genic bacteria (Fig. 3, lane 7a) exhibited a strong cross-reaction with the heaviest component (A) of the VC-16 RNA polymerase (Fig. 3, lane 7b). This cross-reaction demonstrates that the largest component of the RNA polymerase of the sulfate reducer contained structural elements of components A and C of the methanogen enzyme. The new sulfate reducer thus exhibits a previously unknown third type of RNA polymerase (A + C)B′B″ within the archaebacteria, which is phylogenetically removed from those of the two accepted archaebacterial branches. This finding provides evidence for the existence of a third phylogenetic branch within the archaebacterial kingdom.

On the basis of their phylogenetic uniqueness, archaebacterial sulfate reducers may have existed since ancient times. Early Archaean ocean waters were generally poor in sulfate and were thus unfavorable for the presence of sulfate reducers that were thought to have originated later (*24*). This theory is in line with the lack of significant biogenic sulfur isotope fractionation within such sediments (*24*). However, there should have been reasonable quantities of sulfate of magmatic origin present locally within Archaean hydrothermal systems (*25*). Therefore, sulfate reduction by extremely thermophilic archaebacteria could have existed since early Archaean times and may be an ancient type of metabolism.

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Auditory Pathways to the Frontal Cortex of the Mustache Bat, *Pteronotus parnellii*

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In primates, certain areas of the frontal cortex play a role in guiding movements toward visual or auditory objects in space. The projections from auditory centers to the frontal cortex of the bat *Pteronotus parnellii* were examined because echolocating bats utilize auditory cues to guide their movements in space. An area in the frontal cortex receives a direct projection from a division of the auditory thalamus, the suprageniculate nucleus, which in turn receives input from the anterolateral peri-olivary nucleus, an auditory center in the medulla. This pathway to the frontal cortex bypasses the main auditory centers in the midbrain and cortex and could involve as few as four neurons between the cochlea and the frontal cortex. The auditory cortex is also a major source of input to the frontal cortex. This area of the frontal cortex may link the auditory and motor systems by its projections to the superior colliculus.

THE ROLES OF DIFFERENT AREAS OF the mammalian cerebral cortex are established largely by differences in input from the thalamus, interplay between cortical areas, and output to motor centers. Some areas in the frontal cortex receive little or no input from the main sensory relays in the thalamus but are connected with sensory fields of the cortex [including the auditory cortex (*1*)] and provide descending input to motor centers via projections to the deep superior colliculus and basal ganglia (*2*). For example, in primates the frontal eye fields play a role in initiating eye movements toward visual stimuli (*3*), and other frontal areas may play a role in directed movement toward auditory stimuli (*4*). Echolocating bats, because of their unequaled dependence on auditory cues, provide an opportunity to examine cortical connections in animals whose sensory adaptations are radically different from those of species specialized for visual orientation. The echolocation pulses of bats are accompanied by movements of the pinnae, head, and body (*5*) so that successive pulses scan the surrounding space in a manner not unlike that in which a primate scans its environment visually.

We have examined connections between auditory and motor systems in the mustache bat, *Pteronotus parnellii*. We used a combination of electrophysiological and anatomical methods to trace pathways by anterograde or retrograde transport of wheat germ agglutinin conjugated to horseradish peroxidase (WGA-HRP) (*6*). These experiments revealed an auditory pathway that may play an important role in scanning the environment and that, if it exists in other mammals, may provide an anatomical basis for interpreting certain earlier physiological observations.

We first defined the extent of the auditory cortex by its thalamic connections. The cortical target of the ventral division of the medial geniculate body was determined by anterograde and retrograde transport of WGA-HRP (Fig. 1A). The resulting map was consistent with published electrophysiological maps of the auditory cortex (*7*).

We then determined the distant cortical targets of the auditory cortex. The most intriguing finding was a projection to the rostral part of the neocortex, which we refer to here as the frontal cortex (Fig. 1A). Electrophysiological recordings, which were

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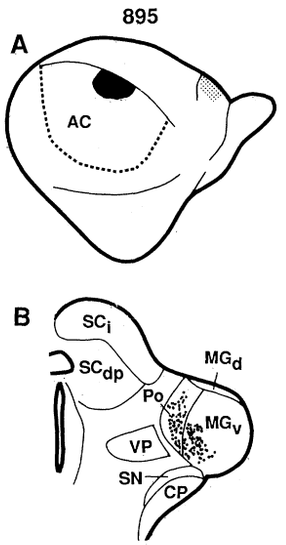
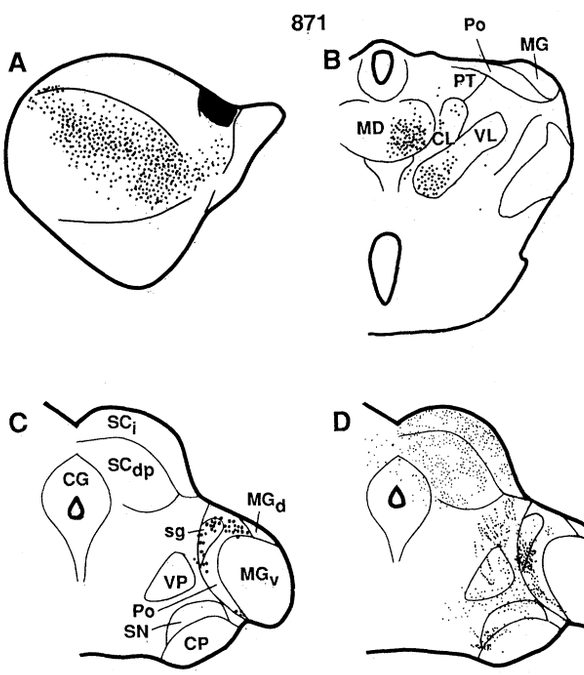


Fig. 1. (**A**) Reconstructed view of the lateral surface of the cortex of *Pteronotus parnellii*, case 895. The blackened area represents the extent of diffusion of WGA-HRP when tetramethyl benzidine is used as the chromagen and the preparation is viewed with dark-field microscopy. This case was chosen as an example of anterograde transport (stippled area) to the frontal cortex after an injection at the dorsal border of the auditory cortex (AC). The extent of the auditory cortex, as determined by analysis of projections from the medial geniculate body in 24 other cases to show retrograde transport from the cortex and 4 cases to show anterograde transport from the medial geniculate body, is the area enclosed by the dorsal fissure (solid line above the injection site) and the dotted line. (**B**) Transverse section showing the location of labeled cells in the medial geniculate (MG) body and posterior thalamic nuclei (Po). Abbreviations: SC, superior colliculus; i, intermediate; dp, deep; d, dorsal; v, ventral; VP, ventral posterior thalamic nucleus; SN, substantia nigra; and CP, cerebral peduncle.

intended primarily to localize injections within acoustically responsive areas, showed robust responses to sound from single units in this region. Injection of WGA-HRP in the auditory region of the frontal cortex revealed many labeled cells (Fig. 2A). We also traced descending projections from the frontal cortex to intermediate and deep layers of the superior colliculus (Fig. 2D). These descending projections are significant as a possible link between the frontal cortex and brainstem motor pathways.

The next step was to identify the sources of ascending pathways to the frontal cortex by retrograde transport of WGA-HRP. The pattern of labeled cells in the thalamic nuclei was similar to that seen after injections in the prefrontal cortex in other mammals (*8*). These thalamic nuclei include mediodorsal and ventrolateral nuclei (Fig. 2B). An unexpected result was that cells in the auditory thalamus were also labeled (Fig. 2C). These cells were located in the suprageniculate nucleus, a cell group easily distinguished from other parts of the auditory thalamus by its location and by its large, darkly staining cells. This pathway from the suprageniculate nucleus to the frontal cortex was confirmed by injection of WGA-HRP into the suprageniculate (Fig. 3A) (*9*). The results showed anterograde transport to the same region of the frontal cortex that is innervated by the auditory cortex (Fig. 3B). Transport to all of the auditory cortical field was also present.

Finally, we examined the auditory input to the suprageniculate nucleus. Figure 3C shows one of two cases in which retrograde transport from the suprageniculate nucleus labeled numerous cells in the anterolateral peri-olivary nucleus (ALPO) (*10*) in addition to the expected finding of labeled cells in the inferior colliculus. We did not find labeled cells in the ALPO in three cases in which injections did not infringe on the suprageniculate nucleus, but were centered in the ventral or dorsal divisions of the medial geniculate body. We then injected WGA-HRP into the ALPO. The result was



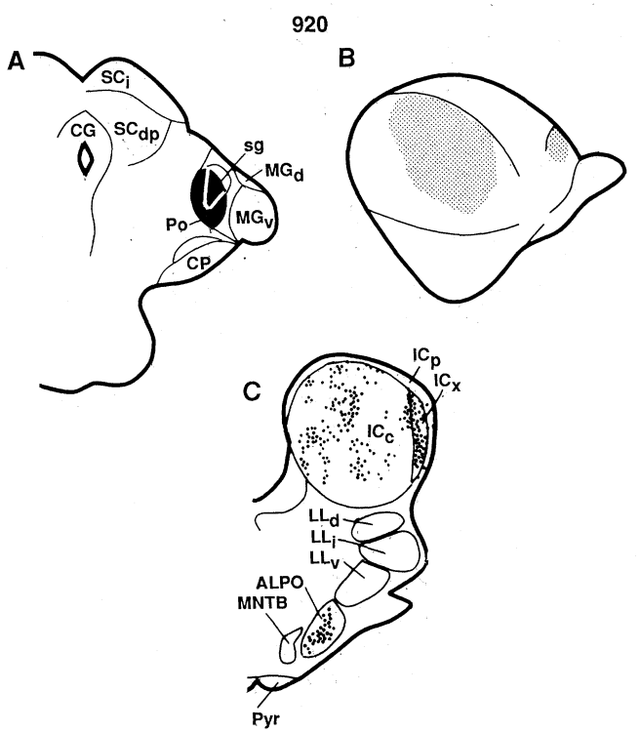


Fig. 2 (**left**). Connections of frontal cortex in case 871. (**A**) Labeled cells in the auditory cortex (lateral view) after an injection in an area of the frontal cortex in which cells respond to sound. (**B**) Labeled cells in mediodorsal (MD) and ventrolateral (VL) thalamic nuclei. (**C**) Labeled cells in the posterior group and suprageniculate (sg) nucleus. (**D**) Anterograde transport to intermediate and deep layers of the superior colliculus. Abbreviations: PT, pretectum; CL, centrolateral thalamic nucleus; and CG, central gray. **Fig. 3** (**right**). Afferent and efferent projections of the suprageniculate nucleus in case 920. (**A**) Injection of WGA-HRP in and around the suprageniculate. (**B**) Anterograde transport to the auditory and the frontal cortex. (**C**) Location of cells labeled by retrograde transport in the inferior colliculus (IC) and the ALPO. Anterograde transport to the frontal cortex and retrograde transport to the ALPO are seen only after injections placed medially and include the suprageniculate nucleus. Retrograde transport is seen in the inferior colliculus after any injection into the auditory thalamus. Abbreviations: LL, nuclei of the lateral lemniscus; MNTB, medial nucleus of the trapezoid body; Pyr, pyramidal tract; p, pericentral; x, external; and c, central.

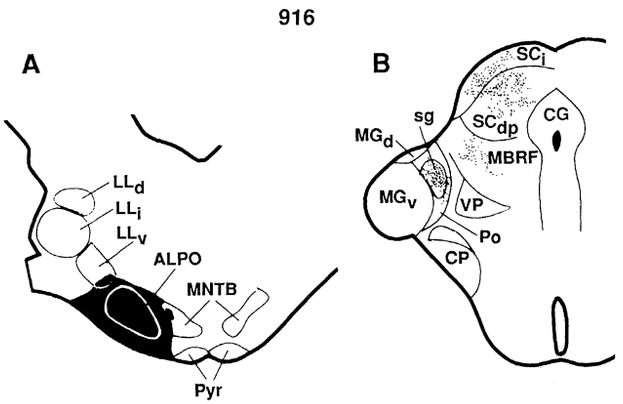


Fig. 4. Projections from the ALPO in case 916. (**A**) Injection site. (**B**) Anterograde transport to the suprageniculate nucleus and superior colliculus. Abbreviation: MBRF, midbrain reticular formation.

dense anterograde transport to the suprageniculate nucleus (Fig. 4A), which confirmed that this nucleus is the thalamic target of the ALPO. This result established a source of auditory input to the suprageniculate nucleus from the medulla, because it had already been shown that the ALPO receives auditory input in *Pteronotus* (*11*).

There are physiological clues that these auditory pathways exist in other mammals. (i) Auditory evoked responses in the frontal cortex persist after ablations of auditory cortex (*12*). This result can be attributed to the pathway from the suprageniculate nucleus. (ii) Auditory evoked responses persist at the auditory cortex after transection of the brachium of the inferior colliculus (*13*). This result can be explained by the pathway from the ALPO: WGA-HRP injections into the ALPO revealed that the labeled fibers to the suprageniculate nucleus traveled ventral to the inferior colliculus and medial and ventral to the brachium of the inferior colliculus. Projections that bypass the inferior colliculus to reach the medial geniculate body were first described by Cajal as constituents of the "central acoustic tract" (*14*). Papez later suggested that the main target of this pathway was the suprageniculate nucleus (*15*). The concept of a "central acoustic tract" became controversial (*16*) until Morest described a set of four subcollicular pathways to the medial geniculate body (*17*), one of which terminates in the suprageniculate nucleus. With the methods available at that time it was not possible to find the cells of origin of this pathway.

Our results identify the ALPO as the major source of auditory pathways that bypass the inferior colliculus to reach the thalamus in the bat; the pathway from suprageniculate nucleus to frontal cortex seems to be the cortical extension of the central acoustic tract (*18*). Through these pathways, auditory information can reach the deep superior colliculus via cortical and subcortical routes that bypass the main auditory centers of the midbrain and cortex (*19*).

The results suggest a role for the frontal cortex in behavior guided by auditory information. The frontal cortex has direct projections to the deep layers of the superior colliculus (Fig. 2D) (*2*), an important source of motor commands for head and pinna movements involved in spatial orientation (*20*). In mammals that rely greatly on vision, such as primates, the deep superior colliculus receives input from the frontal eye fields (*2*). Our finding that the frontal cortex in the bat has a large input from auditory centers and projects to the intermediate and deep layers of the superior colliculus suggests that the frontal cortex may play a role in acoustic orientation in the bat; this role may be analogous to that played by the frontal eye fields in animals that use mainly visual cues for orientation.

We can only speculate on the specific roles the frontal auditory field plays in the behavior of the mustache bat. However, it is not difficult to see parallels between some of the cognitive functions of the frontal cortex (*21*) and the behavior of echolocating bats. Acoustic orientation by bats depends on the use of auditory information to guide many goal-directed behaviors, such as prey identification and interception, obstacle avoidance, and memorization of spatial arrangements such as cave systems (*4*). Our results raise the question of whether the frontal cortex in bats plays a role in these behaviors.

The results are also significant for our view of evolution of brain and behavior. Echolocating bats are phylogenetically old (*22*) and their neocortex is primitive (*23*). It will be important to determine whether functional parallels exist between the frontal cortex of bats and that of primates.

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