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Visual Factors in Sound Localization in Mammals

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ABSTRACT

The ability of mammals to localize sound varies widely among species. During the past decade, evidence has accumulated that this variation cannot be accounted for simply on the basis of the availability of the physical cues for locus. Evidence is presented that a major factor in sound localization is the need to direct the field of best vision to a sound source for further scrutiny. Thus, species with broad fields of best vision (such as visual streaks) require less accurate information regarding the location of a sound source than do species with very narrow fields of best vision (such as foveae). To support this suggestion, data are reported for the width of the field of best vision in the form of retinal ganglion cell isodensity contours for thirteen species of mammals. The possible contribution of other factors including binocular fields, visual acuity, and the degree to which a species is predatory in lifestyle, is also examined.

Key words: perceptual space, hearing, retina, area centralis, sensory integration, ganglion cells

One of the fundamental features of hearing is the ability to localize the source of a sound, particularly brief sounds which may warn of nearby animals (Masterton and Diamond, '73). Because a knowledge of the exact location of such sound sources would seem to be of obvious importance, it would also seem reasonable to assume that all animals are under strong selective pressure to localize sound accurately. Yet not all mammals do so. Tests of the ability to localize sound have shown that sound localization thresholds range from about 1° (e.g., elephants and humans) to more than 25° (e.g., gerbils and horses) with some species (pocket gopher) completely unable to localize brief sounds (Heffner and Heffner, '84; Heffner and Heffner, '82, '88b, '90).

Over the last decade the number of mammalian species with behaviorally determined sound localization thresholds has more than doubled to twenty-three. As more data became available, we began to consider various factors which might account for the variation in acuity among mammals. The first and most obvious factor was the availability of the physical cues to locus. Because the magnitude of the binaural locus cues available to an animal is dependent on head size (Harrison and Downey, '70; Heffner and Heffner, '84), it might be expected that animals with large heads and correspondingly wide-set ears, as indicated by interaural distance, would be better able to localize sound than animals with smaller interaural distances.

Two other potential explanatory factors which we considered have to do with an animal's lifestyle. Because the accuracy with which an animal needs to localize sound may depend on whether it is a predator or prey and whether it is primarily active during the day or night, we also considered trophic level and activity cycle.

Finally, because of mounting evidence indicating close links between hearing and vision (e.g., Jay and Sparks, '84; Knudsen and Knudsen, '89; Meredith and Stein, '86; Whittington et al., '81; Wise and Irvine, '83; Withington-Wray et al., '90), we considered three visual parameters: visual acuity, size of the binocular visual field, and the width of the field of best vision. As will be seen, our analysis indicates that the variation in sound localization acuity in mammals is closely associated with the width of the field of best vision and supports the hypothesis that a primary function of sound localization is to direct the eyes to the source of a sound (Pumphrey, '50).

MATERIALS AND METHODS

Of the seven factors considered here (sound localization acuity and six potential correlates: head size, trophic level, activity cycle, width of field of best vision, visual acuity, and width of binocular field), descriptions or measures of most are available from published sources. Only the visual parameters of width of the field of best vision and width of

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TABLE 1. Values of Parameters Examined as Predictors of Sound Localization Acuity in Mammals

Species	Symbol	Sound localization threshold in deg[1]	Delta t in μsec	Field of best vision in deg	Visual acuity in c/deg[23]	Binocular field in deg	Trophic level
dolphin	Do	1.1[2]	80	—	—	—	1
elephant	E	1.2[3]	3350	—	—	80	3
man	M	1.3[4]	875	.7	67.0[24]	105	2
seal	S	3.2[5]	378	—	3.6[25]	—	1
opossum	Op	4.6[6]	273	15.8	1.8[26]	77	4
pig	P	4.6[7]	498	11.6	8.0	47	2
macaque	Mk	5.0[8]	424	4.3	46.8[27]	111	2
cat	C	5.7[9]	258	4.9	9.0[28]	105	1
dog	D	8.0[10]	435	5.1	8.3	75	1
ferret	F	8.5[11]	180	—	—	—	1
sea lion	Sl	8.8[12]	392	—	4.3[25]	—	1
norway rat domestic	Rd	11.1[13]	150	—	—	76	4
least weasel	W	12.0[14]	76	23.0	2.2	69	1
norway rat wild	Rw	12.8[15]	130	52.8	1.5	35	4
goat	G	18.0[10]	680	—	12.5[29]	23	5
wood rat	Wr	19.0[16]	115	156.2	2.3	85	5
hedgehog	Hh	19.0[17]	167	—	—	35	2
spiny mouse	Sp	19.0[18]	64	—	—	75	5
grasshopper mouse	Gm	19.3[16]	61	68.5	2.3	52	2
horse	H	25.0[19]	684	—	—	28	5
cow	Cw	30.0[10]	1281	132.0	12.4	20	5
gerbil	Gr	27.0[20]	87	200.0	2.0[30]	48	4
kangaroo rat	Kr	27.0[21]	90	—	—	20	5
gopher	Go	90.0[22]	111	166.0	1.7	4	5

[1] Threshold defined as 75% correct for two-choice procedures and 50% detection for conditioned avoidance procedures; [2] Renaud and Popper ('75); [3] R. Heffner and Heffner ('82); [4] R. Heffner and Heffner ('88c); [5] Terhune ('74); [6] Ravizza and Masterton ('72); [7] R. Heffner and Heffner ('89); [8] Brown, et al., ('80), H. Heffner and Heffner ('90); [9] Casseday and Neff ('73), R. Heffner and Heffner ('88c); [10] R. Heffner and Heffner (in press); [11] Kavanagh and Kelly ('87); [12] Moore ('75); [13] Kavanagh and Kelly ('86), Kelly ('80); [14] R. Heffner and Heffner ('87); [15] H. Heffner and Heffner ('85); [16] R. Heffner and Heffner ('88a); [17] Chambers ('71); [18] Mooney ('91); [19] H. Heffner and Heffner ('84); [20] R. Heffner and Heffner ('88b); [21] H. Heffner and Masterton ('80); [22] continuous noise bursts, R. Heffner and Heffner ('90); [23] Calculated based on peak density of ganglion cells except as otherwise noted; [24] Cavonius and Robbins ('73); [25] Schusterman ('72); [26] Average of ganglion cell density and evoked potential measure, Silveira, et al., ('82); [27] Cowey and Ellis ('67) and Cavonius and Robbins ('73); [28] Belleville and Wilkinson ('86) and Jacobson, et al., ('76); [29] Based on peak density of ganglion cells in Hughes and Witteridge ('73); [30] Baker and Emerson ('83).

the binocular fields have been determined specifically for this analysis and only those methods are reported in detail.

Subjects

Eyes for the determinations of width of field of best vision and visual acuity were obtained from adults of wild species or mongrel breeds of domesticated species. Similarly, width of binocular visual fields was determined on living adults of wild species or mongrels of domesticated species.

Sound localization

Interspecies variation among mammals in two-point sound localization acuity around the median sagittal plane is the focus of this report. All of the thresholds have been published and no new thresholds are reported here. Unless otherwise noted, the localization thresholds included for analysis met the following criteria: (1) the behavioral procedure controlled the position and orientation of the animal relative to the sound sources; (2) the stimulus was a complex sound, such as a noise burst or click, which included a broad range of frequencies in order to provide a maximally localizable stimulus; (3) the stimuli were brief (250 msec or less) in order to minimize scanning or homing movements; (4) the test procedure included a penalty for false alarms (reporting a signal when none is present) as well as misses (failure to report the presence of a signal) and most included a correction for false alarms in the performance measure; (5) testing included some angles of sound-source separation that were below threshold, thus assuring that artifacts that could permit the discrimination to be performed on some basis other than locus (such as quality or intensity differences between loudspeakers) were not present. Thresholds meeting such criteria are remarkably replicable despite the use of different behavioral methods of testing (cf. Brown et al., '80; Casseday and Neff, '73; H. Heffner and Heffner, '90; Heffner and Heffner, '88c; Heffner and Masterton, '90).

Interaural distance

The measures of interaural distance around the head in μsec can be used as an estimate of the magnitude of the maximum binaural locus cues available to an animal in the absence of direct measures of interaural time and intensity differences, which are available for very few species. This is a standard measure used because it closely approximates the maximum time required for a sound to travel around the head from one auditory meatus to the other (Masterton et al., '69). Maximum interaural distance can also serve as a relative measure of the maximum interaural intensity difference available to a species even though this value is strongly influenced by the wavelength of the sounds concerned as well. Interaural distances for all of the species have been published in graphic form (e.g., Heffner and Heffner, '87) and their values are listed in Table 1.

Trophic level

Rankings of trophic level, that is, the degree to which a species is predatory or itself preyed upon, were based on published descriptions of each species (Nowak and Paradiso, '83). Species were ranked on a five-point scale with '1' indicating species that are strict predators, such as cats, '2' indicating species that are predatory but are themselves occasionally preyed upon, such as least weasels and grasshopper mice (although problematical, man and macaques are also included here); '3' indicating species that are neither predator nor prey, such as elephants; '4' indicating species that are primarily prey but which catch and eat some meat or scavenge opportunistically, such as some rodents and opossums; and '5' indicating species that are strictly prey, such as cattle and most rodents.

Nocturnal-diurnal activity pattern

As with trophic level, animals were categorized on the basis of published descriptions (Nowak and Paradiso, '83).

However, the descriptions of cyclic activity patterns reveal that few mammals are strictly nocturnal and that even fewer are strictly diurnal. Many species are active at dawn and dusk (crepuscular) or, like the large hoofed animals, are active throughout the day-night cycle, sleeping in short bursts (arrhythmic). Still other species live in dark environments such as oceans or burrows and must function in darkness much of the time regardless of their circadian cycle. Because the requirement for activity under conditions that do not permit good vision would seem to be the relevant factor for the current analysis, species were classified as either primarily active in dark environments or rarely, if ever, active in dark environments.

Width of the field of best vision

There are several ways to determine the width of an animal's best field of vision. The most direct way would be to test visual acuity behaviorally under varying light conditions throughout the retina. However, to do this in a large number of species would be an impractical, if not impossible, task. Fortunately, there is evidence that the anatomical measure of retinal ganglion cell density is a good indicator of spatial resolving power of the individual (for a review, see Pettigrew et al., '88). The most complete evidence is based upon the close agreement between acuity estimates in cats derived from retinal ganglion cell density in the peak density region (e.g., Hughes, '81), behavioral determinations of acuity (e.g., Jacobson et al., '76), and determinations of acuity based on occipital evoked potentials (Harris, '78). Similar agreement between behavioral determinations of acuity, and estimates based on retinal ganglion cell density, have been found in primates (Debruyn et al., '80; Ordy and Samovajski, '68; Rolls and Cowey, '70) and in fish (Collin and Pettigrew, '89).

The variation in visual resolution throughout the retina was estimated by mapping the density of ganglion cells in opossum (*Didelphis virginina*), wild Norway rat (*Rattus norvegicus*), wood rat (*Neotoma floridana*), grasshopper mouse (*Onychomys leucogaster*), gerbil (*Meriones unguiculatus*), pocket gopher (*Geomys bursarius*), cat (*Felis domesticus*), dog (*Canis familiaris*), least weasel (*Mustela nivalis*), pig (*Sus scrofa*), and cow (*Bos taurus*). (Measures for man and macaque were obtained from published retinal analyses.) The region of best acuity was operationally defined as that area containing ganglion cell densities at least 75% of maximum. Because density gradients vary little within a species (Hughes, '77), only one retina was examined for each species except for pig, cat, and dog, for which two retinae were examined, and an average value determined for use in the analyses.

Preparation of retinal wholemounts. Histological preparation of retinal wholemounts followed the procedure described by Stone ('81). Most of the animals were euthanized using an overdose of pentobarbital and perfused through the heart with 0.9% saline followed by 10% formalin, or were obtained as fixed specimens from other investigators. In the case of very large animals (i.e., cow, pig) the orbit was dissected from a freshly killed animal at a slaughterhouse. Formalin was immediately flushed through two punctures in the sclera anterior to the retinal margin and the entire eye immersed in cold formalin for at least 1 week. The dorsal surface was marked with suture through the sclera and labeled as to left or right eye. After removal of the cornea and lens and immersing the entire eye cup in 0.9% saline, the retina was gently teased free from the sclera with a fine brush. The optic nerve was cut and the free-floating retina was slit to enable it to lie flat on a clean slide where the vitreous humor was carefully removed with a fine brush. The cleaned retina was then mounted on a gelatinized slide, covered with a sheet of filter paper, another glass slide, and a 100-g weight. This "sandwich" was immersed in 95% ethanol/4% formalin overnight. The retina was then defatted, rehydrated, stained with 0.05% thionin, dehydrated, cleared and coverslipped. With this method, shrinkage is usually less than 10% and occurs primarily at the edges of the retina and along the radial cuts; cell counts were not taken where shrinkage was noticeable.

Determination of ganglion-cell densities. Ganglion cells were counted under either a 40× objective (pig, cow, cat, dog, grasshopper mouse, wild Norway rat, gerbil, wood rat, pocket gopher, opossum) or 100× objective (least weasel) inside a rectangle encompassing either 6,200 μm^2 or 950 μm^2 respectively. Only nucleoli with at least half of their profile lying within the rectangle were included in the counts. Counts were made at least every 2 mm in the largest retinae and at least every 0.5 mm in small retinae. Counts were routinely taken at 0.1 mm in the areas of greatest change in densities, and often at 0.05 mm (adjacent rectangles) in the region of peak density. Once a slide was positioned on the stage of the microscope for counting, it was not removed until counting was complete in order to avoid errors due to repositioning.

Several morphological criteria for identification of ganglion cells were used in an effort to exclude glial cells and displaced amacrine cells (Hughes, '77, '81; Stone, '78, '81; Wong and Hughes, '87). Cells not clearly in the ganglion cell layer were excluded. Cells smaller than 7 μm in diameter were excluded as probable displaced amacrine cells or glia cells unless they contained obvious Nissl granules; larger cells without Nissl were excluded. In general, small circular cells with smooth borders, large nuclei and nucleoli, and with only a thin shell of cytoplasm and no Nissl substance were considered to be glia; all others clearly within the ganglion cell layer were considered to be ganglion cells.

These criteria proved to be reliable, since recounts at the same location were within 5% of each other. More importantly, as noted in the results, these criteria produced density maps in close agreement with studies on cats which experimentally distinguished between ganglion cells, displaced amacrine cells, and glial cells (Wässle et al., '87; Wong and Hughes, '87). It should be noted that if other mammals are similar to cats, the inclusion of displaced amacrine cells would serve to reduce the density gradient across the retina, since the proportion of displaced amacrine cells increases with distance from the central area. Variation in this effect would serve to lower the correlation between width of field of best vision and the other factors.

The ganglion cell densities in cells/mm^2 were transformed to cells/deg^2 by using a simple linear conversion. For most species the horizon of the retina subsumes approximately 170° (Walls, '42); for cat and rat the values reported by Hughes ('77) were used, and for gerbil, our own measure was used. It should be noted that, at least in macaques, the radial magnification (number of degrees encompassed by 1 mm of retina) is not constant but rather increases toward the periphery (Perry and Cowey, '85). Ignoring this nonlinearity results in a maximum error in macaques of approximately 10% when calculating densities at the periphery of the retina. It should also be pointed out that this nonlinearity is likely to vary with the size and shape of the lens and eye and is unknown for nearly all of the species included in this report. Again, this error would serve to underestimate the density gradient across the retina and thus reduce the correlations of interest here whenever the field of best vision extends to the periphery of the retina.

Defining the region of best acuity. Once ganglion cell densities were known throughout the retinae, the primary measure of interest here could be determined—the horizontal width, in degrees, of the part of the retina that included densities equal to or greater than 75% of the maximum density. This is our operational definition of the field of best vision. Other operational definitions, were also examined such as the region encompassing 90%, 50%, or 25% of maximum, were also examined. Lower criteria encounter a floor effect in retinae with a pronounced visual streak, in that densities do not fall to 50% along the horizontal meridian of the retina. Higher values are affected by relatively minor fluctuations in density near the region of peak density, falling below 90% and then rising again before falling monotonically (e.g., pigs, cattle, wood rat, gerbil, pocket gopher). Thus the "75% of maximum" criterion was used because it was relatively unaffected by floor effects or small variations in density and because it provided a measure that varied across species through the entire range theoretically possible, i.e., less than 1° to more than 180°.

Measures for species possessing a fovea. Because ganglion cells in man and macaques are displaced from the fovea, measures relying on ganglion cell density for estimates of relative or absolute acuity cannot be used. However, it has been shown that measured acuity closely corresponds to cone density in these retinae out to eccentricities of about 10° and to ganglion cell densities beyond 10° (Merigan and Katz, '90). Accordingly, cone densities have been used to estimate the width of the field of best vision in these species and the width of the area with cone densities 75% of maximum has been determined. The values used here were derived from published cone densities for macaques (Wickler et al., '90) and humans (Curcio et al., '87). In both cases a range of values was reported and an average was determined.

Visual acuity

The published values for maximum visual acuity, or two-point resolution, in cycles per degree (c/deg) have been used for human, cat, macaque, gerbil, opossum, rat, and seal. Where published values were not available, maximum acuity is estimated by means of Shannon's sampling theorem (e.g., DeBruyn et al., '80): $(\sqrt{x})/2$ = maximum theoretical resolvable spatial frequency in c/deg, where x = number of ganglion cells/deg^2. Thus, for example, a maximum acuity of 30 c/deg (a 30 c/deg square-wave grating) translates to a minimum resolvable bar width of 1 minute of visual angle. As noted in the results, there was good agreement between visual acuity as estimated by applying the sampling theorem to maximum ganglion cell densities and visual acuity determined behaviorally for cat, gerbil, opossum, and rat, thus suggesting that the estimates for the other species are also reasonable.

Binocular visual fields

The binocular visual fields were defined as the width of the angle of overlap of the retinal fields of the left and right eyes. The horizontal retinal field of each eye was determined as the angle through which light from the narrow beam of an ophthalmoscope could be refracted through the lens and onto the retina. In cats, dogs, monkeys, and humans, this was accomplished in awake individuals (and replicated in dogs under sedation). Other species were examined under ketaset sedation. When necessary (i.e., opossums) the pupils were dilated with Midriacil 1%. Measurement error was approximately plus or minus 5°.

Statistical analysis

Relationships between the factors considered here were determined by using simple and multiple regression analyses (Data Desk 3.0, Odesta Corp.).

RESULTS

The results of this report are of two types: the determination and gathering of values for factors which may correlate with sound localization acuity, and the correlations themselves. We shall first describe the available data on sound localization thresholds and then present the results which consist of new data derived from the ganglion cell density measures (width of the field of best vision and visual acuity) and the determinations of the binocular visual fields. These are followed by ordinal rankings of the lifestyle factors, trophic level, and activity cycle. Finally, the correlations among these factors will be presented. Values for all of the parameters, including sound localization thresholds and interaural distance are listed in Table 1. For convenience, Table 1 also includes a key to the symbols used to indicate each species in the scatterplots.

Sound localization thresholds

The sound localization thresholds for twenty-three species of mammals (with Norway rats represented by both wild and domestic varieties) are listed in Table 1. All were behavioral measures of minimum discriminable angle around the midline (left-right discriminations) using a procedure that controlled the position of the animal relative to the sound sources, and all included a penalty for false alarms as well as misses. Only the threshold for macaques by Brown and colleagues ('80) did not include a correction for false alarms in calculating performance, but their behavioral procedure kept false alarms to a minimum and their thresholds agree closely with thresholds obtained by other investigators (H. Heffner and Heffner, '90). Most of the thresholds were obtained using broad-spectrum noise stimuli, but thresholds for dolphin, seal, and hedgehog are available only for single clicks, and the threshold for kangaroo rats was obtained using a 2/second click train. In animals that have been tested using both noise and click stimuli, clicks tend to support slightly lower localization acuity than brief noise bursts (e.g., Heffner and Heffner, '84; Heffner and Heffner, '82) with the result that actual localization acuity for these four species might be a slight underestimate of their ability compared to the species tested using noise. The threshold for the ferret is an average of the three individuals with the best acuity (Kavanagh and Kelly, '87).

The only significant exception to the criteria for sound localization thresholds is the threshold reported for one species, the pocket gopher (R. Heffner and Heffner, '90). Because pocket gophers were unable to localize brief sounds at all, their threshold could only be determined using a continuously pulsed noise which permitted scanning move-

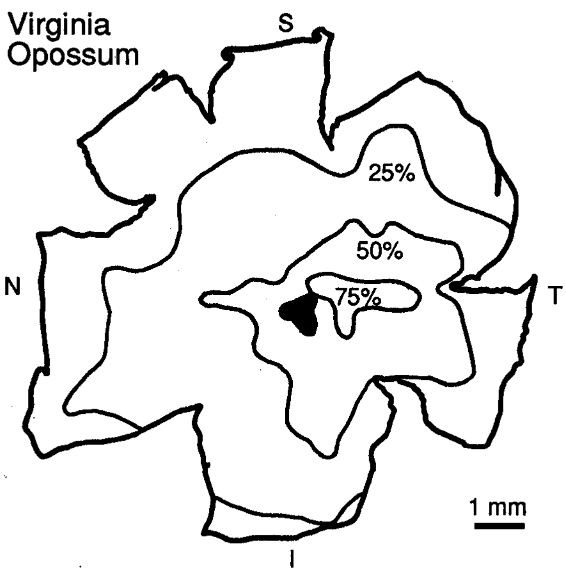

Fig. 1. Ganglion cell isodensity contours for a Virginia opossum. A small streak is evident in the 75% isodensity contour. The optic disk is indicated in black. S, superior; I, inferior; N, nasal; T, temporal.

ments of the head (although these were minimized by a behavioral procedure which required the animal to keep its mouth on a small waterspout). Accordingly, the threshold for the gopher used in the regression analyses may seriously overestimate its acuity. Nevertheless, it is included because it represents an extreme on the scale for sound localization acuity. Thus, it is potentially important in understanding the range of localization acuities in mammals and the relation between especially poor acuity and the other factors examined here. The symbol for the gopher in the scatter plots is marked with an asterisk to emphasize its difference from the other determinations of localization acuity.

Width of the field of best vision and visual acuity

Marsupials. The isodensity contours of the left retina of a Virginia opossum (*Didelphis virginiana*) are illustrated in Figure 1. The overall appearance of the retina is much like that reported previously by Kolb and Wang ('85). The contours are relatively circular with a field of best vision located temporal to the optic disk. Some elongation is evident in the region encompassing cell densities at least 75% of maximum density. The horizontal width of this region measures 15.8°. Maximum ganglion cell density was 3,225 cells/mm^2 (a value within 10% of that reported by Kolb and Wang, '85), which suggests a maximum visual acuity of 2.3 c/deg.

Rodents. Retinae were examined in five species of rodents. Figure 2 illustrates ganglion cell isodensity contours for two species with well differentiated visual streaks, the grasshopper mouse (Cricetidae, *Onychomys leucogaster*) and the gerbil (Cricetidae, *Meriones unguiculatus*). In the grasshopper mouse the streak is obvious in both the regions encompassing 75% and 50% of maximum density and extends further temporally than nasally; ganglion cell density remains above 25% of maximum along the entire horizon of the retina. The region encompassing 75% of maximum density is 68.5° in horizontal width. The visual streak in the gerbil is more marked; ganglion cell densities remain at least 75% of maximum throughout nearly the entire horizontal width of the retina. Because the retinal field of the gerbil encompasses approximately 200° due to its protuberant eyes, the horizontal width of the region encompassing ganglion cell densities at least 75% of maximum was also 200°.

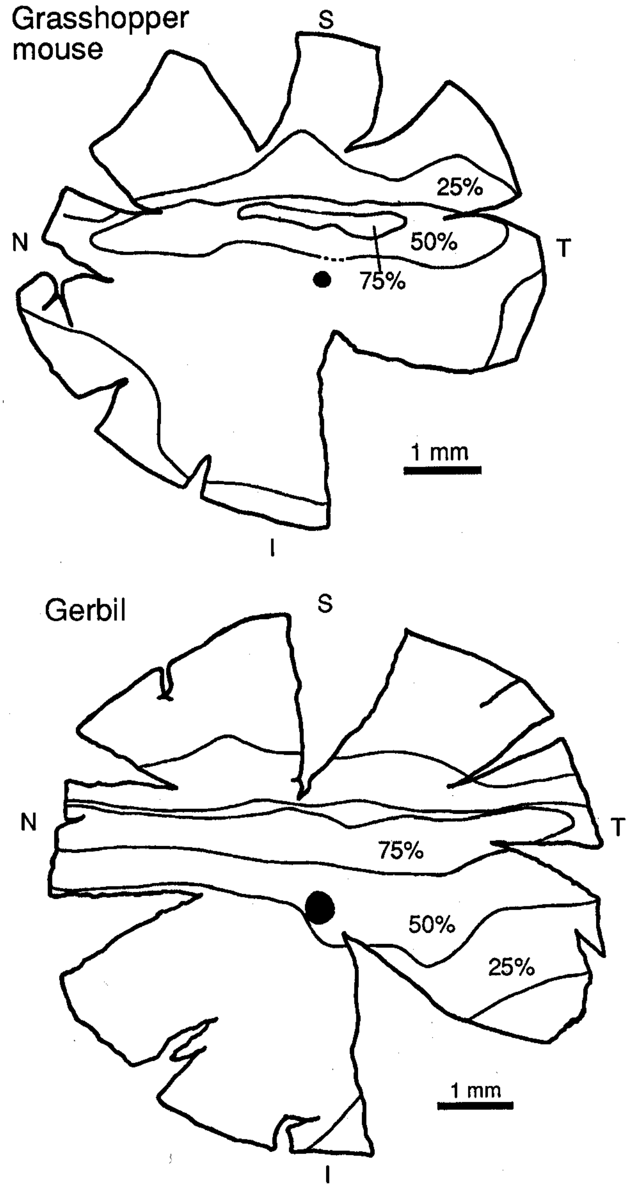

Fig. 2. Ganglion cell isodensity contours for a grasshopper mouse and a gerbil. Both species have a visual streak which is more marked in the gerbil. Abbreviations as in Figure 1.

Maximum densities of 15,000 cells/mm^2 were obtained centrally and dorsal to the optic disk in the grasshopper mouse which suggest a maximum visual acuity of 2.3 c/deg. The maximum density in the gerbil was 15,300 cells/mm^2 in the temporal retina and its behaviorally determined visual acuity is 2.0c/deg (Baker and Emerson, '83).

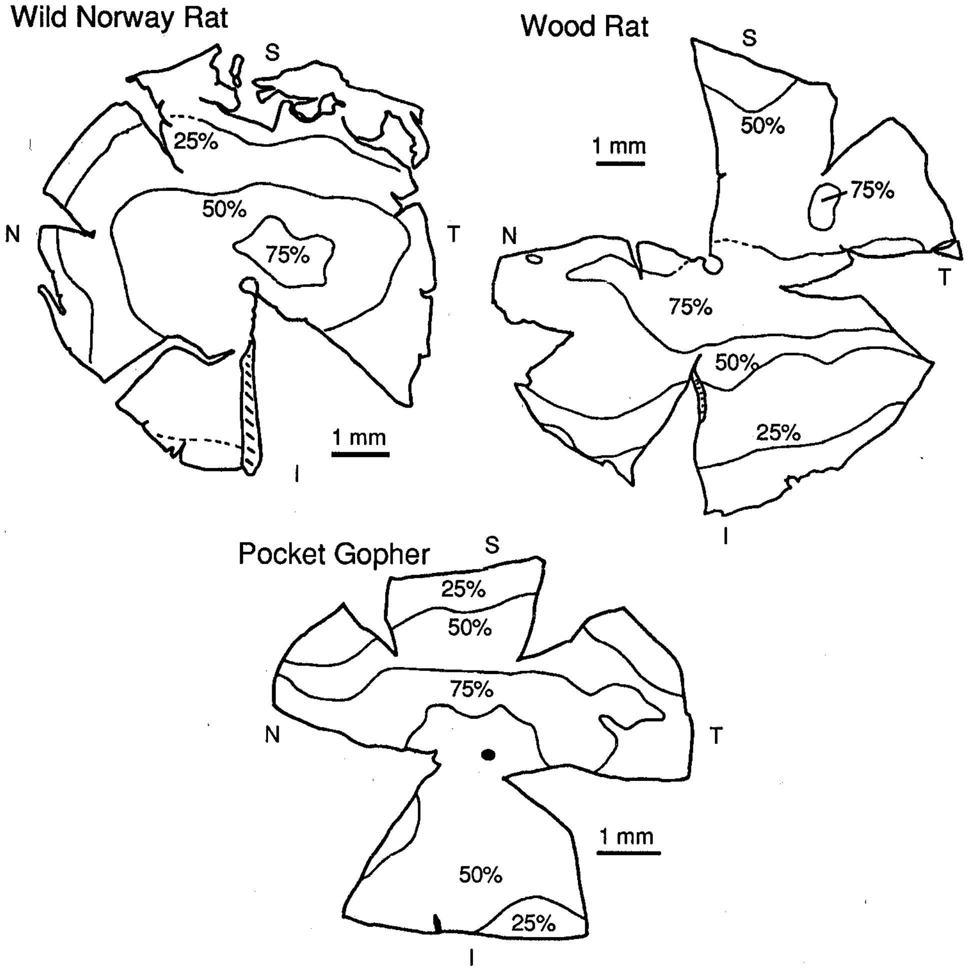

Fig. 3. Ganglion cell isodensity contours for a wild Norway rat, wood rat, and pocket gopher. The density gradients are relatively shallow in all three species with the pocket gopher having the shallowest. Isodensity contours are approximately circular in the Norway rat, but a broad streak is evident in both the wood rat and pocket gopher. Abbreviations as in Figure 1.

Figure 3 illustrates isodensity contours for three species of rodents with less differentiated visual streaks: the wild Norway rat (Muridae, *Rattus norvegicus*), the wood rat (Cricetidae, *Neotoma floridana*), and the pocket gopher (Geomidae, *Geomys bursarius*). The isodensity contours and maximum density for the wild Norway rat are very similar to those reported for domestic Norway rats, both albino and hooded, regardless of whether ganglion cells were labeled with HRP (5,000–6,000 ganglion cells per square mm, Dreher et al., '85) or were identified using morphological criteria with a Nissl stain (6,200–6,500 ganglion cells per square mm, Fukuda, '77). In the wild rat examined here the region encompassing 75% of maximum ganglion cell densities was 52.8° wide and was located slightly superior and temporal to the optic disk. Maximum density was 6,774 cells/mm^2, suggesting a maximum visual acuity of 1.5 c/deg which is similar to the 1.2 c/deg determined behaviorally for pigmented rats (Birch and Jacobs, '79).

The density gradient in the retina of the wood rat is less steep in the horizontal plane than those in the Norway rat, resulting in a broader region encompassing densities at least 75% of maximum. This region is 156.2° wide and extends further temporally than nasally. There is also a small region of high density superior to the visual streak in the temporal retina. The maximum concentration of ganglion cells is located ventral to the optic disk and reaches densities of 10,484 cells/mm^2 corresponding to a maximum visual acuity of 2.3 c/deg.

The pocket gopher is of special interest because it is a burrowing mammal which spends nearly all of its time underground. It has numerous specializations for this lifestyle, including reduced ability to regulate body temperature, the absence of pinnae, vestigial auditory sensitivity and localization ability, and small eyes (R. Heffner and Heffner, '90; Nevo and Reig, '90). Nevertheless, the retina of the gopher is a generalized avascular retina, containing both cones and rods, and suggests evolution from a diurnal or crepuscular ancestor (Feldman and Phillips, '84). The ganglion cell isodensity contours displayed in Figure 3 reveal very shallow density gradients both horizontally and vertically making it the most homogeneous retina examined. The region encompassing densities at least 75% of maximum encompass 166° of the horizon in the pocket gopher. Maximum concentrations of ganglion cells were found superior to the optic disk and peaked at 8,870 cells/mm^2, suggesting a maximum visual acuity of 1.7 c/deg.

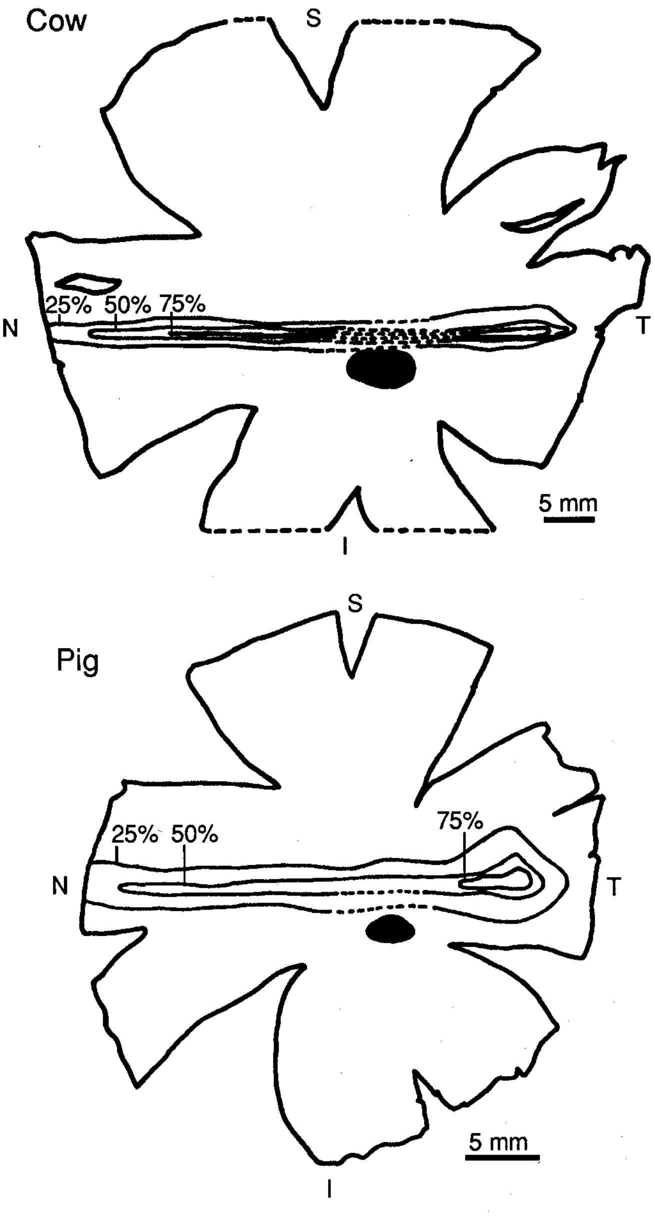

Fig. 4. Ganglion cell isodensity contours for a cow and pig. Both species have a marked visual streak, but a relatively narrow area of greatest density is present in the pig. Dashed lines at the superior and inferior margin of the cow retina indicate edges of the microscope slide. Abbreviations as in Figure 1.

Artiodactyls. Retinal ganglion cell isodensity contours are illustrated for two Artiodactyls in Figure 4. The cow (Bovidae, *Bos taurus*) represents an exclusively prey species and the pig (Suidae, *Sus scrofa*) represents a generalized artiodactyl and one of the few members of this order that is often predatory in its habits. The ganglion cell layer of the cow illustrated here is much like that described previously (Hebel, '76; Hebel and Holländer, '79), with a dramatic streak just superior to the optic disk and a peak density of 6,130 cells/mm^2 located far temporally. This maximum density in such a large eye suggests a maximum visual acuity of 12.4 c/deg. The horizontal width of the region encompassing densities 75% of maximum or greater is 132°.

The results for the domestic pig are also very similar to those reported previously (Hebel, '76; Hughes, '77) and show a combination of a visual streak in the 25% and 50% contours, but a relatively narrow field of best vision in the contour representing 75% of maximum density. This field of best vision encompasses 11.6° along the horizon. The maximum ganglion cell density was located far temporally; the density of 6,615 cells/mm^2 agrees closely with previous reports (Hebel, '76; Hughes, '77) and predicts a maximum visual acuity of 8.0 c/deg.

Carnivores. Figure 5 illustrates ganglion cell isodensity contours for three carnivores: domestic mongrel dog (Canidae, *Canis familiaris*), domestic cat (Felidae, *Felis domesticus*), and the smallest extant member of the order, the least weasel (Mustelidae, *Mustela nivalis*). All three species are strongly predatory, but because of its small size, the least weasel is also occasionally preyed upon. The ganglion cell density gradients are steep in dogs but a small streak is evident in the region encompassing densities of 25% of maximum (c.f. Hughes, '77). However, the highest densities are concentrated in a relatively small region so that the width of the region encompassing 75% of maximum density is only 5.1° wide. The maximum density of 7742 cells/mm^2 agrees closely with that reported previously (Hughes, '77) and suggests a maximum visual acuity of 8.3 c/deg.

The isodensity contours for the cat are similar in shape to the many previously published analyses of the ganglion cell layer of cats (e.g., Hughes, '75, '81; Rowe and Stone, '76). The concentration gradient is even steeper than in dogs and a streak is only evident in the gradient encompassing densities 25% of maximum. The contour representing densities 75% or more of maximum encompasses only 4.9°. Maximum density in the retina reported here is 9670 cells/mm^2 which is well within the range of recent reports using Nissl stains (Hughes, '75) or HRP-labeled ganglion cells (Hughes, '81). This maximum density suggests a maximum resolution of 8.9 c/deg which is intermediate between behaviorally determined thresholds of 8.5 and 9.7 c/deg.

The ganglion cell distribution in the least weasel differs from that in the other two carnivores examined here, in that its density gradient is less steep. Densities barely fall to 25% of maximum in the horizontal plane and a distinct streak is evident in the 50% contour. In both the 50% and the 75% contours there is a slight extension superiorly of the area of maximum concentration. A similar appearance of isodensity contours (without the extension) has been reported for the domestic pigmented ferret (Henderson, '85; Vitek et al., '85). The width of the 75% contour is 23.0° in the least weasel. The maximum ganglion cell density found in the retina of the least weasel was 17,895 cells/mm^2. This density is at least three times that found in the much larger domestic ferret (c.f. Henderson, '85; Vitek et al., '85), but is comparable to the maximum densities found in some other small species (gerbils and grasshopper mice). This maximum density in such a small retina suggests a maximum visual acuity of 2.2 c/deg.

Primates. As noted in the methods, the region of best acuity cannot be determined from ganglion cell counts in species in which ganglion cells are absent from the fovea. Accordingly, we have relied on published reports of cone densities in the fovea for both macaques and humans. In man (Curcio et al., '87), maximum cone densities ranged from 96,900 to 281,000 per mm^2, but the width of the

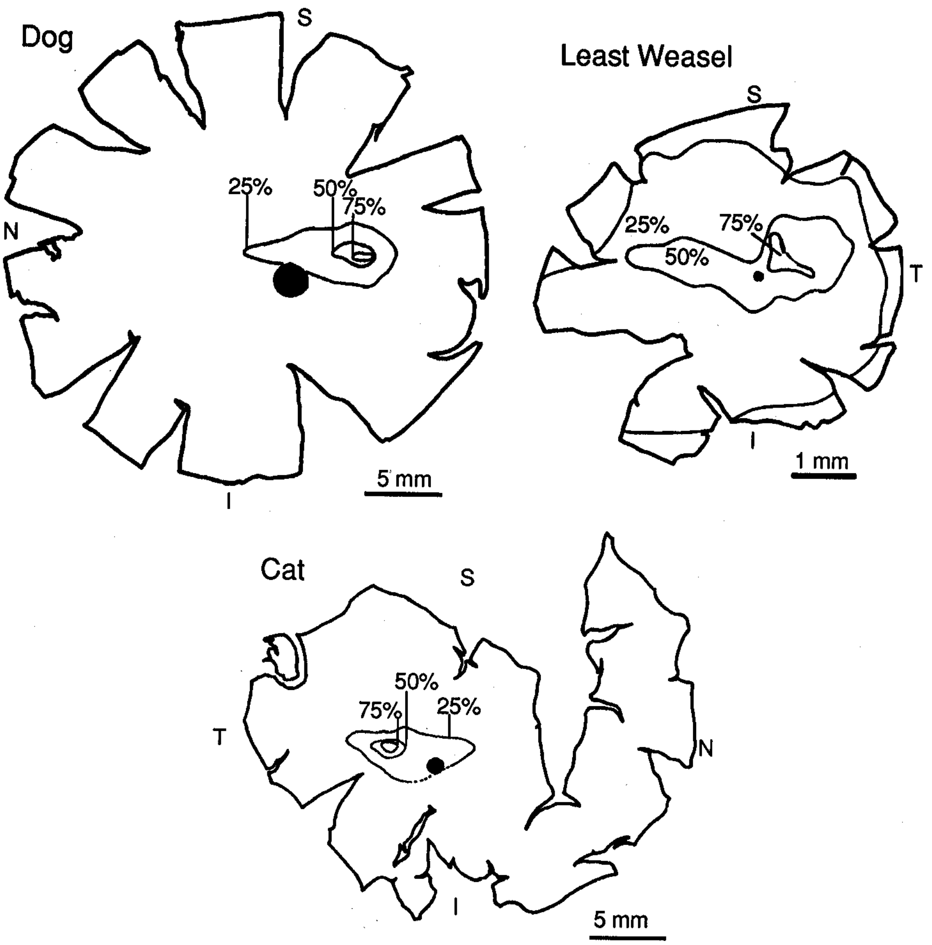

Fig. 5. Ganglion cell isodensity contours for a dog, cat, and least weasel. Density gradients are steep in the dog and cat, but a narrow streak is evident in the 25% contour. The least weasel has a less steep density gradient and a broad streak evident in the 50% contour but a narrow region of highest ganglion cell density. Abbreviations as in Figure 1.

region encompassing densities at least 75% of maximum ranged only from 0.4° to 0.97° and we have used an average value of 0.7° to represent man in our correlations. A representative visual acuity for man is 67 c/deg (Cavonius and Robbins, '73).

For the rhesus macaque (Wikler et al., '90) maximum cone densities ranged from less than 80,000 to approximately 190,000 cones per mm^2. By replotting the published values and measuring the width of the region encompassing cone densities at least 75% of maximum for the extremes of the published range, we determined the horizontal width of this visual field to be from 3.1° to 5.42° with a median value of 4.3°. The representative visual acuity for macaques is 46.8 c/deg based on behavioral tests (Cavonius and Robbins, '73; Cowey and Ellis, '67).

Binocular visual fields

The measures of horizontal width in degrees of the binocular visual fields of the species covered in this report are listed in Table 1. They range from the very small binocular field of the pocket gopher (4°) to the large binocular fields of man, macaque, and cat (105–111°).

Lifestyle factors

Trophic level. The rankings of the degree to which a species is predator or prey, as suggested by published descriptions of their habits, are listed in Table 1, with 1 being strictly predatory and 5 being strictly prey.

Activity cycle. Among the twenty-four animals in the sample, only man and macaques show minimal activity in the dark—all others spend a significant part of their active time foraging and avoiding predators in the dark. Thus, contrary to expectation, the diurnal species are among those with good localization acuity and animals active in darkness cover the entire range from very good to very poor acuity. However, our sample contains too few strictly diurnal species for reliable analysis and the relation between sound localization and activity pattern cannot be pursued further until additional and more diverse diurnal species are examined.

Statistical analyses of correlates of sound localization acuity

A matrix of the first-order correlation coefficients among all of the factors is displayed in Table 2. The relationships

TABLE 2. First-Order Correlation Coefficients

	Sound localization threshold	Inter-aural distance	Binocular visual field	Field of best vision	Visual acuity	Trophic level[1]
sound localization	1.000					
interaural distance	−0.404	1.000				
binocular visual field	−0.732	0.103	1.000			
field of best vision	0.911	−0.542	−0.611	1.000		
visual acuity	−0.532	0.762	0.336	−0.747	1.000	
trophic level	0.606	−0.026	−0.536	0.729	−0.240	1.000

[1] All factors logarithmic except trophic level.

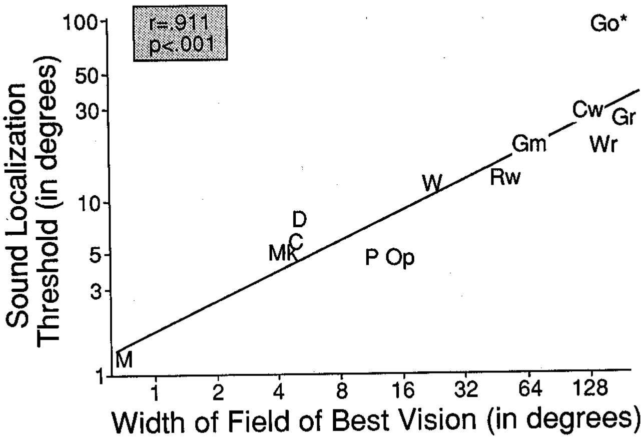

Fig. 6. Relationship between width of field of best vision and sound localization threshold for thirteen species of mammals (note log scales). Species with a narrow field of best vision have much smaller sound localization thresholds (greater acuity) than species with a broad field of best vision. In this and subsequent figures, a shaded box indicates a statistically reliable correlation. Abbreviations for this and subsequent figures: Cat, C; cow, Cw; dog, D, dolphin, Do; elephant, E; ferret, F; gerbil, Gr; goat, G; gopher, Go; grasshopper mouse, Gm; hedgehog, Hh; horse, H; kangaroo rat, Kr; macaque, Mk; man, M; Norway rat domestic, Rd; Norway rat wild, Rw; opossum, Op; pig, P; sea lion, Sl; seal, S; spiny mouse, Sp; weasel, W; wood rat, Wr; * indicates that the threshold for gophers is based on long-duration stimuli because they were unable to localize brief sounds.

between the log of sound localization threshold and each of the five potentially predictive factors are illustrated in Figures 6–8. The strongest correlation (Fig. 6) is with the log of the width of the field of best vision (r = .911) which accounts for 83% of the variance. As illustrated, species with a narrow field of best vision have the smallest sound localization thresholds and those with broad fields of best vision have the largest.

Despite the strength of this relationship, we considered the possibility that this correlation might be spurious and due instead to a common relation of both sound localization and width of field of best vision to one of the other potential explanatory factors. Accordingly, each of these factors was, in turn, removed mathematically from the relationship using partial correlations (Fig. 7). Even after the removal of the influence of absolute visual acuity, width of the binocular visual field, trophic level, or interaural distance, the correspondence between sound localization acuity and width of the field of best vision remains high and reliable (r = .842, .873, .862, .868 respectively). Thus, the relationship between sound localization and width of the field of best vision does not seem to depend on a common relationship with any of the other factors so far proposed. Indeed, a multiple correlation using all of these potential explanatory factors increased the amount of variance accounted for by only 13%. Accordingly it seems that the major correlate of sound localization acuity is the width of the field of best vision. The other factors that have so far been suggested seem to contribute minimally.

Nevertheless, as noted previously and illustrated in Figure 8 (left column), there does seem to be a recognizable correspondence between these other factors and acuity of sound localization among mammals. Thus, as above, it seemed appropriate to examine each of these, in turn, to determine whether their relation to sound localization might be accounted for by a common relation to width of the field of best vision (Fig. 8, right column).

As listed in Table 2, the width of the field of best vision is reliably correlated with both visual acuity (r = -.747) and with width of binocular visual field (r = -.611). Removing the contribution of the width of the field of best vision from the correlations of visual acuity and width of binocular fields with sound localization threshold reduces those correlations to insignificance (Fig. 8, right column). It should be noted that the relationship between binocular visual fields and sound localization appears to remain strong even after removing the influence of the width of the field of best vision. However, this high correlation is due to the fact that regression analyses can be strongly affected by even a single extreme value. In this example, the correlation is determined almost exclusively by the extreme case of the fossorial pocket gopher with its very high leverage value of 0.8. Without the pocket gopher this correlation also falls to insignificance. Tests with additional species which, like the gopher, have very small binocular fields may provide insight into whether the gopher is an indicator of the importance of binocular vision or merely a unique aberration. With the data currently available it seems that any correspondence between visual acuity or binocular fields and sound localization acuity is due primarily to their common correlation with the width of the field of best vision. Species with the best sound localization acuity tend to have both good visual acuity and a narrow field of best vision. Similarly, good sound localizers tend to have both large binocular visual fields and a narrow field of best vision. Partial correlational analyses indicate that it is the width of the field of best vision that is the primary factor.

Trophic level, the degree to which a species is a predator or prey, is also significantly correlated with sound localization acuity (r = .606) and with width of the field of best vision (r = .729), but as shown in Figure 8, removal of the influence of field of best vision reduces the correlation between trophic level and sound localization acuity to insignificance. Again, good localizers tend to be predatory in their habits and have a narrow field of best vision; it is the latter factor that seems to be primary.

With the accumulation of a more representative sample of mammals, interaural distance has become a relatively unreliable predictor of sound localization acuity. As illustrated in Figure 8, even the marginal predictiveness of this factor is eliminated when the influence of the width of the field of best vision is removed mathematically. Surprisingly, it seems that interaural distance is just a weak correlate of the main factor, the width of the field of best vision, and has no direct significance for sound localization acuity.

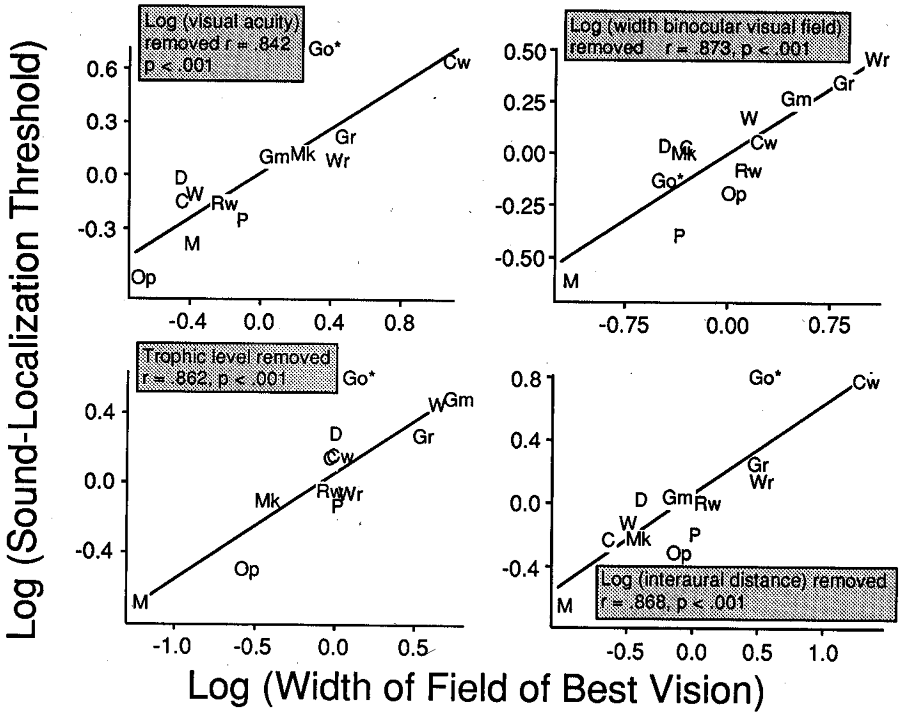

Fig. 7. Relationships between width of field of best vision and sound localization threshold with the effect of each of the other factors removed mathematically (note all scales are logarithmic except trophic level). The correlation coefficient remains high and reliable despite the removal of the contribution of visual acuity, width of the binocular visual field, trophic level, or interaural distance. For key to symbols see Table 1 or Figure 6.

DISCUSSION

The strong correlation between sound localization acuity in the horizontal plane and the horizontal width of the field of best vision lends credibility to the suggestion that an important source of selective pressure for sound localization in mammals is the precision required of the behavior that it directs, specifically, the orientation of vision for further examination of sound sources. It is important to note at the outset, however, that it is relative acuity that is important, rather than absolute visual acuity. When an animal directs its vision, it uses the best vision it possesses regardless of how good or poor that vision is. Even though there is some correspondence between absolute visual acuity and sound localization acuity, that relationship is due to the common correlation of each with the width of the field of best vision. In other words, animals with narrow areas of best vision tend to have better localization acuity regardless of their visual acuity.

Vision, in turn, is strongly influenced by an animal's lifestyle, with the result that lifestyle factors become apparent correlates of auditory abilities as well. For example, predators have more frontally placed eyes and consequently larger binocular fields than prey species (r = -.536 among the current sample; cf. Hughes, '77). Similarly, predators tend to have smaller fields of best vision (r = .729). Thus, the visual parameter of width of the field of best vision serves as a basis for the observed first-order correlations between sound localization acuity, trophic level, and width of binocular visual fields, and the addition of these factors in a multiple correlation adds minimally (13%) to the variance that can be accounted for.

In attempting to identify a single factor that can account for much of the interspecies differences in sound localization in mammals, we have concluded, along with other investigators, that audition seems to coordinate closely with vision. In other words, the precision of auditory localization may depend on the precision required of the resulting behavior. One of the most consistent behaviors to result from hearing a sound is the orienting reflex which turns the head and eyes toward a sound source for visual scrutiny (Hafter and DeMaio, '75; Pumphrey, '50). This orienting reflex to sound is even faster and more accurate than the orienting reflex to a brief flash of light (Whittington et al., '81). Indeed, it has even been demonstrated in owls that vision calibrates sound localization during development—that is, owls hearing a brief sound orient to the perceived location of a visual stimulus even when that stimulus has been artificially displaced by prisms from the actual sound source (Knudsen and Knudsen, '89). Further evidence that vision and sound localization are closely linked, are the congruent auditory-visual maps of space in the superior colliculus and the dependence of the auditory map upon visual input for normal development (Jay and Sparks, '84; Meredith and Stein, '86; Wise and Irvine, '83; Withington-Wray et al., '90).

Thus, in phylogeny as well as in ontogeny, it seems that the precision required of directional *information* from the auditory system may depend on the precision required of directional *responses*. When an animal hears a sound and directs its vision toward the source, *it is the region of its eyes capable of the most acute vision that is directed.* In man this is the fovea, an area encompassing only 1–2° of the horizon,

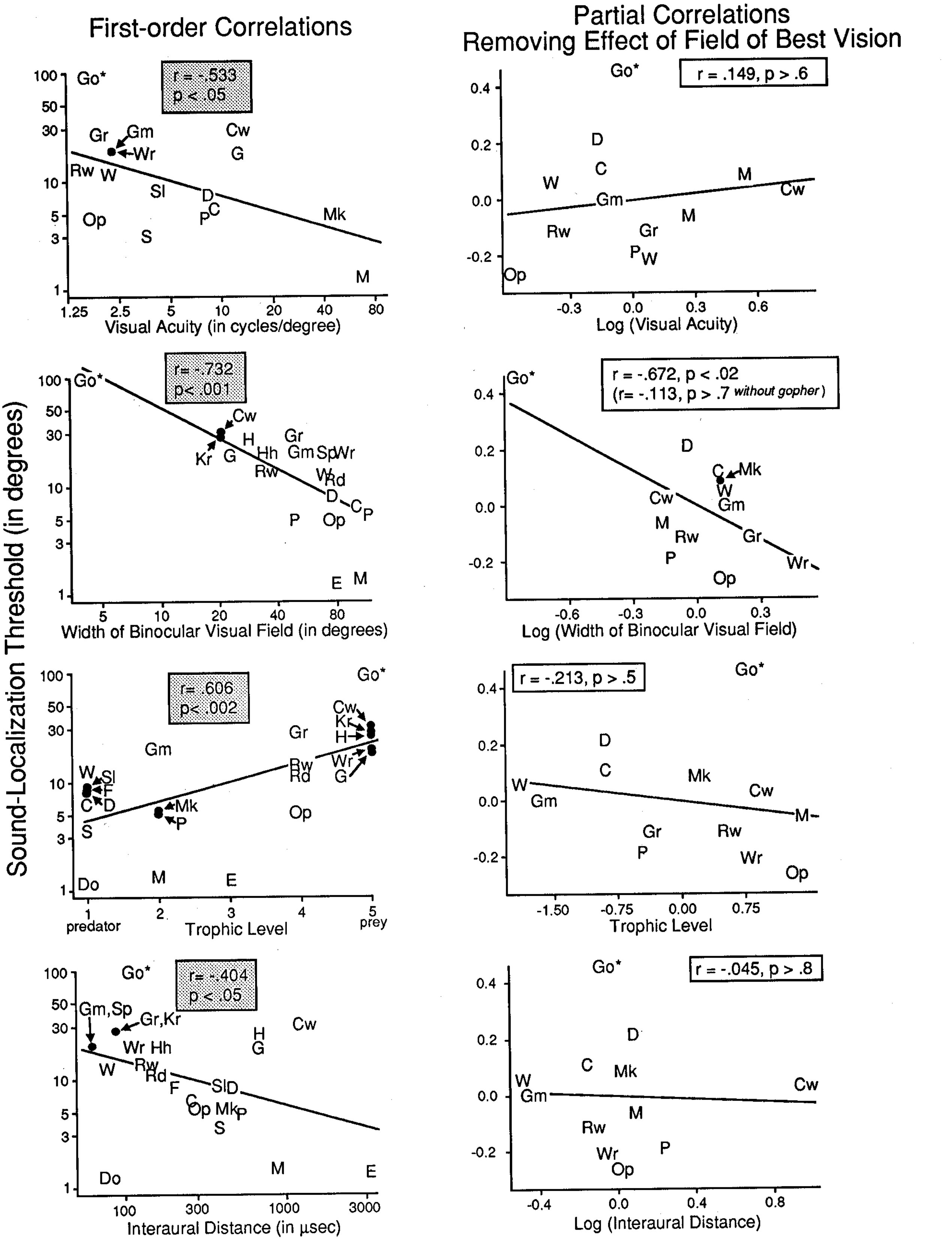

Fig. 8. Left column: relationship between sound localization threshold and four factors suggested to contribute to the variation in localization acuity; each factor is significantly correlated with localization threshold. Right column: each of the relationships collapses entirely after the contribution of width of field of best vision has been mathematically removed. Note log scales for all factors except trophic level; correlation coefficients and associated probabilities are shaded when statistically reliable and unshaded when not reliable; for key to symbols see Table 1 or Figure 6.

which suggests that man's auditory localization acuity must also be in that range in order to direct his narrow fovea without error. However, most mammals do not have a fovea, but rather, have a broader region of best vision. For example, in some rodents and hoofed mammals, the region of the retina capable of acute vision is so broad that it encompasses nearly all of the horizon and is called a visual streak (for a review of the variation in retinal topography, see Hughes, '77). It seems reasonable that a species with a visual streak encompassing as much as 180° of the horizon would not need a very precise auditory indication of locus to enable it to bring a sound source into such a broad field of good vision.

Before continuing, it is appropriate to indicate some of the limitations and strengths of this analysis and to examine some possible predictions generated by the correlations presented.

Limitations of the sample

The most serious limitation to these conclusions is the small available sample. Among the many species of mammals, sound localization thresholds have been published for only twenty-four, and, of these, two are actually wild and domesticated varieties of the same species (Norway rat). The sample is further limited by the availability of determinations of the width of the field of best vision to only thirteen species. However, the width of the field of best vision can be estimated from published data for four additional species: horses and goats, both poor localizers (Heffner and Heffner, '84; Heffner and Heffner, in press), have broad visual streaks (Hebel, '76; Hughes and Whitteridge, '73) as might now be predicted. On the other hand, elephants have a relatively narrow field of best vision (Stone and Halasz, '89) and very acute sound localization (Heffner and Heffner, '82) as might also be predicted. Ferrets have an intermediate visual streak (Henderson, '85; Vitek et al., '85) in keeping with their moderate localization acuity (Kavanagh and Kelly, '87). These four additional species bring the number which supports the hypothesis to seventeen.

Although the sample is small, it is nevertheless representative of mammals in general along a number of relevant dimensions. Five orders of mammals are represented, including 4 families of rodents and 2 families of artiodactyls, groups often underrepresented in comparative analyses. On the other hand only two primates are included, a group often overrepresented with the result that a comparative analysis becomes dominated by their neural and sensory specializations. The largest deviation from a representative sample is the absence of bats owing to the fact that passive sound localization thresholds have not been determined for any bat species.

A broad range of lifestyles is also represented. The sample of thirteen species for which complete information is available includes species ranging from strict predators to those that serve as prey and are exclusive herbivores. Similarly, a wide variety of circadian rhythms are represented in the sample. Nevertheless, additional species that are strictly diurnal are needed in order adequately to examine the contribution of that factor to the variation in localization acuity. Both surface and exclusively subterranean species are included. Unfortunately, retinal analyses for aquatic mammals remain unavailable; it will be important to examine aquatic mammals, some of which may relegate vision to a lesser role, owing to the limited light available to those that spend much of their time submerged. In such cases, vision may no longer be a strong force influencing sound localization.

The sample includes a broad range of interaural distances—from some of the smallest mice (maximum interaural time differences of 61 μsec) to some of the largest land dwellers (cattle, 1,281 μsec). The only potentially important group not represented are the large predators because of the difficulties encountered in carrying out behavioral tests with such species.

Finally, the maximum ranges of both the visual and the auditory parameters are included in this small sample so that future surprises are not likely to result from an initial sample covering only a truncated range of the relevant parameters.

Strengths

One of the strengths of the correlation between sound localization and width of field of best vision is that it accommodates several species that are deviant, in attempts to predict localization acuity using other factors. For example, humans, pigs, gerbils, and wood rats deviate most from the regression line relating width of binocular fields to sound localization acuity, but these species are accurately predicted by the width of the field of best vision. Similarly, the large hoofed mammals which diminish the correlation between interaural distance and sound localization are also accurately predicted by the width of the field of best vision.

Special cases

Subterranean species. There is one diverse group of mammals for which neither visual form nor auditory locus may be useful information. These are species that live exclusively underground. The dark environment of burrows renders vision relatively useless in scrutinizing objects so that there is little need for the ears to direct the eyes. Indeed, in the pocket gopher, the ganglion cell density gradients are shallow and nowhere do they fall below 25% of maximum, thus making its retina the most homogeneous retina examined. Similarly, auditory locus seems to have little relevance in their one-dimensional world and their sound localization is by far the least acute so far observed among mammals (R. Heffner and Heffner, '90). Even though the localization acuity of the subterranean gopher is overestimated (owing to the necessity of testing using long-duration stimuli), it still represents an extreme value on all of the regression plots, suggesting that it is truly unusual. Thus, the pocket gopher is clearly the most extreme case in the sample. At least two other subterranean species (naked mole rat, *Heterocephalus glaber*, and blind mole rat, *Spalax eherenbergi*) appear to be similarly deviant (Heffner and Heffner, unpublished observations).

Echolocators. Although the need to direct the gaze appears to be the major factor determining "passive" localization acuity in mammals, this relationship may not apply to the use of "active" echolocation particularly by animals, such as microchiropteran bats which no longer rely on vision for scrutinizing their environment. In addition to locating objects in space, echolocators use audition to examine the shape, distance, motion, and identity of objects—analyses carried out by vision in non-echolocators (Neuweiler, '90). Thus, even though microchiropteran bats have exquisite ability to locate objects using sonar, they have low density gradients among their retinal ganglion cells (Pettigrew et al., '88) resulting in relatively broad areas of best vision. Such broad areas of best vision would predict that their accurate echolocation may be accompanied by relatively poor "passive" sound localization acuity.

Significance and implications

The significance of the analysis reported here is not simply that we are able to accommodate a wide range of species with a single relatively simple factor in a long-standing effort to account for the wide species differences in sound localization. The results also give new importance to an old idea: visual orientation to an auditory stimulus is not only a convenient function, it is also an important factor in the evolution of hearing and may begin to explain the puzzling correspondence of the sizes of major nuclei in the brainstem dealing with sound localization and eye movements (Irving and Harrison, '67). Thus, we suggest that a primary function of audition, in addition to serving as a detector of sound sources (nearly always another animal), is to direct visual attention for further analysis. The degree of selective pressure for acuity in sound localization, in its turn, exerts profound effects on basic auditory sensitivity (e.g., R. Heffner and Heffner, '82, '90; Masterton et al., '69).

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