Comparative Study of Sound Localization and its Anatomical Correlates in Mammals

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Heffner RS. *Comparative study of sound localization and its anatomical correlates in mammals.* Acta Otolaryngol (Stockh) 1997; Suppl 532: 46–53.

One of the fundamental features of hearing is the ability to localize the sources of sounds, particularly brief sounds, which may warn of nearby animals. Yet not all mammals localize sound equally well with threshold acuity ranging from about 1° for elephants and humans to more than 25° for gerbils and horses and a near absence of localization in some subterranean species. During the past decade evidence has accumulated that this variation cannot be accounted for simply by the availability of the physical cues for locus. Nor does it appear to be a function of an animal's lifestyle. Rather sound-localization acuity in mammals appears to be a function of the precision required of the visual orienting response to sound. Thus the neural integration of hearing and vision in cortex, as well as in multimodal subcortical structures, is a reflection of their behavioral integration and evolutionary coupling. *Key words: evolution, vision, spatial perception, retina, sound localization, orienting, auditory space.*

INTRODUCTION

A major source of selective pressure in the evolution of mammalian hearing has been the utility of sound localization. Indeed, the importance of sound localization is indicated by the fact that much of the auditory system of mammals is devoted to the perception of auditory space, and this seems to be true of auditory cortex as well as of lower auditory structures. However, unlike auditory brainstem structures, cortex seems to have limited involvement in an analysis of the cues for spatial locus and no systematic maps of auditory space have been revealed in cortex (although cortical neurons do retain the responsiveness to binaural locus cues that is generated in lower centers (1)). Instead, cortex appears to be more involved in integrating auditory space with other sensory representations of space and in orchestrating responses to sound sources that will result in the identification of those sources (e.g., 2, 3). Thus it should come as no surprise that the evolutionary selective pressure underlying the remarkable variation in sound-localization abilities may have involved the visual orienting response to sound and the integration of auditory and visual space (4). It is a description of the sound-localization abilities of mammals and their relation to visual parameters that is the subject of this chapter.

THE IMPORTANCE OF LOCALIZING SOUND SOURCES

There are several reasons for believing sound-localization to be important to mammals (the focus here is on mammals as much less is known about sound localization in other vertebrates). First of all, nearly all mammals localize sound (the subterranean species that live exclusively in the one-dimensional world of underground burrows being the exception). Second, most structures in the auditory nervous system respond to the cues for locus and seem to be involved in localizing sound. Finally, locus information is useful for directing our responses–which way to turn and look, which way to run. Thus there is evidence to suggest that there is strong selective pressure for sound localization and certainly much neural processing is devoted to it.

Such a belief in the importance of sound localization forces us to ask the question: If it's so important, why do mammals vary so much in their ability to localize? Is there some morphological variable, or neurological constraint, or difference in habitat or lifestyle that affects sound-localizing abilities of different species?

BEHAVIORAL TESTS

In order to tease out factors affecting sound localization, we must determine the abilities of a wide range of different species. We must ask the same questions of animals as different as mice and elephants and still have confidence that the answers are valid and comparable from one species to another. Because psychoacoustic methods underlie the data upon which all our conclusions rest regarding the evolution and mechanisms of sound localization, a brief consideration of those methods and our confidence in them is in order.

To determine an animal's localization acuity, it is trained to make one response to sounds emanating from one location, and a different response to sounds emanating from a different location. Those sound sources are then brought closer and closer until the animal no longer responds above chance. There are
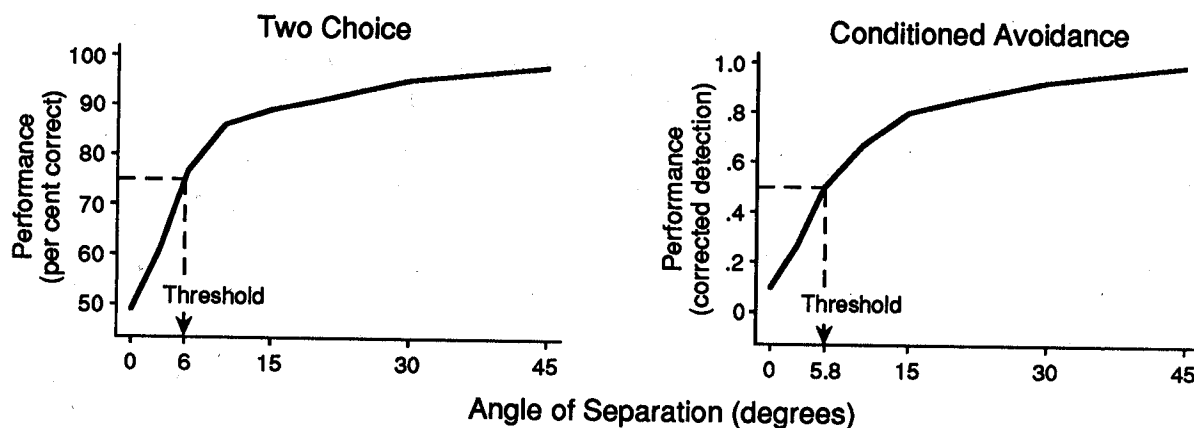
Fig. 1. Sound-localization acuity in cats determined using two-choice and conditioned avoidance test procedures (modified from ref [9]). *Arrows* indicate angle at threshold; note the similarity of results in the two procedures.

three procedures commonly used. One is called a 'two-choice' and animals are trained to first make an observing response to turn on a sound (5). The observing response usually involves placing the head in a central location with respect to the sound sources thus assuring stable sound levels and directions. If a sound then comes from the animal's left, the animal responds by touching a left key or lever, and if the sound comes from its right, it responds by touching a right key or lever. Animals are always rewarded for correct responses and errors are usually punished by a short wait, or time-out.

A second procedure is 'conditioned avoidance' (6). In this procedure an animal makes a steady response, such as drinking from a spout, as long as sounds are emitted from sources at one location, and it makes a different response, letting go of the spout, whenever a sound occurs at another location. Drinking from the spout serves to fix the animal's head relative to the sound sources again assuring reliable sound levels and directions. Errors are punished by a mild shock when the animal fails to respond to a change in location (misses), and by foregoing the reward when they respond in the absence of a change (false alarms).

The third procedure, known as 'go/no-go,' is similar to conditioned avoidance in that animals make one response while waiting for the target signal and a different response when the target occurs. However, unlike the conditioned avoidance procedure in which the animals are rewarded for correct rejections as well as hits, in the go/no-go procedure they are rewarded only for hits thereby predisposing them to high false alarm rates. Performance in the go/no-go procedure can also be hindered by the absence of punishment for misses. This procedure has been used most with primates where careful training has resulted in valid measures (7).

In all three procedures, threshold has traditionally been defined as the midpoint between perfect performance and random performance: 75% correct in the two-choice procedure and 50% detection (preferably corrected for false alarm rate) in the conditioned avoidance and go/no-go procedures. Over 25 years of experience with these procedures has convinced us that as long as the acoustics are well controlled and the animals are trained to high levels of performance, the thresholds are reliable and valid. The same thresholds are achieved even when animals are re-tested years later and results of different procedures agree closely with each other when carried out in the same species or individuals (8, 9). Fig. 1 illustrates sound-localization performance of cats tested with two different procedures; note the similar shape of the curves and the similar thresholds obtained.

EXPLAINING THE VARIATION IN SOUND LOCALIZATION

Physical factors

Traditional explanations of the wide variation in sound-localization acuity among different species were based on the physics of sound localization. The most powerful physical cues to sound location are interaural differences in the time of arrival of a signal at the two ears and differences in the intensity of different spectral components at the two ears (10). That is to say, a sound from an animal's right both arrives at the right ear before arriving at the left ear, and its high-frequency components are louder at the right ear than at the left. Both of these cues are of greater magnitude in species with more widely spaced ears. If all animals are under intense selective pressure to localize as well as possible, limited only by the cues available to them, then it might reasonably be ex-
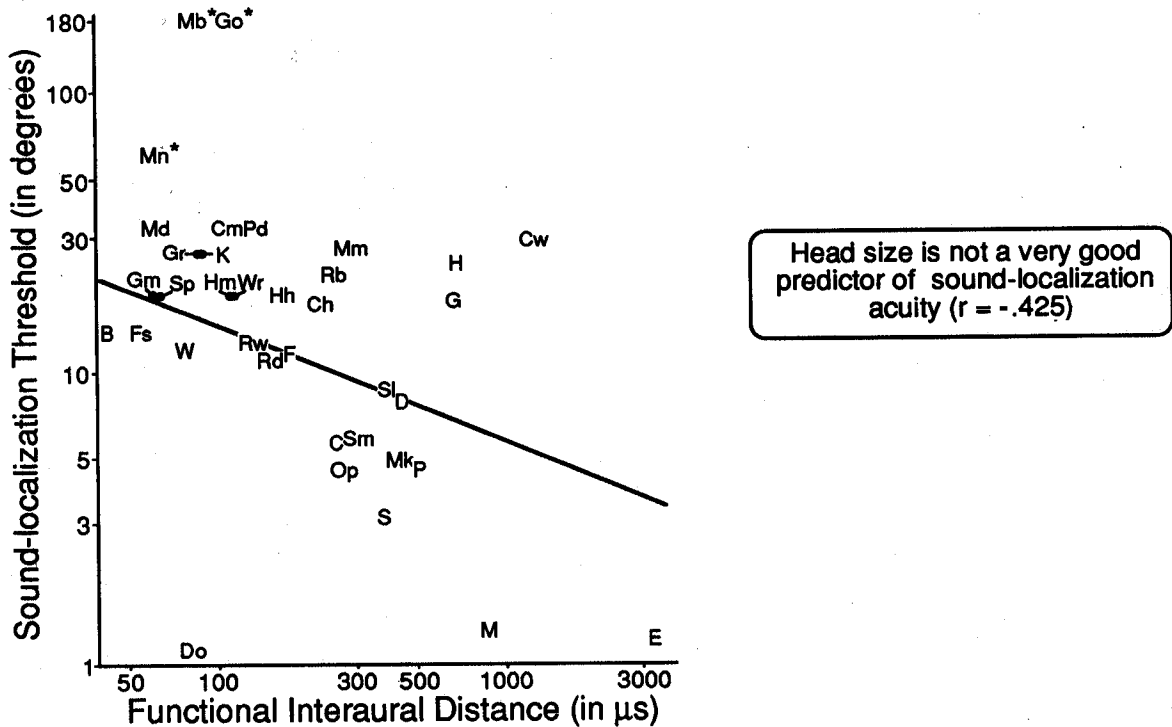
Fig. 2. The relation between functional interaural distance and sound-localization acuity among 36 species of mammals. In this and subsequent figures an asterisk (*) indicates subterranean species tested with a long-duration signal permitting scanning as well as binaural analysis; regression lines for statistically significant correlations are indicated by *solid lines* and those for non-significant correlations are indicated by *dashed lines*; B big brown bat, C cat, Ch chinchilla, Cm chipmunk, Cw cow, D dog, Do dolphin, E elephant, F ferret, Fs fox squirrel, G goat, Gm grasshopper mouse, Go* pocket gopher, Gr gerbil, H horse, Hh hedgehog, Hm hamster, K kangaroo rat, M man, Mb* blind mole rat, Md domestic mouse, Mk macaque, Mm marmot, Mn* naked mole rat, Op opossum, P pig, Pd prairie dog, Rb domestic rabbit, Rd domestic Norway rat, Rw wild Norway rat, S seal, Sl sea lion, Sm, squirrel monkey, Sp spiny mouse, W least weasel, Wr wood rat. All correlation figures updated from ref. (4).

pected that sound localization in different species would be predicted by functional head size—the time it takes a sound to travel from one ear to the other.

As Fig. 2 illustrates, functional interaural distance is not a very satisfactory predictor of sound-localization acuity among the 36 species of mammals so far examined. Even when the degenerate subterranean species (*) are excluded, the correlation coefficient is low ($r = -0.425$, $p = 0.014$). Although statistically reliable, head size, and by implication, the magnitude of the physical cues, is not a good predictor of localization acuity and many species are distant outliers.

Biological factors
With physical factors being relatively poor predictors of localization acuity, the question remained as to why some species are so much more accurate localizers than others and our attention turned to biological factors. We examined factors such as trophic level (whether predators or prey are more accurate localizers), nocturnal and diurnal activity cycles, habitat, and phyletic lineage. Not only were such factors

difficult to quantify, they also proved unable to satisfactorily account for the variation in sound-localization acuity.

We next considered that the key might lie in the responses rather than in the stimuli: In other words, what do animals do with locus information? The first response upon hearing an unexpected sound is usually an orienting reflex that turns the head and eyes toward the sound source (11–14). This is a relatively low-level neural function that can occur in the absence of auditory cortex (15). This visual orientation to a brief sound is faster than and as accurate as the visual orientation to a brief spot of light (16). Cognitive psychologists have also pointed out that even when orienting movements are prevented, attention is still oriented in the direction of the sound (15). Findings such as these point to the fundamental importance of orienting to sound sources.

A simple measure of what is being oriented in the visual orienting response would permit us to explore visual orienting as a potential factor influencing variation in localization acuity. One measure is the size of
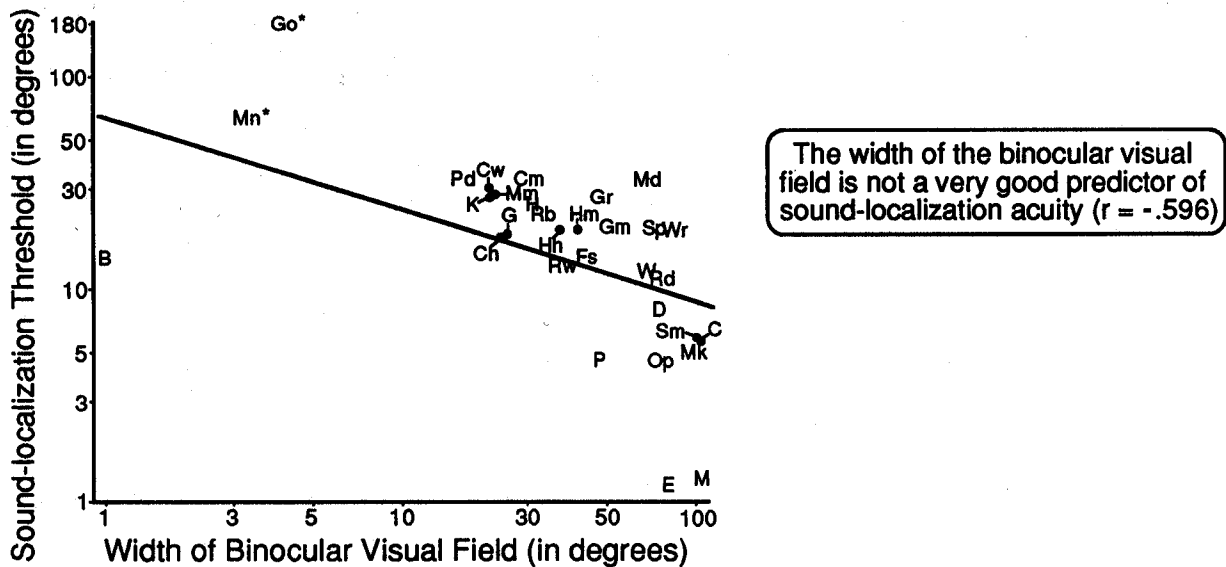
Fig. 3. The relation between binocular visual fields and sound-localization acuity among 31 species. (See Fig. 2 for key.)

the binocular visual fields. As shown in Fig. 3, the relation between the size of the binocular visual fields and localization acuity is strong ($r = -0.596$, $p = 0.0004$). However the correlation is heavily influenced by species with degenerate vision (big brown bat and subterranean rodents), and among the cluster of more typical species, there are several deviant cases (pig, mouse, opossum) indicating that binocular vision, while related, may not be the factor most relevant to sound localization.

Upon further consideration, we realized that when we orient to a sound source, it is not just our binocular field that is turned, or even the eye, but the part of the eye with the best visual acuity. In humans and other primates this is the fovea and the orientation is referred to as 'foveation'. But most animals don't have a fovea, instead they have a larger region of comparatively good vision (sometimes called an 'area centralis'). Many animals even have their best vision spread across the horizon of their retina in a 'visual streak'.

It is likely that if animals are orienting their field of most acute vision, then their hearing would have to provide more accurate locus information if they possessed narrow fields of best vision than if their field of best vision were broad. In other words, animals with a narrow fovea should need more acute locus information in order to direct their fovea to a sound source, but animals with a visual streak should need only an approximate indication of a sound's location in order to capture it within their broad field of good vision. Extreme examples of the latter are horses and rabbits with laterally directed eyes and a visual streak that encompasses virtually the entire horizon.

In order to examine the validity of this prediction, it was necessary to obtain a measure of the size of the field of best vision in every animal that had been tested for sound localization. This is not practical behaviorally, but a good anatomical estimate of visual acuity is available in the form of retinal ganglion cell densities. Retinal ganglion cells are the final common pathway out of the retina and are a limiting factor in visual acuity. But most important, the density of the ganglion cells in the retina has been shown time and again to be a good estimate of behavioral visual acuity (e.g., 18–20). Accordingly, we determined the density of the ganglion cells throughout the retina using retinal wholemounts in as many species as possible. Because there is no commonly accepted measure of the 'field of best vision' that could be used to compare across species, we arbitrarily defined the area of best acuity as the region with ganglion-cell densities at least 75% of maximum. Other criteria such as 90% of maximum or 50% of maximum were also considered, but these are subject to ceiling and floor effects and thus do not provide a scale that can accommodate many species.

The region of densest ganglion cell packing is usually located in the central or temporal retina. Density falls toward the periphery and with it, acuity. We have calculated the width of the area that has at least 75% of maximum acuity, in degrees, for most of the species that have been tested in sound localization. As was already well established, we found that different species have very differently shaped isodensity contours in their retina and that their fields of best vision vary from about 1° for humans to over
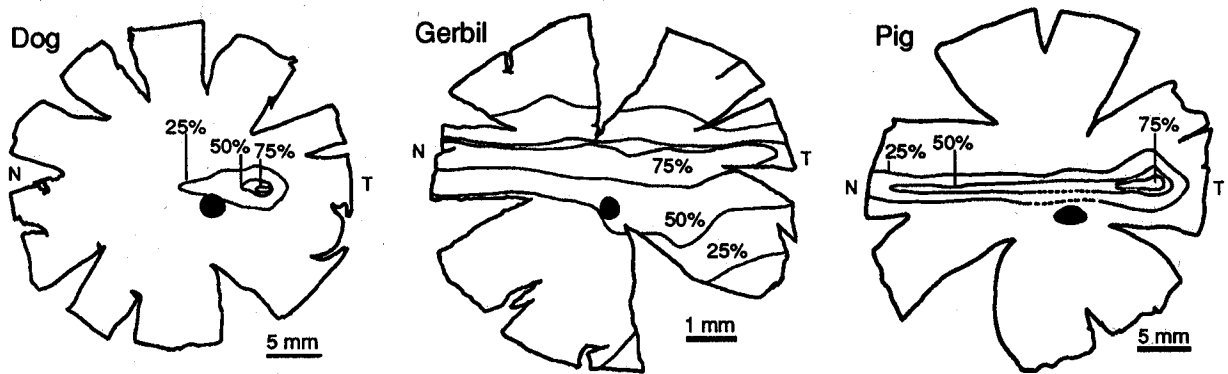
Fig. 4. Retinal isodensity contours for three species of mammals expressed as 25%, 50%, and 75% of maximum density. N, nasal; T, temporal; black area is optic disc.

180° for some rodents. Fig. 4 illustrates the configuration of the retinae of three species. Dogs have a hint of a streak in the 25% contour and the 75% contour defines a relatively narrow 5° field of best vision. Gerbils have a marked streak in all of their isodensity contours and the 75% contour encompasses approximately 200° (as the retinal field is 200° and the 75% contour encompasses the entire retinal field). The last example, pigs, illustrates a somewhat unusual configuration with a well defined streak accompanied by a relatively narrow field of best vision of 11°.

Fig. 5 illustrates the relation between the width of the field of best vision and sound-localization acuity for the 24 species currently available. As can be seen, the width of the field of best vision is a reliable predictor of sound-localization acuity. Animals with narrow fields of best vision are very accurate localizers and animals with broad fields of best vision are poor localizers ($r = 0.922$, $p < 0.0001$). However, species that spend all their time underground deviate from the regression line and their inclusion into the calculation of the correlation coefficient lowers it to $r = 0.855$. Because there is little use of visual orienting in the dark and sound travels poorly underground, both hearing and vision are degenerate in pocket gophers, naked mole rats, and blind mole rats—indeed, since blind mole rats have eyes that are buried in muscle below the skin, they have no field of vision and a value cannot be obtained for them (21–23). Thus it comes as no surprise that the two senses are not well coordinated in subterranean species and that they have drifted away from the common mammalian plan.

This strong relationship between the width of the field of best vision and sound-localization acuity lends credibility to the suggestion that an important source of selective pressure for sound localization in mammals is the precision required of the behavior it directs—namely the orientation of vision for scrutiny of sound sources. The sample is now 24 species, and it is representative of mammals in several relevant features: First, a wide range of body sizes and interaural distances, from mice and bats to humans and cows, are represented. Second, the sample is taxonomically and phyletically broad with nine orders of mammals represented (including eight families of rodents and two families of artiodactyls—groups commonly underrepresented in comparative studies). The sample also includes a bat (B) although this important group remains underrepresented; note that the bat's passive sound-localization acuity conforms to the mammalian plan despite its auditory specialization for active sonar. Third, the sample includes a broad range of lifestyles including strict predators and exclusive prey, surface and subterranean dwellers, and both nocturnal, diurnal, and arrhythmic activity patterns. The generality of the relationship seems broad, but it will be important to continue testing it by examining species of unusual auditory abilities (such as dolphins and additional bats with different echolocating patterns) or of pivotal taxonomic status such as primitive primates and rodents. Finally, it will be of interest to determine whether this relationship applies to birds with their different auditory and visual systems, but subject to at least some of the same selective pressures as mammals.

It must be stressed that it is relative visual acuity that is important and not absolute visual acuity. This is because an animal directing its vision uses the best vision it has regardless of how good or poor that vision may be. As shown in Fig. 6, visual acuity is not a reliable predictor of sound-localization acuity. The correlation coefficient is only $r = -0.306$ ($p = 0.106$) and many species are strongly deviant.

Vision, of course, is strongly influenced by an animal's lifestyle, with the result that lifestyle factors can become apparent correlates of auditory abilities.
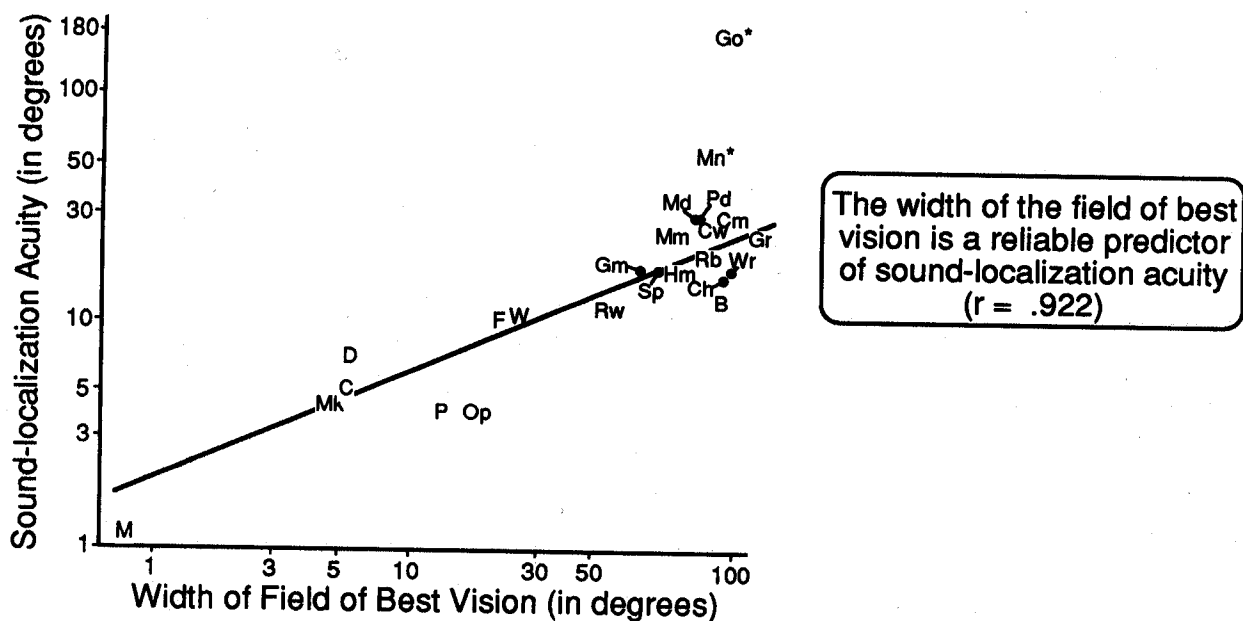
Fig. 5. The relation between the width of the field of best vision and sound-localization acuity among 24 species of mammals. (See Fig. 2 for key.)

An example of this correspondence is the relation between trophic level and sound-localization acuity—predatory species tend to be better localizers than prey species ($r = 0.643$). However predators also tend to have their best vision directed forward and, more importantly, concentrated in a relatively narrow region; as a result, when the influence of field of best vision is removed mathematically, the correlation between trophic level and sound localization collapses to insignificance ($r = 0.132$).

Finally, it is appropriate to ask whether interaural distance, and by implication the physical cues for locus, play a noticeable role in the variation of mammalian sound localization. Although surprising, we are forced to conclude that the evolutionary influence of the physical locus cues may be minimal. As illustrated in Fig. 7, if we factor out the contribution of field of best vision from the correlation between interaural distance and sound-localization acuity, there seems to be no remaining influence of interaural distance. On the other hand, the correlation between field of best vision and sound-localization acuity remains robust after partialing out the influence of interaural distance. Within broad limits, selective pressure seems able to overcome the physical limitations of a small interaural distance to provide localization acuity adequate to direct the eyes. Conversely, the lack of selective pressure for good localization results in poor acuity regardless of how far apart the ears and how large the physical cues for locus. It

seems as though the physical cues in the environment provide potential information, and biological organisms evolve ways to derive that information whenever there is a selective advantage for doing so.

CONCLUSION

In conclusion, a primary function of audition is to direct visual attention for scrutiny of sound sources. This function seems to have been a major source of selective pressure affecting the evolution of sound localization among mammals. This function is also reflected in the organization of the nervous system. Nearly thirty years ago Irving & Harrison (24) reported a puzzling correspondence between the size of the medial superior olivary nucleus in the brainstem, which analyzes interaural time differences, and the 6th nerve nucleus, which turns the eyes in azimuth. The establishment of a strong functional relationship between sound localization and vision makes it easy to understand why a nucleus that analyzes sound location should be related to a motor nucleus that turns the eyes.

More recently we have seen that selective pressure for coordination between sound localization and vision is also reflected in the congruent maps of auditory and visual space found in the superior colliculi of mammals and birds (11, 14). Coordination between auditory and visual space at a cortical level is also likely to become more apparent as investigators
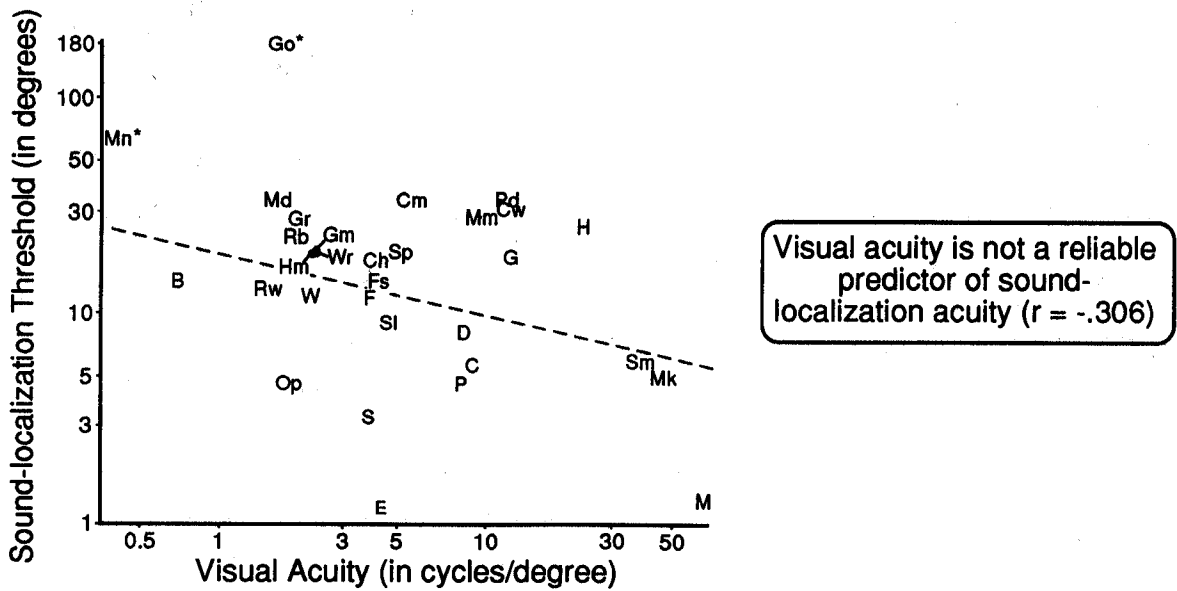
Fig. 6. The relation between visual acuity and sound-localization acuity among 30 species of mammals. (See Fig. 2 for key.)

increasingly include multiple modalities in electrophysiological studies of behaving animals (e.g., 2, 13).

The recognition of the importance of the coordination of the senses has an important implication for the study of sound localization. The evolution of hearing is best understood in intact and behaving animals in their ecological context—the relation of

hearing to other senses is not only important, it may be paramount. Animals do not use each of their senses in isolation, but rather in coordination to obtain information about their environment. It is objects and other animals that are important to survival. Lights, sounds, and odors are merely the medium by which these objects and animals are detected and their significance interpreted.
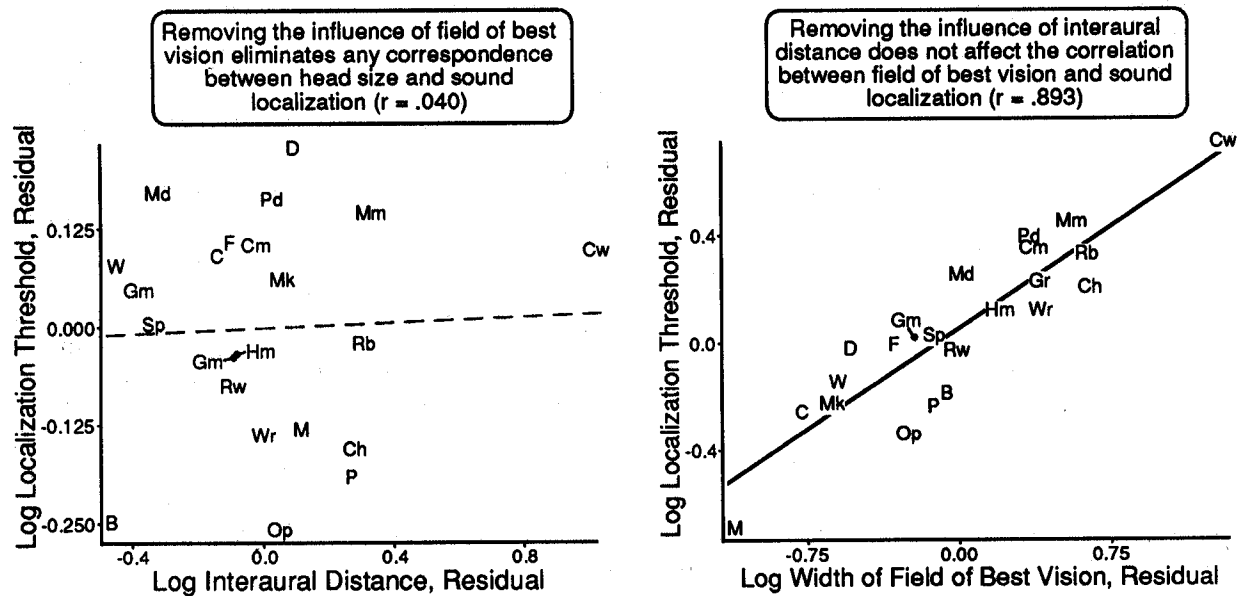

Fig. 7. Residual correlations: On the left, the correlation collapses between interaural distance and sound-localization acuity after partialing out the influence of field of best vision. On the right, the correlation between field of best vision and sound localization acuity remains robust after partialing out the influence of interaural distance. (See Fig. 2 for key.)

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