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Visual and Nonvisual Auditory Systems in Mammals

Anatomical evidence indicates two kinds of auditory pathways and suggests two kinds of hearing in mammals.

J. M. Harrison and R. Irving

It is generally assumed by those interested in the study of the anatomy and physiology of mammalian hearing that the auditory system is essentially the same in all mammals (*1*). In work on the comparative anatomy of the auditory system of the brain stem (*2*) it has been shown that the various structures which comprise the system vary in size relative to other parts of the brain, but the underlying assumption appears to be that all the various structures are present in all mammals. For example, the auditory system is very large in many bats (*3*) and relatively small in many primates (*4*), but in both groups of animals it is assumed to consist of the same components. In this article we are concerned with variations in the size of the components of the auditory system of the brain stem in mammals and with evaluation of the idea that not all components of the auditory system are present in all mammalian species.

Anatomical work has shown that the cochlear nucleus (in cat and rat) contains groups of different classes of nerve cells and that the nerve fibers which arise from each of these cell groups terminate in different nuclei of the superior olivary complex (*5, 6*). That is, above the level of the cochlear nucleus the auditory system consists of a number of separate pathways rather than a single pathway. One implication of this finding is that one or more of the pathways may be associated with behaviorally distinct aspects of hearing. This can be illustrated by a well-known analogous problem in vision. The retinas of many mammalian species contain primary light receptors which can be divided, on anatomical grounds, into two classes, rods and cones. Schultze was the first to note (*7, 8*) that the rods and cones are distributed differently in the retinas of different animals. He investigated the relation between the distribution of rods and cones in the retina and the nocturnal and diurnal habits of a large number of vertebrates and came to the conclusion that there were two kinds of vision rather than one. The idea of two kinds of vision was later elaborated by Ramon y Cajal's finding (*9*) that there were different kinds of bipolar cells associated with the rods and cones—in other words, that there were at least two visual pathways as well as two classes of receptors. It is now well established that there are two major classes of vision, scotopic and photopic. While most mammals have retinas containing both rods and cones and possess both photopic and scotopic vision, some have retinas containing only rods (many species of bats, hedgehogs, some primates, many rodents), while others have retinas containing only cones (many species of squirrels) (*10*).

This method of correlating structure with broad behavioral characteristics may be adopted in looking for particular behavioral characteristics of the several auditory pathways. One may examine the relation between the presence or absence (or changes in relative sizes) of any of these pathways and some aspect of the animal's normal behavioral environment (*11*). To this end we have examined the nuclei of the superior olivary complex in a number of mammalian species and have correlated variations in the relative sizes of the nuclei in different mammals with the behavior of the animal. The results of these observations are presented here.

Superior Olivary Complex

The nuclei of the superior olivary complex receive nerve fibers from the cochlear nucleus, and the fibers which arise in the complex pass to higher levels in the auditory system. The nuclei of the superior olivary complex with which we are concerned may be seen in Fig. 1, a cross section of the medulla of the chinchilla. The material was prepared as follows. Each animal was anesthetized with nembutal and perfused through the aorta with normal saline followed by chilled fixing fluid containing alcohol, formalin, and acetic acid. After a further period of fixation the brain was dissected out of the skull and cut into serial sections 16 microns thick. Every other section was mounted and impregnated by the protargol silver method of Bodian (*12*).

The comparative study of groups of nerve cells (nuclei) of the nervous system imposes certain restrictions upon the way these nuclei can be defined, and in the interests of clarity it is necessary to make these restrictions explicit. The nuclei shown in Fig. 1 have names—lateral superior olivary nucleus and medial superior olivary

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nucleus—which reflect the relative position of the two nuclei. However, their relative position cannot be used as a criterion in a comparison of these two nuclei from species to species because in some other species their spatial arrangement might be quite different (dorsal and ventral, for example), although the nuclei, recognized by other criteria, might be the same. This problem becomes particularly acute if one of the nuclei is absent; is the remaining nucleus to be called the "medial" or the "lateral" superior olivary nucleus? A classification based upon purely internal morphological criteria completely avoids this confusion. The criteria used in the study discussed here were, briefly, as follows. The medial superior olivary nucleus (Fig. 1) consists of an irregular column of cells each of which has a medially and a laterally directed dendrite. The medial and lateral dendrites, but not the cell bodies, are embedded in a fine neuropil. Synaptic endings consist of boutons densely distributed on the dendrites. The lateral superior olivary nucleus (Fig. 1) consists of a region of fine neuropil in which are embedded fusiform cells. Small synaptic endings (boutons) may be seen on the base of the dendrites of the cells. The neuropil also contains a coarse component.

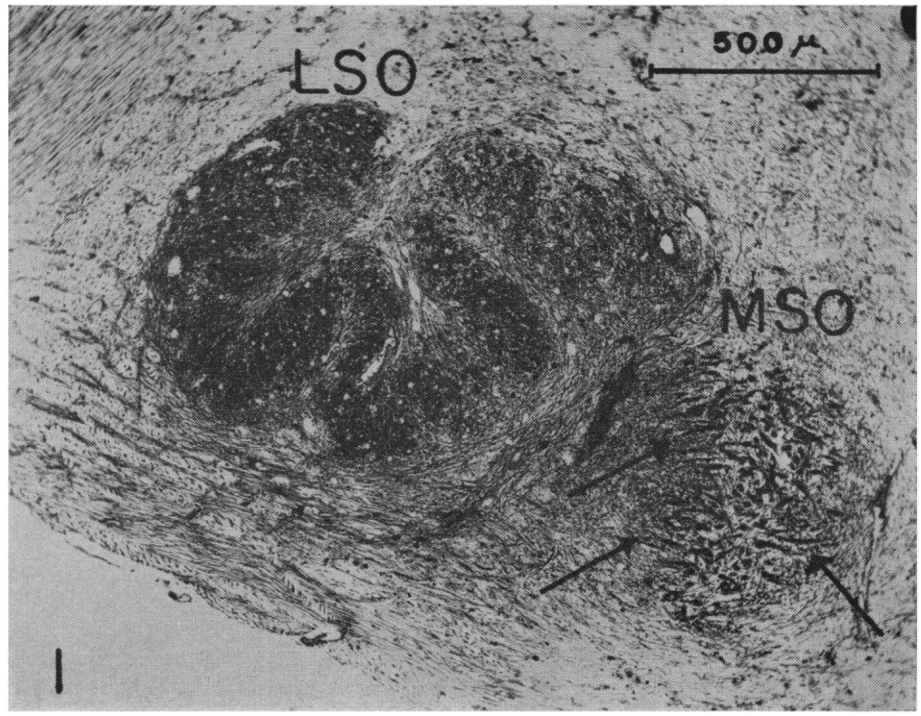


Fig. 1. Transverse section through the medulla of the chinchilla, showing the superior olivary complex. The medial superior olive (*MSO*) consists of a column of nerve cells; medially and laterally directed dendrites of the cells are indicated by the arrows. The lateral superior olive (*LSO*) consists of a region of neuropil in which fusiform nerve cells are embedded. (Protargol silver impregnation method of Bodian.)

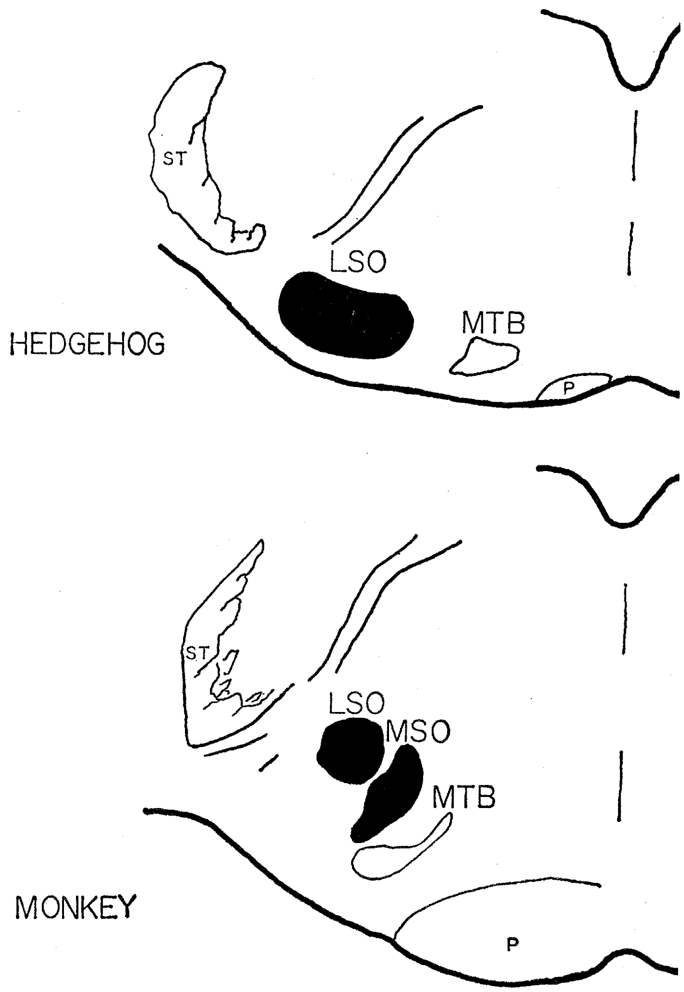
A comparison of the superior olivary complex in different mammalian species reveals that the nuclei of the complex vary greatly in relative size.

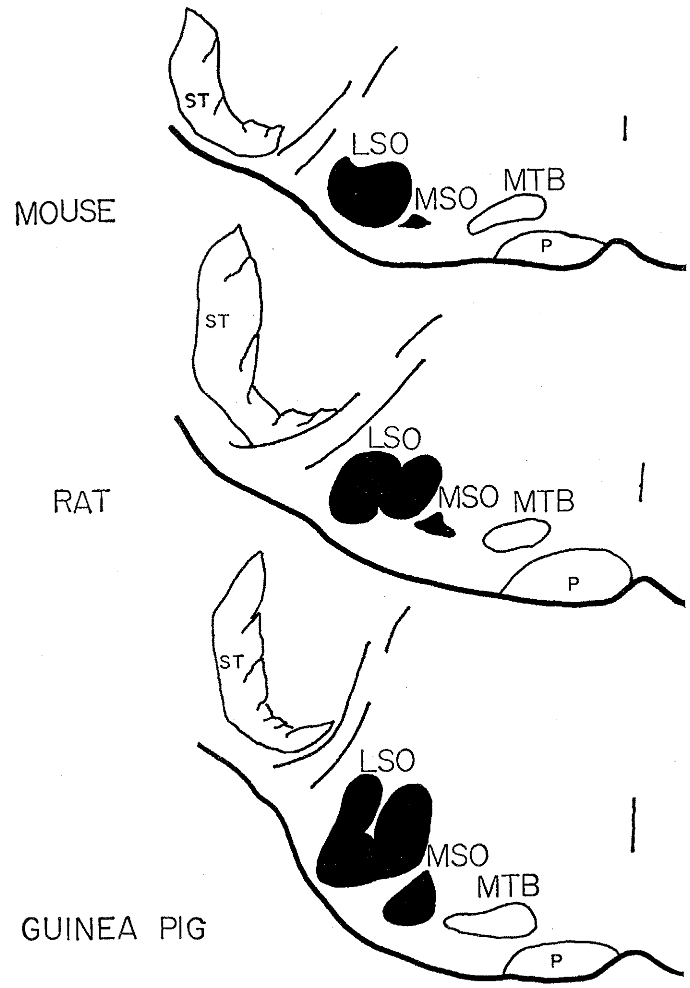
The superior olivary complex of two mammals of different taxonomic orders, hedgehog (*Erinaceus europaeus,* an insectivore) and monkey (*Macaca speciosus,* a primate), is shown schematically in Fig. 2. The medial superior olivary nucleus is absent in the hedgehog and is, relative to the rest of the superior olivary complex, prominent in the monkey. On the other hand, the lateral superior olivary nucleus is relatively well developed in the hedgehog and is relatively poorly developed in the monkey. The same variation of relative size of the medial and lateral superior olivary nuclei is also found within a taxonomic order. The superior olivary complex for three rodents, mouse (*Mus musculus*), albino rat (*Rattus norvegicus*), and guinea pig (*Cavia porcellus*), is shown schematically in Fig. 3. In the mouse the lateral superior olivary nucleus is prominent as compared to the medial superior olive, which is almost completely absent, while in the guinea pig both these structures are well developed. In the rat the relative sizes of the two nuclei are intermediate between their sizes in the mouse and in the guinea pig (*13*).

There are anatomical and physiological data which strongly implicate the medial superior olivary nucleus in auditory localization. The medial superior olivary nucleus receives nerve fibers from the cochlear nuclei of both sides (*5, 14*), and physiological work has shown that the spike discharges of the cells are determined by the time and intensity differences of pairs of clicks delivered one click to each ear (*15*). It is therefore surprising to find that this nucleus is absent or much reduced in size in some mammals. Because of the suggested role of the medial superior olivary nucleus in auditory localization it was decided to examine the superior olivary complex of animals known to have well-developed auditory behavior —the echolocating animals, bat (*16*) and dolphin (*17*). Three species of bat (*Corollia perspicillata, Myotis lucifuga,* and *Phyllostomus hastatus*) and one dolphin (*Tursiops truncatus*) were examined; the superior olivary complex of one species of bat and that of the dolphin are shown schematically in Fig. 4. None of these animals has a medial superior olivary nucleus. The lateral superior olivary nucleus, however, is prominent in all of them.

It is clear from the foregoing observations that the lateral superior olivary nucleus is most prominent in echolocators and in some nocturnal animals (in whose retinas rods predominate)—in particular, the guinea pig, chinchilla, and cat. The prominence of the lateral superior olivary nucleus in echolocators and in some nocturnal mammals suggests that it plays a critical role in the mediation of fine auditory discriminations. It is also to be noted that the lateral superior nucleus is present in all the mammalian species that we examined.

The medial superior olivary nucleus is exceedingly variable in size, and in the echolocators is conspicuously absent; it is therefore reasonable to conclude that the medial nucleus is not an essential nucleus for auditory localization in mammals. The medial nucleus is prominent in diurnal animals and also in nocturnal animals with large eyes (cat, chinchilla, guinea pig) and, presumably, good night vision. This finding suggests that the medial nucleus may be connected in some way with the visual system and that it may play some role in visual behavior. We decided to investigate this possibility by measuring the relationship between the size of the medial superior olivary nucleus and a nucleus in the visual system.





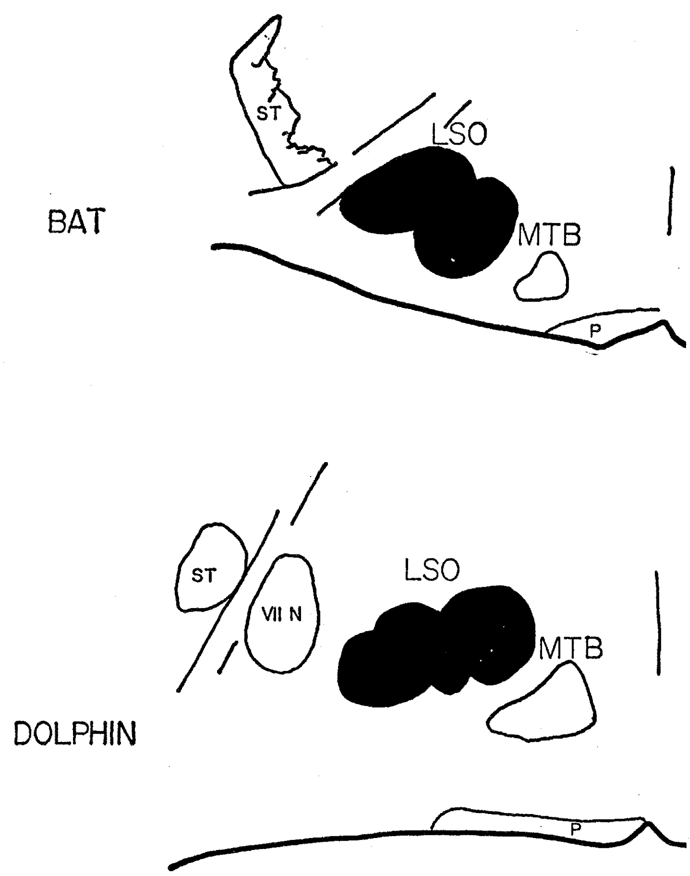


Fig. 2 (top left). Schematic transverse section through the medulla in hedgehog (*Erinaceus europaeus*) and monkey (*Macaca speciosus*), showing the lateral (*LSO*) and medial (*MSO*) superior olivary nuclei. (*MTB*) Medial nucleus of the trapezoid body; (*P*) pyramidal tract; (*ST*) spinal tract of trigeminal nerve.

Fig. 3 (top right). Schematic transverse section through the medulla in mouse (*Mus musculus*), rat (*Rattus norvegicus*), and guinea pig (*Cavia porcellus*), showing the lateral (*LSO*) and medial (*MSO*)Superior olivary nuclei. (*MTB*) Medial nucleus of the trapezoid body; (*P*) pyramidal tract; (*ST*) spinal tract of trigeminal nerve.

Fig. 4 (left). Schematic transverse section through the medulla of bat (*Phyllostomus hastatus*) and dolphin (*Tursiops truncatus*), showing the lateral (*LSO*) and medial (*MSO*) superior olivary nuclei. (*MTB*) Medial nucleus of the trapezoid body; (*P*) pyramidal tract; (*ST*) spinal tract of trigeminal nerve; (*VII N*) nucleus of 7th nerve.

Quantitative Considerations

In order to obtain a measure of this relationship, nerve cells were counted in the medial superior olive and also in one of the nuclei of the extrinsic ocular muscles (the 6th nucleus) in a number of species. The nerve cells of each nucleus were counted as follows. Each mounted section was scanned at an intermediate magnification (approximately 300), and all nerve cells in which the nucleus was present and its outline was complete were counted by means of an ocular grid. Since the nuclei of the nerve cells are smaller than the thickness of the sections, and since only every other serial section was counted, no cell was counted twice. The number obtained was multiplied by 2 to give the count for the nucleus. The majority of the nuclei were recounted after an interval of 2 or 3 months without reference to the original count; the variation between initial and second counts varied by no more than 10 percent. The results are given in Table 1 and in Figs. 5 and 6. In the diurnal primates (with cone-cell fovea) of Fig. 5, there is an approximately linear relationship between the number of cells in the medial superior olive and the number in the nucleus of the 6th nerve. In the group of nocturnal rodents (in whose retinas rods predominate), the relationship between the number of cells in these two nuclei is also approximately linear (Fig. 6). In the light of these two functions, the count for the squirrel is of particular interest. This animal has a cone-cell retina, and it is to be expected that the count will not fall on the curve for nocturnal rodents (Fig. 6). This it does not do. But it does fall on an extension of the curve for the diurnal primates of Fig. 5.

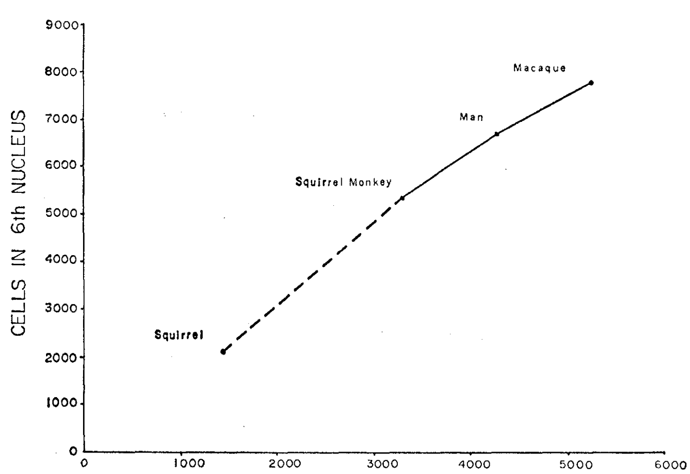
The data of Table 1 give some idea of the relationship between the size of the medial superior olivary nucleus and the 6th nucleus in other taxonomic orders. The curve for the rodents of Fig. 6, if extended, crosses the ordinate at approximately 110 cells for the 6th nucleus, at zero cells for the medial superior olive. This value for the 6th nucleus is a little higher than the observed number of cells in this nucleus in the bats (between 85 and 40 cells), animals in which no medial superior olivary nucleus has been found. This suggests that the function for bats, if any species are found with a medial superior olive, may be displaced downward from the function of Fig. 6, for rodents.

The dolphin is a particularly interesting case. As shown in Table 1, this animal has no medial superior olivary nucleus but has a relatively large number of cells (about 1150) in the 6th nucleus. At first sight this finding may appear to run counter to the idea that the medial superior olive is in some way related to vision. Consideration of the visual and auditory apparatus of the dolphin, however, shows that this is not the case. The external auditory canal is closed, the tympanic membrane is loose, and the ossicles are immobile. Sound from the water reaches the middle ear not by conduction through the external canal and ossicles but directly through the tissue of the animal's head. This arrangement is efficient in water but inefficient in air, and the animal is partially deaf (with auditory range diminished by probably 60 decibels or more) when its head is out of water (*18*). From behavioral observations of the dolphin (*Tursiops truncatus*), Scheville and Lawrence (*17*) concluded that it uses vision principally when its head is out of water. Vision and audition are not functional at the same time, and a medial superior olive is not needed for interaction between the two sensory systems.

The cat has a well-developed auditory system, including a large medial superior olive and a retina in which rods predominate (*7*). When plotted on the graphs, the point representing the cat falls on an extension of the line for animals with rod cells (Fig. 6) rather than on the line for animals with cone cells (Fig. 5). This suggests that the relationship between the size of the medial superior olive and the 6th nucleus may be nearly the same in carnivores as in rodents.

Conclusions

The major conclusion from these observations is that the medial superior olive is a part of the auditory system



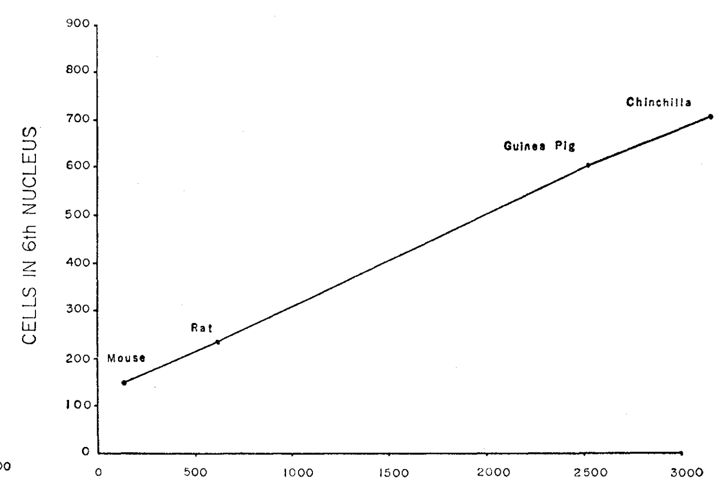


Fig 5 (left). Graph showing the relation between the number of cells in the medial superior olive (*MSO*) and in the 6th nucleus in squirrel monkey, man, and macaque. These three animals have cone-cell foveas. Note the almost linear relation between the sizes of the two nuclei. The squirrel is a rodent with a pure cone-cell retina. Note that the cell count for this animal fits approximately on an extension of the primate function. Fig. 6 (right). Graph showing the relation between the number of cells in the medial superior olive (*MSO*) and the 6th nucleus in mouse, rat, guinea pig, and chinchilla. Note the almost linear relation between the sizes of the two nuclei. The scale of this figure differs from that of Fig. 5.

Table 1. The number of nerve cells in the 6th nucleus and the medial superior olivary nucleus, and the type of retina in various mammals.

Animal	Number of cells, 6th nucleus		Number of cells, medial olivary nucleus		Retina type
	Left	Right	Left	Right	
Dolphin	1200	1100	0	0	Rod
Man	7260	6070	4240	4280	Cone fovea
Macaque monkey	7895	7660	5545	4960	Cone fovea
Cat	1180	950	5980	5810	Predominantly rod
Squirrel monkey	5526	5112	3167	3390	Cone fovea
Chinchilla	692	736	3136	3178	Rod (?)
Guinea pig	542	662	2628	2466	Rod
Rat	260	210	638	594	Rod
Squirrel	2086	2114	1386	1465	Cone
Hedgehog	308	386	0	0	Rod
Mouse	130	168	146	110	Rod
Bat					
Carollia	74	84	0	0	Rod
Phyllostomus	54	20	0	0	Rod
Myotis	36	44	0	0	Rod

which is in some way related to vision. The current idea that the medial superior olive is the essential nucleus for auditory localization is not upheld. The functional relationship between the medial superior olivary nucleus and the 6th nucleus differs for nocturnal and diurnal animals, suggesting the existence of nocturnal and diurnal auditory systems. A minor conclusion is that the lateral superior olive is an essential structure for audition and that it may be an essential structure for auditory localization.

One interpretation of these conclusions is that there are at least two auditory systems, one (which includes the medial superior olive) concerned with the pointing of the head and eye in the direction of a source of sound, and a second (which includes the lateral superior olive) concerned with the control of the rest of behavior by the direction and other aspects of sound. According to this interpretation, the medial superior olive will be well developed in all diurnal animals and in nocturnal animals with good vision (such as cats), while the lateral superior olive will be well developed in nocturnal animals.

Summary

Examination of the structural organization of the auditory system of the brain stem shows that the system is composed of a number of separate ascending pathways. This suggests that there may be at least two auditory systems, analogous to the rod and cone pathways in vision. We examined this possibility by investigating the variation in relative size of the medial and lateral superior olivary nuclei in a number of different mammalian species.

The lateral superior olive is present in the hedgehog (an insectivore), cat (a carnivore), and squirrel monkey (a primate), but the medial superior olive is absent in the hedgehog. In a group of animals of the same taxonomic order (rodents) the lateral superior olive was present in all species examined, but the medial superior olive was almost wholly absent in the mouse and very prominent in the chinchilla and guinea pig. The absence of the medial superior olive in some animals is surprising because recent anatomical and physiological work has implicated the nucleus in auditory localization. Because of this implication, the medial and lateral olivary nuclei were examined in three species of bat and one dolphin, all echolocating animals. The medial superior olive was absent in these animals, and the lateral superior olive was prominent.

These observations support the idea that the medial and lateral superior olives are nuclei on two different ascending auditory systems. It was also noted that the medial superior olive was always well developed in animals with well-developed eyes, and this suggested that the nucleus is in some way related to the visual system. We examined this idea by studying the relation between the numbers of cells in the medial superior olive and in the nucleus of the 6th cranial nerve (one of the motor nuclei concerned with eye movement) in a number of mammalian species. An approximately linear function was found between the sizes of the 6th nucleus and of the medial superior olive in three primates with cone-cell retinas (squirrel monkey, man, and macaque) and four rodents with rod-cell retinas (mouse, rat, guinea pig, and chinchilla). The cell numbers for the ground squirrel (a rodent with cone-cell retina) fitted an extension of the primate curve, and the cell numbers for the cat (in whose retina rods predominate) fitted an extension of the rodent curve. Thus, it is clear that the medial superior olive is related to the visual system, and that it is present in animals with cone-cell fovea and retina (diurnal animals) and animals with rod-cell retina (that is, nocturnal animals) having good vision. In nonvisual nocturnal animals the nucleus is small or absent. The medial superior olive is probably not concerned with auditory localization in the psychophysical sense but is probably concerned with the movement of head and eyes in the direction of a sound in space. Localization in the psychophysical sense and fine auditory discrimination probably depend upon the ascending pathway which includes the lateral superior olive.

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Science Broadcasting in Britain

In presenting science to a wide audience BBC television aims for more than just explanation of scientific findings.

Aubrey E. Singer

Every year, as part of its general programming aimed at broad audiences in peak hours, the British Broadcasting Corporation broadcasts a total of about 140 hours of science on radio and television.

Some 34 hours of this output are accounted for by the very-high-frequency television channel, BBC-1, with its eight 50-minute documentaries and weekly half-hour magazine-style program "Tomorrow's World." The documentaries have included a broad review of research on structure and function of viruses, vignettes of Francis Crick, Maurice Wilkins, John Kendrew, and Max Perutz when they received Nobel prizes in 1962, current problems in astronomy narrated by Fred Hoyle, exploratory interviews with four psychiatrists working in different areas of their field, a look at French plans and achievements in technology, and "Challenge," an annual review of the year's developments in science, technology, and medicine. "Tomorrow's World" is lighter, and may include an item on a new technical development in cars or a film on high-speed photography.

About 40 hours of science programs a year are transmitted over the ultra-high-frequency channel, BBC-2, mainly through the alternating fortnightly programs "Horizon" and "Life." Among the presentations of "Horizon" have been profiles of Joseph Needham, Albert Szent-Györgyi, and Richard Gregory.

BBC radio broadcasts about 60 hours of science a year. Its science broadcasting ranges over Home, Light, and Third programs, Network Three, and Schools, and includes such programs as "Science Survey," "Science Review," and "Who Knows?," special Third Program talks and series, and extensive educational programming.

BBC television's science programming for a general audience is primarily the responsibility of the Features and Science group. Over the last nine years we in this group have become, so to speak, prime contractors responsible for producing science television programs during peak hours. Ours is not, of course, the only effort the BBC makes to explain the substance of scientific and technological discoveries and to discuss their impact on everyday life, but it may serve as an example of the total effort.

In our effort to make our broadcasting coherent, we have over the years worked out some general ideas about science broadcasting. Broadcasting not only affects but is affected by the climate of opinion. Its ideas and attitudes arise from the community at large, and broadcasting journalism assimilates, manipulates, and amplifies these trends and then reflects the image back at its source. Hence the science broadcaster must gain his sense of direction by considering what the public knows and what it thinks about science. Broadcasting policy must be formulated in the light of the facts that the public hears much more than it used to about science and its impact, that the widening flood of scientific information makes it difficult for either scientist or layman to keep up, and that the dangers inherent in some of the most exciting fields of science make it difficult for laymen to trust scientists. Broadcasting must also do its part to ensure against the danger that education, faced with a flood of facts, will degenerate, as Jacques Ellul puts it in *The Technological Society*, from "an unpredictable and exciting adventure in human enlightenment" into merely "an exercise in conformity and an apprenticeship to whatsoever gadgetry is useful in a technical world."

Planning the Programs

Before looking at program policy in detail, however, it might be best to explore the origin of program ideas as well as the machinery we have for consultation with the scientists themselves.

The machinery most used by the producer when seeking ideas or advice on stories is informal. By and large he draws on his relationships with scientists who have appeared on our program in the past. (Of course, for reasons of temperament or misunderstanding things sometimes turn sour between a producer and his scientist-performer, but usually the producer and scientist end by maintaining a lasting informal association.) These associations, and our reputation built up over the years, serve as a point of entry into the world of science.

In contrast to this informal machinery, the formal point of contact is the

The author is head of the Feature and Science department of the British Broadcasting Corporation's television service in London. This article is adapted from a lecture delivered 16 February 1966 at Broadcasting House, London.