, should lead to a more complete understanding of both the functions and mechanisms of hearing in mammals.

The purpose of the present report is to increase the sample of hoofed mammals examined for sound localization in order to determine how widespread is the phenomenon of poor acuity, loss of the binaural intensity cue and poor development of the SOC. The domestic pig *(Sus scrofa)* was selected as a subject based on both its phyletic heritage and its lifestyle. Like cattle, pigs belong to the Artiodactyla, a large and successful order consisting almost exclusively of large prey animals. However, pigs are members of the most primitive family in the order and are less specialized in their digestive physiology and behavior than bovids. Of particular interest is the fact that the domestic pig's wild ancestors in Asia, and their feral form in North America, are both rarely preyed upon but rather are, themselves, frequent predators. Thus, the degree of similarity of the sound localization ability of pigs to that of other hoofed mammals, and to that of more predatory species, may indicate whether sound localization is a conservative character common to all members of an order, or a character that changes more rapidly in response to the selective pressures peculiar to the lifestyle of each species.

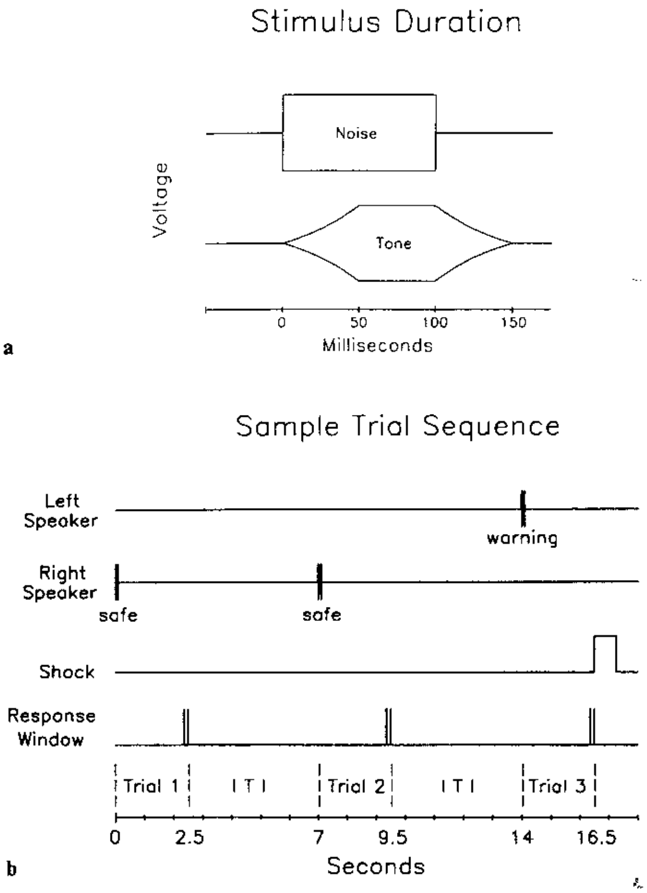

Fig. 1. a Stimuli used in sound localization. The noise stimulus had an abrupt onset and a 100-ms duration; the pure-tone stimuli had a 50-ms rise-decay and remained at full amplitude for 50 ms. **b** Sample trial sequence in which two safe (right) trials were followed by a warning (left) trial; note that shock follows the warning trial and occurs after the animal's response has been determined (i.e. at the end of the 'response window'). ITI = Intertrial interval.

Materials and Methods

Subjects

Three adolescent female pigs (referred to as A, B and C) of three different breeds (Duroc, Hampshire and Yorkshire, respectively) were used in these tests. The animals were housed together in a room with free access to food. Water was used as a reward and was available only in the test sessions. The animals were weighed daily to monitor their deprivational state. A complete audiogram of each animal, obtained previously, gave no indication of auditory disease, and the animals remained healthy throughout testing.

Behavioral Apparatus

Testing was conducted in a quiet cement block room, 3.15 × 2.55 × 2.44 m, the walls and ceiling of which had been lined with eggcrate foam and the floor carpeted to reduce sound reflection. A double door with fiberglas insulation between the doors was installed to attenuate sounds emanating from outside the room. A nearby, sonically isolated room housed the behavioral control and stimulus generation equipment and a television monitor for viewing the animals. The animals were tested in a wood frame stall, 1.35 m long by 0.55 m high by 0.5 m wide. The top and front of the stall were enclosed with a welded wire (5 × 10 cm mesh) arch 0.65 m above the sides of the stall. The pigs stood on a 27-cm high platform with their ears 22 cm above the side of the stall. A water spout 50 cm above the platform protruded into the wire mesh within easy reach of the pigs. The water spout was connected to a solenoid water valve and an 8-liter reservoir, both located in an adjacent room. The water spout was also connected to an electronic circuit which detected when the animal made contact with the spout, and mild electric shocks could be delivered through the spout and the metal floor.

Acoustic Apparatus

Noise localization thresholds were determined for a single 100-ms burst of broadband noise with a fast (10-μs) rise-decay. Considerable effort was expended to be sure that the pigs had no cue other than the locus of the sound source on which to base their responses. The electrical signal was produced by a noise generator (Grason Stadler 1285) and was then led to a programmable attenuator (Coulbourn S85-08) which randomly varied the intensity of the noise burst over a 7-dB range in order to guard against possible speaker differences. From there the signal was sent to either a left or right line, which, in turn, led to a rise-decay gate (Coulbourn S84-04), then to an amplifier (Crown D75), and finally to one of two loudspeakers mounted on a perimeter bar (1 m radius) at ear level. Thresholds were determined using both dome tweeters and Koss 1-in (2.54-cm) ministereo headphone receivers (which facilitated testing at small angles of separation). In a final effort to ensure against slight quality differences between speakers that might serve as a confounding cue, threshold determination was replicated with the spectrum of the noise randomly varied between three different spectra produced by three different settings of a graphic equalizer (Symmetric Sound Systems EQ-3) inserted between the noise generator and the programmable attenuator. There were no differences in performance or threshold between the two determinations, or with the two different transducers, so the data were combined.

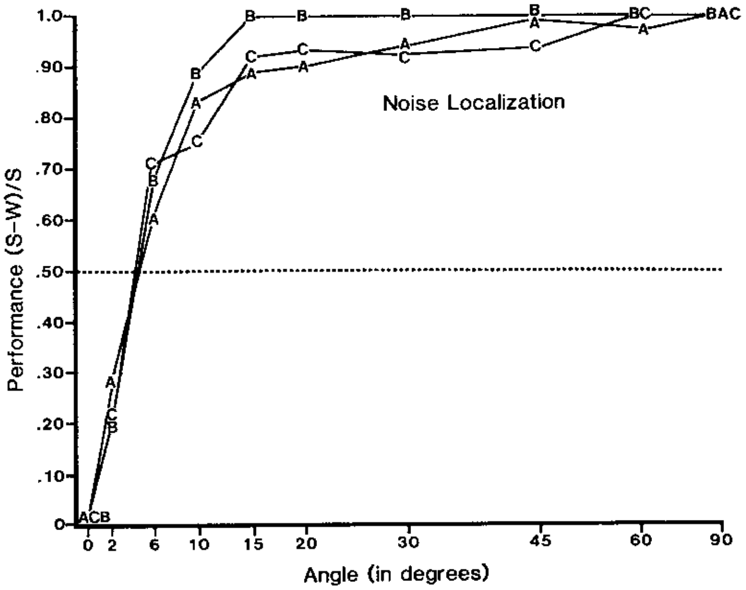

Fig. 2. Sound localization performance of three pigs using a single burst of broadband noise (100 ms duration). Note good performance at angles of azimuth as small as 10°, 50% detection threshold at 4.5° and close agreement among animals. A, B and C represent individual animals. Dashed line indicates 50% detection. A score of 1.0 indicates perfect detection, and a score of 0.0 indicates random performance (for further explanation see Psychophysical Procedures).

Pure-tone localization was examined at a fixed angle of 60° for single tone bursts of 100 ms duration and 50 ms rise-decay, permitting full amplitude for 50 ms (fig. 1). The tones were produced by an oscillator (Hewlett-Packard 209A) and led to a programmable attenuator (Coulbourn S85-08) which randomized intensities over a 4-dB range. From there the signal was sent to either a left or right line, then led to a rise-decay gate (Coulbourn S84-04), audio filter (Krohn Hite 3202), amplifier (Coulbourn S82-24) and, finally, to one of two loudspeakers placed on the perimeter bar (5-in woofers, dome tweeters or ribbon tweeters, depending on the frequency being produced).

Audiograms for the three pigs had been determined previously. Their hearing range at 60 dB intensity extends from approximately 40 Hz to 40 kHz, with a broad range of good sensitivity between 250 Hz and 16 kHz. All stimuli, whether noise or tone, were presented at an average of 45 dB above threshold.

Psychophysical Procedures

A conditioned avoidance procedure was used for testing. A thirsty animal was trained to drink steadily from the water spout in order to receive a steady trickle of water (35–65 ml/min) while listening to a noise burst emitted every 7 s from the speaker on its right side. It was then trained to break contact with the spout whenever the noise burst was emitted from the speaker to its left by following the left noise bursts by a mild electric shock from the spout. Breaking contact in this way allowed the animal to avoid the shock and served as an indication that the animal detected a shift in the locus of the sound source. To provide feedback for successful avoidance, a light in front of the animal was flashed during shock delivery. To reduce the effect 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 a trial although the trial was presented as usual. This criterion was applied equally to left and right trials and did not bias the results.

The test procedure, diagrammed in figure 1, consisted of presenting 2.5-second trials separated by 4.5-second intertrial intervals (i.e. one trial every 7 s). Each trial was either a 'safe' trial during which the signal came from the right, or a 'warning' trial in which the signal came from the left. Warning trials occurred randomly with a probability of 0.20. No trial was given in the 2.5 s immediately following a warning trial in order to allow an animal sufficient time to return to the spout.

Performance was quantified by detecting spout contact in each of the ten 15-ms time intervals during the final 150 ms of every trial. This measure of 'time in contact' was averaged separately for safe trials (S) and warning trials (W) for each angle of speaker separation, and a measure of discrimination was then expressed in the form (S–W)/S. In trained animals the measure varied from near 0.0 (failure to detect the shift in locus) to 1.0 for perfect detection.

For a second statistical analysis, the probability that the two samples of scores, S and W, belonged to the same population was determined for each block of trials at each angle (Mann-Whitney U test). Thresholds were determined by reducing the angular separation between the speakers until the pigs could no longer distinguish between them above a level expected by chance ($p < 0.01$). For comparison with other species, the 50% detection threshold (a performance score of 0.50) was used.

Anatomical Methods

The materials used consisted of the normal brains of three pigs. The animals were euthanized and then perfused through the heart with 0.9% saline followed by 10% formalin. The brains were prepared for frozen sectioning by immersion in a cryoprotectant (25% glycerine) and cut in either coronal, sagittal or horizontal sections 20–33 μm thick. Alternate series of sections were stained with either thionine or Protargol. The superior olives were compared with similarly stained material from numerous other species including cats, dogs, horses, cattle, goats, sheep, deer, elephants and numerous small species. Cats and horses were chosen for illustration because they best illustrate the relation of pigs to a well-known carnivore and to a representative hoofed animal. All illustrations are of sections through the largest extent of the nucleus.

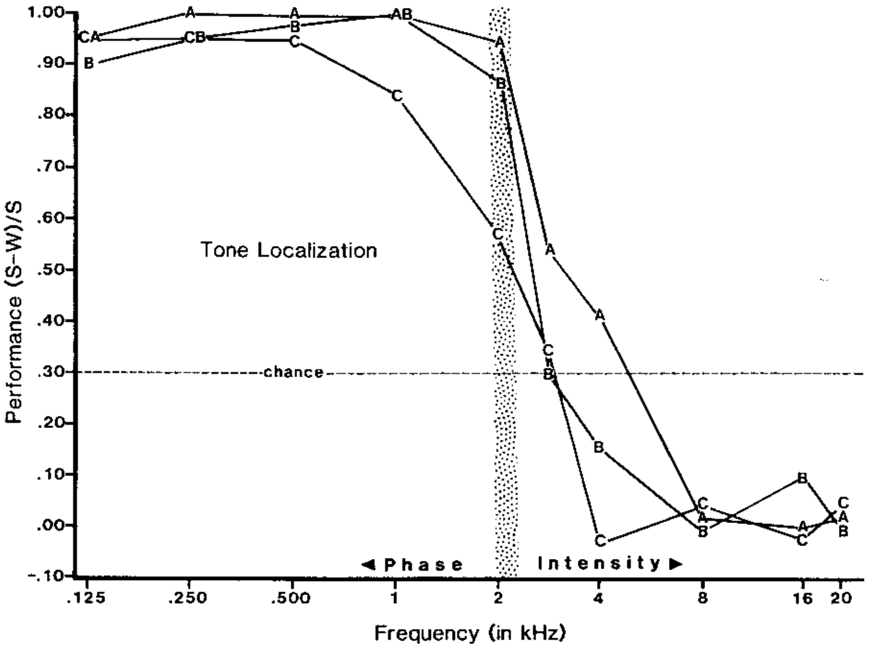

Fig. 3. Ability of three pigs to localize pure-tone pips 30° left vs. 30° right of midline (100 ms duration, 50 ms rise-decay). Stippled bar indicates the calculated frequency above which the interaural phase-difference cue becomes ambiguous and the animals are forced to rely on the interaural intensity-difference cue. Note that pigs perform well at low frequencies where the phase cue is available, but performance falls rapidly to chance at frequencies requiring the use of the intensity cue. A, B and C represent individual animals; performance levels below the dashed line are not statistically different from chance.

Results

Noise Localization

Figure 2 illustrates the ability of the three pigs to localize a single 100-ms burst of broadband noise. Each animal performed very well at angles larger than 10°. At smaller angles, performance fell rapidly to chance at 2.5° with 50% detection thresholds at 4.5°. False alarm rates generally remained low (below 5%), and the fall in performance at small angles was due primarily to a drop in detection rate.

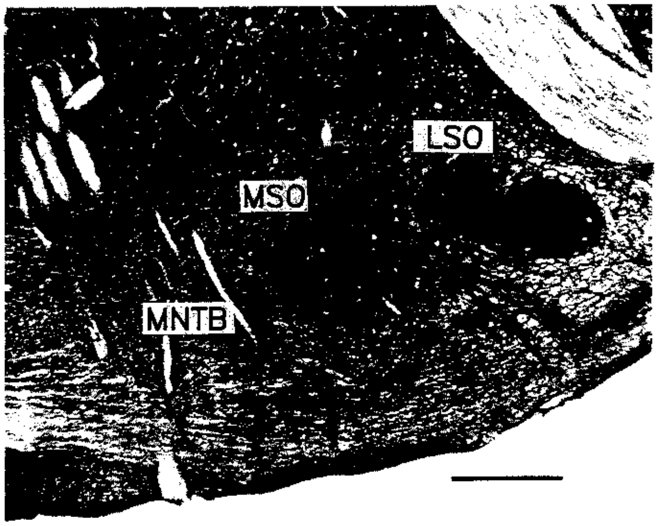

Fig. 4. Coronal section through the SOC at the level of its maximum size in a pig. In comparison to other large hoofed mammals, the neuropil is dense and the size relatively large in relation to the cross-sectional area of the brainstem at this level. MNTB = Medial nucleus of the trapezoid body. Protargol stain. Scale bar = 1 mm.

Pure-Tone Localization

To explore the ability of pigs to localize sound sources using binaural time and intensity cues alone, the animals were also tested for their ability to localize a brief tone pip at frequencies from 125 Hz to 20 kHz. Intensity-difference cues are not produced by low-frequency tones and phase-difference cues become ambiguous at high frequencies; thus, the ability to localize low-frequency pure tones indicates that an animal can use the binaural phase-difference cue, and the ability to localize high-frequency pure tones indicates that it can use the binaural intensity-difference cue [e.g. 13, 23]. At 60° separation, the calculated frequency above which the phase cue becomes ambiguous for an animal with a spherical head and the interaural distance of an adult pig is 2.075 kHz (indicated by the vertical stippled bar in fig. 2) [for the formula for calculating the frequency of ambiguity, see ref. 1, 19]. Therefore, for pure tones above approximately 2 kHz, a pig would be predicted to be forced to rely on binaural intensity differences to localize.

Figure 3 illustrates the ability of three pigs to localize single pure-tone pips from speakers separated by 60°. The performance of the pigs at frequencies of

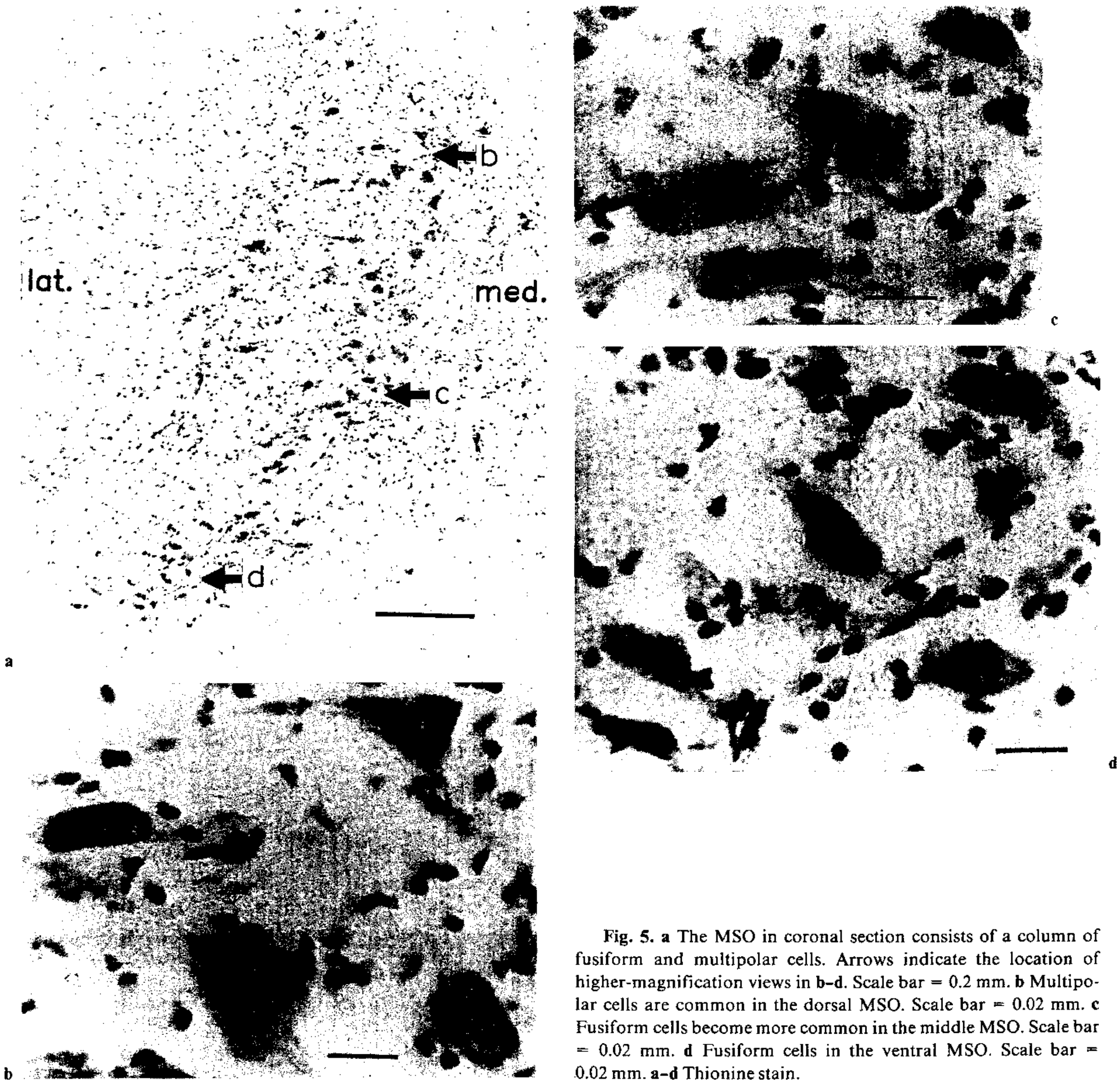

Fig. 5. **a** The MSO in coronal section consists of a column of fusiform and multipolar cells. Arrows indicate the location of higher-magnification views in **b–d**. Scale bar = 0.2 mm. **b** Multipolar cells are common in the dorsal MSO. Scale bar = 0.02 mm. **c** Fusiform cells become more common in the middle MSO. Scale bar = 0.02 mm. **d** Fusiform cells in the ventral MSO. Scale bar = 0.02 mm. **a–d** Thionine stain.

1 kHz and below was excellent. Above 1 kHz their performance began to fall. By 2.8 kHz their performance was near chance, and for all higher frequencies the pigs were unable to distinguish between the two sound sources. These results indicate that pigs easily use the binaural phase-difference cue present in low frequencies, however, they have little or no ability to use the binaural intensity-difference cue present in the high frequencies despite their good sensitivity to those frequencies.

It should be noted that monaural locus cues were greatly reduced, if not eliminated, in the present tests due to the use of pure tones (which eliminated spectral cues) and random intensity variation (which eliminated the monaural intensity cue).

Superior Olivary Complex

The SOC of a pig is illustrated in figure 4. The SOC is large and well defined by its neuropil. The medial superior olive (MSO), illustrated in figure 5a, is a large column of densely stacked fusiform neurons much like those seen in cats. Figures 5b–d illustrate the typical fusiform shape and medial-lateral orientation of the neurons in the MSO. The presence of these typical neurons suggests that in the pig, as in other more thoroughly studied species, the MSO cells receive input from both the contralateral and ipsilateral cochlear nuclei and are well-suited to compare the auditory input to the two ears.

The lateral superior olive (LSO) is illustrated in figure 6a. It is also large and, compared to that of horses and cattle, contains more densely packed cells [11]. However, compared to those in cats, the cells of the LSO in pigs are somewhat sparse. The majority of neurons in the LSO (fig. 6b, c) appear to be fusiform in coronal section and oriented perpendicular to the borders of the nucleus. This configuration is similar to that in cats and suggests that the neurons are aligned along isofrequency planes and are well suited to function as comparators of interaural intensity differences [17]. However, many multipolar cells are present as well; in horizontal sections, such as illustrated in figure 7a, these neurons have a multipolar appearance and are not oriented toward the borders of the nucleus. These multipolar neurons may correspond to the 'multiplanar' cells which make up 11% of the cells in the LSO of cats and have been suggested to be responsive to broader bandwidths and serve a function different from that of the fusiform cells [17, 22]. The medial nucleus of the trapezoid body contains large, darkly stained cells, illustrated in figure 8, which receive typical calyx endings from large fibers in the trapezoid body.

In figure 9, the configuration of the SOC at the level of its greatest extent is illustrated for pigs, domestic cats and horses. Examination of serial sections from several individuals of each species reveals that the SOC of pigs resembles more closely the SOC of cats than it resembles the SOC of large hoofed mammals in size relative to cross-sectional area of the brainstem, in configuration of MSO and LSO, and in density of neural elements.

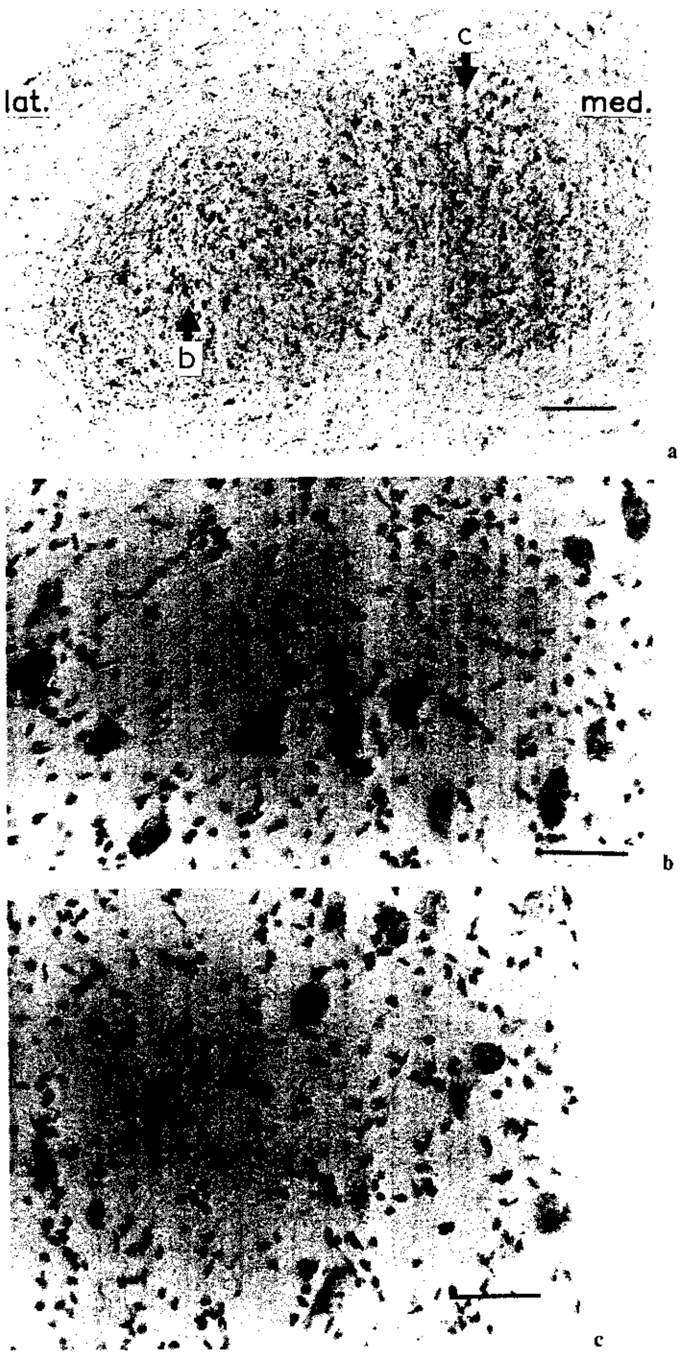

Fig. 6. a The LSO in coronal section is in the form of an 'M' and contains multipolar as well as fusiform cells oriented toward the borders of the nucleus. Arrows indicate the location of higher-magnification views in **b** and **c**. Scale bar = 0.2 mm. **b, c** Higher-power views of lateral and medial portions of the LSO illustrating the low density of neurons and the presence of multipolar cells. Scale bar = 0.05 mm. **a–c** Thionine stain.

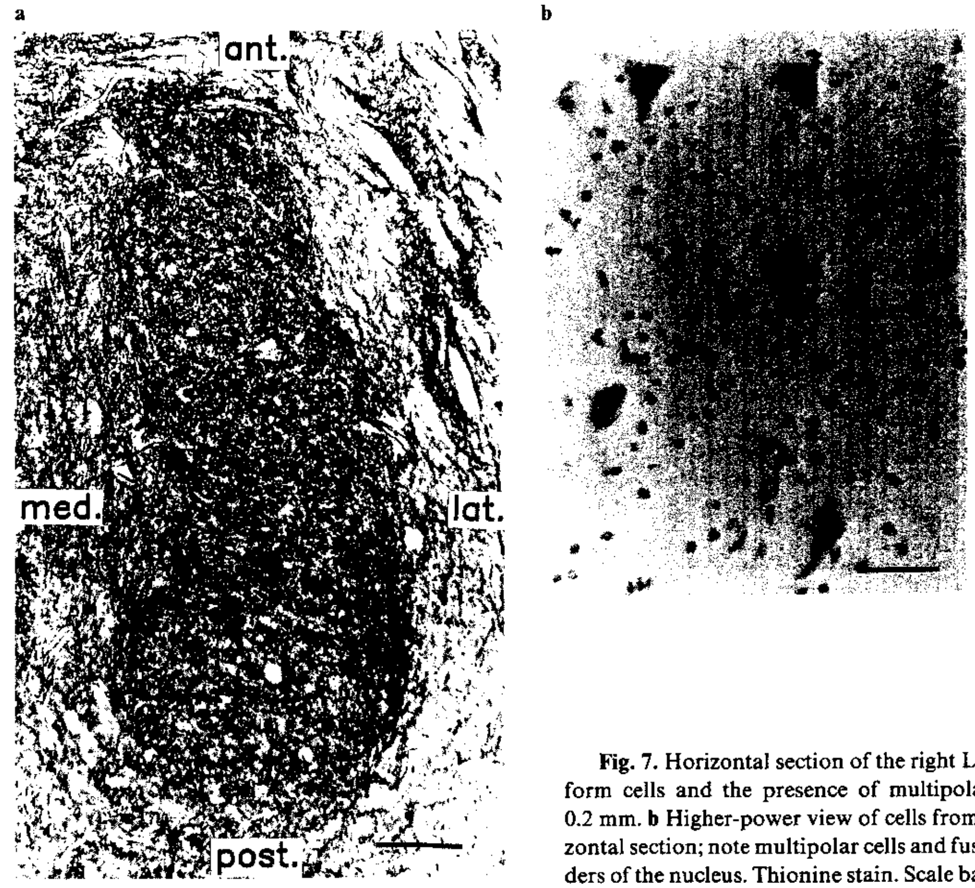

Fig. 7. Horizontal section of the right LSO. **a** Note varying orientation of fusiform cells and the presence of multipolar cells. Protargol stain. Scale bar = 0.2 mm. **b** Higher-power view of cells from the middle region of the LSO in horizontal section; note multipolar cells and fusiform cells oriented parallel to the borders of the nucleus. Thionine stain. Scale bar = 0.02 mm.

Fig. 8. Cells and neuropil in the medial nucleus of the trapezoid body illustrating calyx-type endings; the parts of each ending visible in the plane of focus are drawn and a dashed line surrounds the cell body. Protargol stain. Scale bar = 0.01 mm in **a** and 0.02 mm in **b**.

Discussion

Localization Acuity

The 4.5° sound localization threshold of pigs is smaller than that of most mammals [for recent reviews, see ref. 11, 14]. Indeed, with an interaural distance between that of humans and horses, and the large interaural differences in time and intensity that result, good acuity might be expected. But by having such good acuity, pigs are notable among hoofed mammals as all three of the other hoofed mammals examined to date (horses, cattle, goats) are poor localizers despite their large interaural distances [9].

In seeking the source of selective pressure for this unusual feature of pigs, several unique features of the lifestyle of pigs may be relevant. For example, pigs are *not* as specialized for herbivory as the other hoofed mammals, and, unlike them, are rarely prey. Rather, pigs are themselves more often predators to be reckoned with, as their large canines attest. This relatively predatory lifestyle may be a factor in their localization acuity; as we have previously noted, among smaller mammals predators seem to be under stronger selective pressure than prey to localize accurately. For example, the smallest extant member of the Carnivora is a more accurate localizer than any rodent yet examined, including those with much larger interaural distances [13]. Similarly, a predatory rodent, the grasshopper mouse, is a more accurate localizer than its interaural distance would predict [14]. Pigs may share in the selective pressure on predators since they are more accurate localizers than the other members of the Artiodactyla which are exclusively prey.

On the other hand, pigs are members of the least specialized family of Artiodactyla, and localization acuity commensurate with their interaural distance may simply be a primitive character which the other artiodactyls have lost as part of their specialization. Further tests with other unspecialized but nonpredatory artiodactyls might clarify this issue.

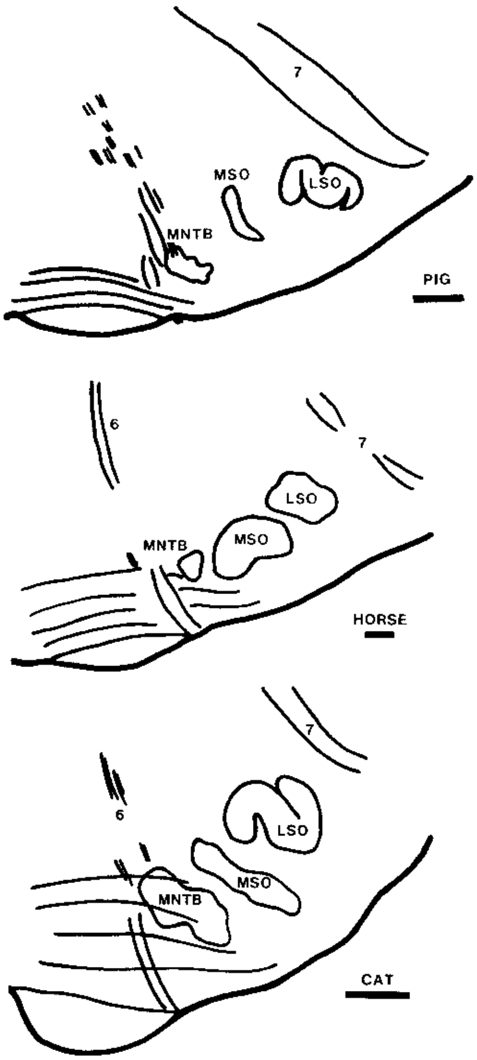

Fig. 9. Comparison of the SOC in a pig, a horse and a cat. '6' and '7' indicate the sixth and seventh cranial nerves. MNTB = Medial nucleus of trapezoid body. Scale bars = 1 mm.

Use of Binaural Cues

The inability of pigs to localize high-frequency pure tones indicates that they are virtually unable to use interaural intensity differences to localize sound. Of the two binaural cues for localizing pure tones, only the interaural intensity difference should be available to pigs for frequencies above approximately 2 kHz at a speaker separation of 60°. The remaining, but limited, ability of pigs to localize frequencies one half octave higher than the theoretical limit of the phase cue suggests that there may be a small residual ability to use the interaural intensity-difference cue. The variation among the three individuals in the exact frequency at which they fell to chance may be due to variation in the ability to use what, in pigs, may be a vestigial ability – i.e. perception of interaural intensity differences. On the other hand, there is room for some error in the theoretical calculations of the upper frequency limit of binaural phase differences because they are based on a sphere of the same diameter as the head of an animal. It is possible that a small-magnitude phase cue is actually available to pigs at slightly higher frequencies than would be expected if their heads were smooth spheres. Nevertheless, despite the possibility of some residual ability to use the binaural intensity-difference cue, it seems clear that pigs do not use this cue for most of the frequency range for which it should be available – indeed, the intensity difference between the two ears typically increases at higher frequencies where pigs perform at chance [6, 7].

Most mammals studied so far are able to use both binaural phase- and intensity-difference cues to localize. These include tree shrews, macaques, squirrel monkeys, humans, Norway rats, kangaroo rats, gerbils, cats and least weasels [1, 3, 4, 8, 13, 15, 20, 21]. Nevertheless, there appear to exist species that rely primarily or exclusively on only one of these binaural cues. The first to be discovered was the hedgehog [20] which does not use the binaural phase cue. More recently we have found species, including horses and cattle, that do not use the binaural intensity cue, and elephants that are capable of using it only over a restricted range [11, 12]. The pig is the fifth species known to have absent or restricted use of one of the interaural localization cues.

Like the other species that do not use the binaural intensity cue, the pig is a large mammal (adult body weight exceeding 100 kg), suggesting that perhaps there is some common factor in this group that reduces the usefulness of the binaural intensity cue. One possibility is that for species with very large heads there are many situations in which the intensity difference between the two ears would be so great that a sound would be audible in the near ear and *in*audible in the far ear. In such a situation the source could be localized only to the hemifield and further precision would depend on monaural cues. The inability of elephants to localize pure tones in the upper two octaves of their hearing range [10] suggests that the limited utility of the interaural intensity difference at very high frequencies may contribute to restriction or loss of ability to use the cue in large-headed species. On the other hand, humans are able to localize high-frequency pure tones (although this ability has not yet been examined for the upper octave of human hearing) [21], indicating that not every large species necessarily loses this ability and suggesting that more than one factor may be involved.

Pigs differ from the other hoofed mammals that do not use the binaural intensity-difference cue in one important respect – whereas the others are poor localizers, pigs are very accurate localizers. Thus, the suggestion that species such as horses have given up the use of one of the main binaural locus cues because they are under minimal selective pressure to localize and can be sufficiently accurate without the intensity cue cannot be applied to pigs. The acuity of pigs is as good as that of cats and monkeys, yet, unlike cats and monkeys, pigs achieve their good acuity without assistance from the interaural intensity-difference cue.

In conclusion, we cannot yet say why some species use only one of the binaural difference cues to localize sound. The finding that pigs, which are accurate localizers, use the interaural phase cue (and probably time cues in general), and not the interaural intensity-difference cue, has eliminated some plausible explanations. A more satisfactory explanation must await analyses of the use of binaural cues in species that represent different taxonomic groups and lifestyles.

Superior Olivary Complex

So far, in attempting to understand what appear to be the unusual aspects of sound localization in pigs (their good acuity and their inability to use the interaural intensity cue), we have examined the possible influences of heritage and habitus. It is also appropriate to look at a different level and examine in pigs the neural structures that are known to play a role in the localization of sound and the early analysis of binaural locus cues – the SOC.

The SOC provides the first opportunity for input from the two ears to interact and is the main binaural nucleus in the brainstem. The functions of its two main components have not yet been completely defined, but it is clear that they play different roles in the localization of sound. Cells in the MSO are responsive to low frequencies, and the firing rate of many of these cells is affected by the phase relationship between the stimuli at the two ears, whereas most (although not all) remain relatively insensitive to interaural intensity differences [5, for a review, see ref. 18]. The LSO, on the other hand, is primarily responsive to high frequencies, and its neurons are strongly affected by transient and ongoing intensity differences at the two ears [2, 5, 18, 27]. These differences suggest that the MSO is important for the analysis of binaural time cues and that the LSO is important for the analysis of binaural intensity cues.

The conclusion that the MSO subserves localization based on time cues and the LSO subserves localization based on intensity cues is supported by the fact that hedgehogs lack both an MSO and the ability to use the binaural phase cue [20]. Similarly, the LSO of horses and cattle is small, diffuse and disorganized, and these species lack the ability to use the binaural intensity cue [9, 11, 16]. However, data for pigs suggest that the MSO-time, LSO-intensity dichotomy is somewhat more complicated than it first appears. Even though pigs lack the ability to use the binaural intensity cue, they possess a relatively large and well-developed LSO comparable to that of species like cats, weasels and rats which do use the binaural intensity cue [13, 20]. Thus, it is likely that the LSO serves an additional function or functions in pigs and that these are present only to a limited extent, if at all, in horses.

Although we as yet have no evidence as to what the different functions of the LSO might be, at least one possibility comes to mind: it is already known that species vary in the location of olivocochlear neurons - in the hilus of the LSO in cats and in the lateral portion of the body of the LSO in rodents [25, 26]. It is possible that the LSO remains as a source of afferents to the cochlea in species whose LSO lacks the ability to analyze binaural intensity differences.

Finally, there exists in the LSO (in addition to the characteristic fusiform neurons) a variety of cell types coupled with a variety of response characteristics [17, 22, 24]. Such evidence suggests that the function of the LSO may not be restricted simply to an analysis of interaural intensity differences. It is not unlikely that several analyses may be performed by the different cell types in the LSO and these may be differentially emphasized in different species. Further insight into the nature of the contribution of the LSO to hearing will undoubtedly be suggested by electrophysiological and antomical investigations of species with atypical abilities.

Acknowledgements

This research was supported by National Institutes of Health grant NS 17850 to the Bureau of Child Research, University of Kansas, and Biomedical Sciences Support grant R07037 to the University of Kansas. We thank Brenda Anderson for her assistance in this project.

References

1 Brown CH, Beecher MO, Moody DB, et al: Localization of tones by old world monkeys. J Acoust Soc Am 1978;65:1484-1492.

2 Caird D, Klinke R: Processing of binaural stimuli by cat superior olivary complex neurons. Exp Brain Res 1983;52:385-399.

3 Casseday JH, Neff WD: Localization of pure tones. J Acoust Soc Am 1973;72:365-372.

4 Don M, Starr A: Lateralization performance of squirrel monkey *(Saimiri sciureus)* to binaural click signals. J Neurophysiol 1972;35:493-500.

5 Goldberg JM: Physiological studies of auditory nuclei of the pons; in Keidel WD, Neff WD (eds): Handbook of Sensory Physiology, V/2. New York, Springer, 1975, pp 109-144.

6 Harrison JM, Downey P: Intensity changes at the ear as a function of the azimuth of a tone source: A comparative study. J Acoust Soc Am 1970;47:1509-1518.

7 Heffner HE, Heffner RS: Sound localization in large mammals: Localization of complex sounds by horses. Behav Neurosci 1984;98:541-555.

8 Heffner HE, Masterton B: Hearing in glires: Domestic rabbit, cotton rat, feral house mouse, and kangaroo rat. J Acoust Soc Am 1980;68:1584-1599.

9 Heffner RS: Sound localization and the superior olivary complex in horses and cattle. J Acoust Soc Am 1981;69:10S.

10 Heffner RS, Heffner HE: Hearing in the elephant *(Elephas maximus)*: Absolute sensitivity, frequency discrimination, and sound localization. J Comp Physiol Psychol 1982;96:926-944.

11 Heffner RS, Heffner HE: Localization of tones by horses: Use of binaural cues and the role of the superior olivary complex. Behav Neurosci 1986;100:93-103.

12 Heffner RS, Heffner HE: Variation in the use of binaural localization cues among mammals. Abstr Ninth Midwinter Res Meet Assoc Res Otolaryngol 1986;108.

13 Heffner RS, Heffner HE: Localization of noise, use of binaural cues, and a description of the superior olivary complex in the smallest carnivore, the least weasel *(Mustela nivalis)*. Behav Neurosci 1987;101:701-708.

14 Heffner RS, Heffner HE: Sound localization in a predatory rodent, the Northern grasshopper mouse *(Onychomys leucogaster)*. J Comp Psychol 1988;102:66-71.

15 Heffner RS, Heffner HE: Sound localization and use of binaural cues by the gerbil *(Meriones unguiculatus)*. Behav Neurosci 1988;102:422-428.

16 Heffner RS, Heffner HE: Interaural phase and intensity discrimination in the horse using dichotically presented stimuli. Abstr Eleventh Midwinter Res Meet Assoc Res Otolaryngol 1988; 233.

17 Helfert RH, Schwartz IR: Morphological evidence for the existence of multiple neuronal classes in the cat lateral superior olivary nucleus. J Comp Neurol 1986;244:533-549.

18 Irvine DRF: Progress in Sensory Physiology, vol 7: The Auditory Brainstem. New York, Springer, 1986.

19 Kuhn GF: Model for the interaural time differences in the azimuthal plane. J Acoust Soc Am 1977;62:157-167.

20 Masterton B, Thompson GC, Bechtold JK, et al: Neuroanatomical basis of binaural phase-difference analysis for sound localization: A comparative study. J Comp Physiol Psychol 1975; 89:379-386.

21 Mills AW: Auditory localization; in Tobias JV (ed): Foundations of Modern Auditory Theory. New York, Academic Press, 1972, vol 2, pp 301–348.

22 Scheibel ME, Scheibel AB: Neuropil organization in the superior olive of the cat. Exp Neurol 1974;43:339–348.

23 Stevens SS, Newman EB: The localization of actual sources of sound. Am J Psychol 1936;48:297–306.

24 Tsuchitani C: Lower auditory brainstem structures of the cat; in Naunton RF, Fernandez C (eds): Evoked Electrical Activity in the Auditory Nervous System. New York, Academic Press, 1978, pp 373–401.

25 Warr WB: Olivocochlear and vestibular efferent neurons of the feline brain stem: Their location, morphology and number determined by retrograde axonal transport and acetylcholinesterase histochemistry. J Comp Neurol 1975;161:159–182.

26 White JS, Warr WB: The dual origins of the olivocochlear bundle in the albino rat. J Comp Neurol 1983;219:203–214.

27 Yin TCT, Kuwada S: Neuronal mechanisms of binaural interaction; in Edelman G, Ga W, Cowan W (eds): Dynamic Aspects of Neocortical Function. New York, Wiley, 1984, pp 263–313.

Rickye S. Heffner
Department of Psychology
University of Toledo
2801 Bancroft
Toledo, OH 43606 (USA)