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PHYSIOLOGICAL BASIS FOR DETECTION OF SOUND AND VIBRATION IN SNAKES

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INTRODUCTION

The study of sensory systems in animals with anatomical and physiological specializations different from those of higher mammals can contribute much to our understanding of general principles underlying sensation. Sensory systems in snakes have recently attracted some attention. Infrared reception has been studied peripherally (Bullock & Cowles, 1952; Bullock & Diecke, 1956; Bullock & Barrett, 1968) and centrally (Barrett, 1969). A peripheral tactile vibratory response has been reported (Proske, 1969). The auditory system has been largely overlooked. Improved understanding of sensory systems in snakes will certainly improve our understanding of the biology of snakes, and in addition, may shed light on fundamental processes underlying sensation in other animals.

The lack of interest in the auditory system of the snake may be in part because what behavioural evidence can be found indicates that snakes do not hear but may perceive vibrations from the substrate (Manning, 1923; Crawford & Holmes, 1966). The anatomical arrangement of the middle ear has been interpreted as a specialization for reception of vibratory signals from the substrate (Tumarkin, 1949; Bellairs & Underwood, 1951). The columella has an elastic articulation with the quadrate; the quadrate articulates with the mandible which is in contact with the ground. Thus the columella is in direct communication with the substrate.

The history of the physiology of snake audition began with an unsuccessful attempt by Adrian (1938) to record responses from an excised VIII nerve preparation in one snake. Wever & Vernon (1960) demonstrated a peripheral auditory response, cochlear microphonics, for sound stimulation and for bone vibration. They suggested that the quadrate bone takes the place of the tympanic membrane as receiver of sound energy. In preliminary accounts, Hartline & Campbell (1968, 1969) reported midbrain responses to sound and vibration. They attributed the responses to the inner ear on the basis of changes in the responses caused by destruction of the spinal cord or the inner ear.

In this paper the responses of midbrain centres to sound and vibration are more fully explored. The VIII nerve, and in addition, the spinal cord, mediate responses to these stimuli. The vibration-sensitive mechanoreceptors in ventral skin (reported by Proske, 1969) presumably contribute to the responses mediated by the spinal cord. I shall attempt to elucidate the origin of the VIII nerve responses and to explain their persistence if stimuli are localized at a portion of the body surface remote from the head. I will compare responses of the VIII nerve and spinal systems, which by virtue of their properties gather information about overlapping sets of stimuli, but neither of which seems to signal whether the stimulus arrived through air or through substrate.

METHODS

Experiments were carried out on species of the families Boidae, Colubridae, and Crotalidae. Crotalids yielded the easiest dissections and were used for the experiments cited unless otherwise specified. The main results have been verified for species of all three families. Room temperature was 26–29 °C, within the snakes' normal activity range (Brattstrom, 1965). But temperature of the snakes was not monitored. Anaesthetic was administered intraperitoneally at a dosage of 15–30 mg sodium pentobarbital per kg of body weight or 10–20 mg sodium thiopental per kg body weight. Snakes recovered in 5–6 h from pentobarbital or in 1–2 h from thiopental. When anaesthesia was deep, artificial respiration was used; air was injected into the airsac at about the middle of the body and was allowed to escape continuously through the intubated trachea.

The dissection exposed one or both tectal lobes. Electrodes were metal-filled glass micropipettes of 5–20 μ tip diameter, or flame-sharpened tungsten needles, insulated to within about 10 μ of their tips. These electrodes were plated with gold and platinum (Dowben & Rose, 1953). Recordings were made below the tectal surface at positions and depths corresponding to the torus semicircularis, homologue of the mammalian inferior colliculus (Huber & Crosby, 1926). Conventional methods of amplification and oscilloscope display were used. High-frequency and low-frequency cut-offs were generally 2 kHz and 2 Hz respectively.

A block diagram of the experimental arrangement is provided in Fig. 1, to which the reader is referred for details. A 'tone-burst modulator' (see legend of Fig. 1) generated sinusoidal stimuli whose envelopes had a linear rise, constant amplitude plateau, and linear fall, each of controllable duration. The tone burst was fed through an attenuator, a power amplifier, and a matching transformer to the final transducer. For sound, either an 8 in. loudspeaker or a 4 in. loudspeaker with an orifice restricted for local sound delivery was used. In the former case, that of 'general-field' sound, resonances in the sound-proofed experimental chamber and loudspeaker defects produced a sound field around the snake with peaks and nulls of ± 5 dB relative to the intensity at the monitor microphone. In the case of local sound, intensity was measured at the surface of the snake's skin adjacent to the sound orifice, which was itself 1 cm from the snake's body. A microphone probe consisting of a no. 15 gauge hypodermic needle coupled to a calibrated microphone was employed.

A piezoelectric ceramic cylinder provided vibrations to drive either a hypodermic needle 'vibrating probe' or a small 'vibrating platform' on which a portion of the snake could lie (Fig. 2). The displacement was calculated from manufacturer's specifications and measured with an optical system dependent on reflexion of light from the vibrating surface. The system is a variant of the commercially available 'Fotonic Sensor' of Mechanical Technology, Inc. (Latham, N.Y.), and will be described by other authors.

This vibration-calibrating system is capable of 10 Å resolution without employing phase-sensitive techniques of signal detection. Calibration curves for peak-to-peak

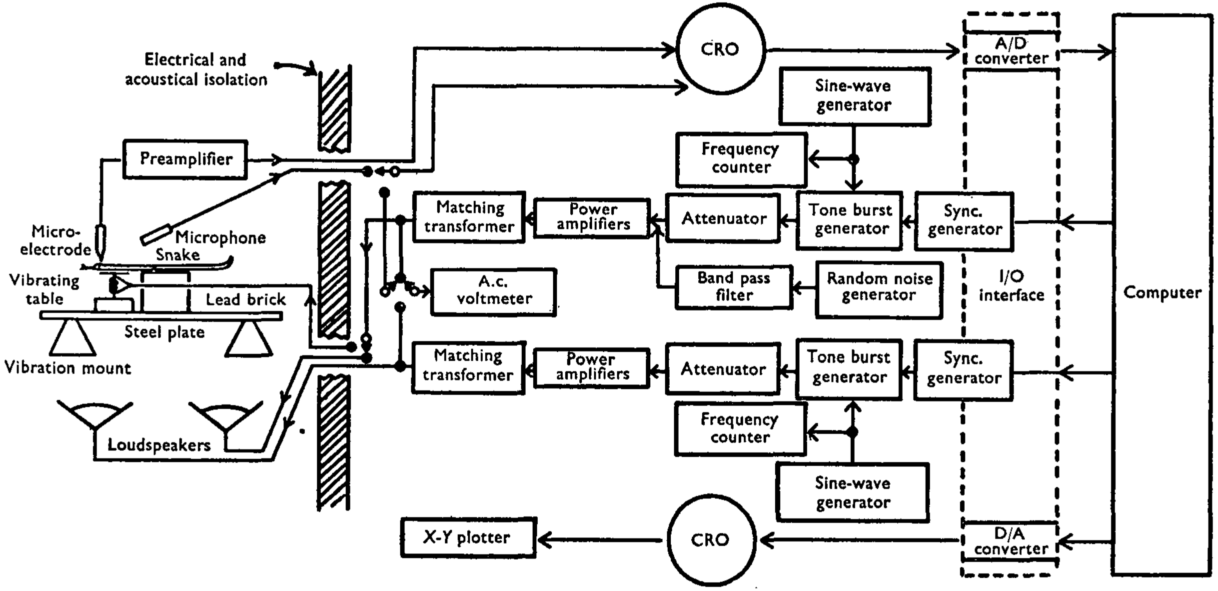


Fig. 1. Block diagram of apparatus: Lead brick augments the mass of the experimental table at the point where the snake lies, and lowers the resonant frequency of the suspension. Vibration mounts are 'Barry Mount' and impart *c.* 5 Hz resonant frequency to the table. The tone-burst modulator was either (1) a special unit designed and built by Mr R. H. Hamstra, Jr., with amplitude on–off ratio better than 90 dB and with no measurable click transients, or (2) a Grason Stadtler electronic switch.

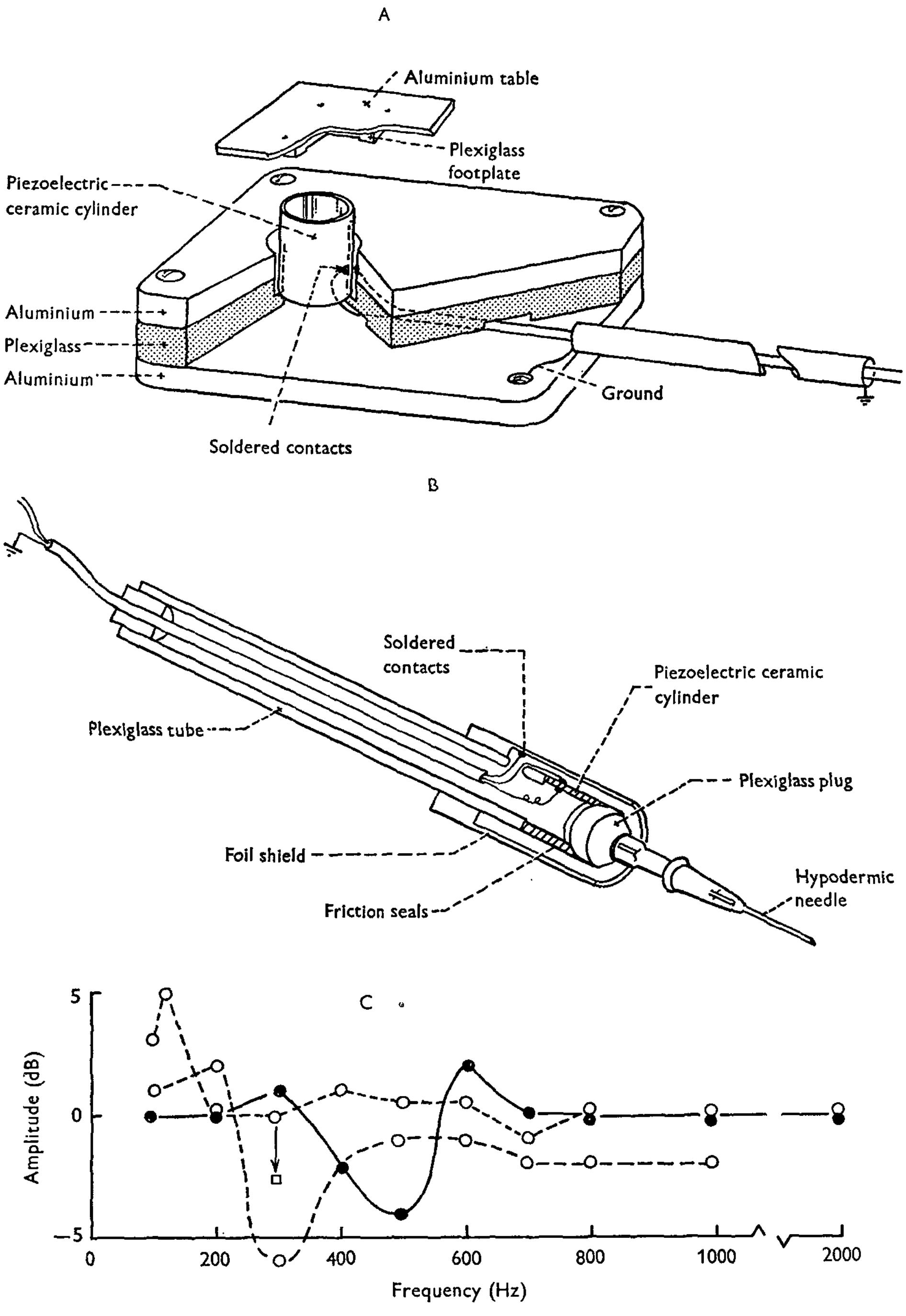


Fig. 2. Vibrating table, vibrating probe, and frequency responses: Vibrating table (A) and vibrating probe (B) both use the same piezoelectric ceramic element: part no. 8-8031-5 cylinder from Clevite Corp. (Bedford, Ohio). The manufacturer's specifications give the relation between applied voltage and increase of cylinder length, $d_{31} = 1{\cdot}7 \times 10^{-12}$ m/V. Cylinder thickness = 0·031 in.; length = 0·5 in. Calculated vibration amplitude per applied volt is 37 Å/V peak to peak (p-p). (C) shows calibration curves for a vibrating platform: 0 dB = *c.* 40 Å/V, p-p. Unloaded platform, ●; same platform loaded with 50 g, ○ (two separate runs on different days); single □ shows effect of loading with 200 g in one run.

(p-p) displacement versus frequency are provided in Fig. 2C. The shapes of the curves are similar for two vibrating probes and two vibrating platforms (flat within 5 dB to 2000 Hz). Absolute amplitude calibration (vibrator displacement per applied volt) was about 40 Å/V. Variation in this measured figure was as much as 30% (*c.* 3 dB) for different vibrating elements. Measurements were repeatable on different days and at different temperatures to within 20% (2 dB) for a given element. The mechanical impedance of these vibrators was more than sufficient for these experiments, in which loading of the platform with more than 50 g was very rare. The effect of loading on the frequency response of one unit is shown in Fig. 2C. One platform was loaded with 150 g; the measurement at 200 Hz showed an attenuation of only 2 dB. I feel justified in reporting absolute amplitudes based on calibrations made infrequently and believe them to be accurate to within 5 dB and consistent to within 2 dB at different frequencies.

The presence of spontaneous slow-wave activity and the lack of uniformity of responses to identical stimuli necessitated averaging in most cases. The signal was fed to an A/D converter which digitized at a rate of 1 or 2 kHz (1 or 0·5 msec per point); the clock controlling the A/D converter was accurate to 5%. The input was filtered (low pass) at 2 kHz. Controls and internal consistency of the results indicate that this filtering, which does not meet the ideal sampling theorem conditions, is adequate. Seven bits of the conversion were kept, which was more than a sufficient number to assure faithful convergence of the average; the sum was no more than twelve bits. Experiments were controlled and data were collected by a digital computer (Digital Equipment Corporation PDP-8: software description available on request).

Two features of the computer system are noteworthy: (1) to prevent spurious signals from showing up in the averaged response, the computer delivered stimulus-synchronization pulses at intervals whose mean is given as the repetition period (RP in figure legends) and which had a random jitter of $\frac{1}{4}$ the mean interval; (2) if responses to two different stimuli (*a* and *b*) were to be compared, these stimuli were presented in alternating sequence and the response averages (A and B) were calculated for each concurrently. This method eliminates possible effects of drift, and is superior to comparison of two responses averaged sequentially. In addition, two separate averages were usually calculated for each type of stimulus. Thus the data area of the computer was divided into four parts for a given averaging sequence. The response to every other repetition of stimulus *a* was pooled to give an average A_1; the responses to alternate *a* stimuli were pooled to give an independent average A_2. Concurrently and in a similar fashion, B_1 and B_2 were formed.

RESULTS

General character of responses

Examples of midbrain responses to stimulation with a sound click are shown in Fig. 3. The variability in response shape illustrated here or, more commonly, variability in latency, was encountered in many midbrain recordings. Averaging in this case does not produce the ideal noise-free response, but rather a mean response which may be unlike any single response (Brazier, 1964). This does not constitute an objection in the interpretation of the data presented below. A typical click-evoked response for either system for focal recording (judged by amplitude of slow waves and presence of spike responses) had an initial negative peak with 35–50 msec latency (auditory system) or 25–35 msec latency (spinal system) and 10–30 msec duration. This was followed by a slow positive wave lasting as long as 100 msec. Responses could be preceded by a sharp positive peak, the positive slow wave could be reduced or absent, and late negative waves were sometimes observed. Occasionally, as the electrode was advanced, a gradual reversal of polarities was observed, affecting one or several components of the response. This phenomenon is common in mammalian records (Amassian *et al.* 1964). In general, latency and width decreased and amplitude increased with increasing stimulus intensity. Units have been recorded and usually appear no earlier than the initial negative peak. With decreasing intensities of stimulation the spikes are progressively delayed with respect to the peak and become more variable in latency. In deeply anaesthetized or anoxic snakes the spike responses are absent but the evoked slow potentials persist. According to the interpretation of other investigators in other animals, this suggests that the major part of the response is due to input to the recording area and does not depend on local spiking (Amassian *et al.* 1964).

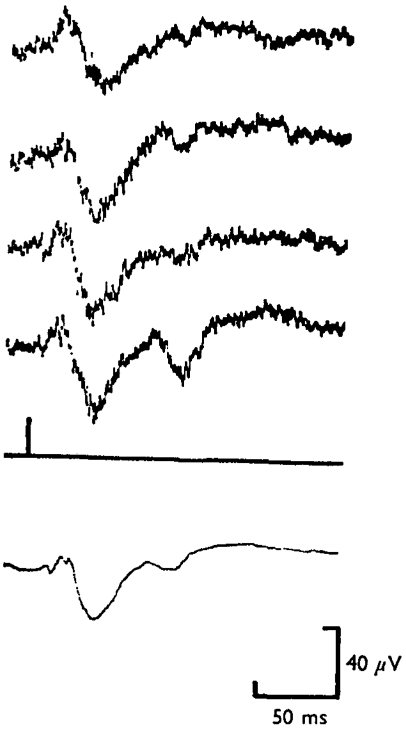


Fig. 3. Representative responses and average. Vibration (click) stimulus indicated by mark in fifth line. The responses of the auditory system are shown in four instances of ten which were added to obtain the resultant average (last line). Note the variability of latency and shape of the individual responses. The vertical calibration applies to all response traces including average. Negative is downward in this and all succeeding figures. *Crotalus cerastes.*

The shape of the averaged response is affected by the repetition period and by the rise time of the tone stimulus. In a series of averages, in which only the repetition period was varied, it was found that full recovery from one stimulus, (as judged by comparing response amplitude at a given repetition period with its amplitude at 10 sec repetition period), depended on the intensity of the stimulus but usually required more than 2 sec. Using such an interval, or a longer one which would allow full recovery, would necessitate allowing a long time to compute any average or set of averages. Long averaging times were undesirable because of response drift and experimental design. Consequently, a repetition period of 1–1·5 sec was chosen as a compromise between drift and incomplete recovery. The effect of decreasing rise time of a tone burst was primarily to decrease the latency. Another effect was to sharpen the initial negative peak slightly. These effects are treated more fully in the following publication (Hartline, 1971).

Responses were also affected by anaesthesia. Animals with previously implanted electrodes were anaesthetized and allowed to recover while responses were monitored. Deep anaesthesia resulted in lower response amplitudes and in elimination of some detail in the response shape. These effects, probably due to anoxia, could be partially reversed by artificial respiration. For most results, the effect of anaesthesia was not important.

Distinction between VIII nerve and spinal systems

In order to facilitate presentation, the data are organized around the main conclusions reached, which are as follows. Information about both sound and vibration is carried by each of two separate sensory systems. One is termed the 'VIII nerve system' or 'auditory system' because the inner ear and eighth cranial nerve subserve its responses. The designation does not imply that recordings were made directly from the VIII nerve. The second is termed the 'spinal system' or 'somatic system'. Midbrain response of this system requires an intact spinal cord, and evidently originates in skin receptors, perhaps those reported by Proske (1969). The differences between responses of the VIII nerve system and of the spinal system, apart from their sensory origins are: (1) anatomical distribution in the midbrain; (2) frequency response, the spinal system being sensitive to a wider range than the VIII nerve system; (3) sensitivity, the VIII nerve system being 20 dB more sensitive to airborne sound than the spinal system.

The responses of the VIII nerve system persist on destruction of the spinal cord and are abolished by destruction of the inner ears. Adequate natural stimuli, effective if delivered to head or body, are either air-borne sound or vibration of the substrate. The auditory frequency-sensitivity curves are peaked between 200 and 400 Hz, both for sound and vibration, and have approximately the same shape for both. Sensitivity has been demonstrated at the best frequency (frequency of lowest threshold) to sounds of 35 dB SPL (SPL: relative to 0·0002 dyne/cm^2 r.m.s.) and to vibrations of 1–2 Å p-p.

The responses of the somatic system persist on destruction of the inner ears but are abolished by subsequent spinal section or by cooling of the cord. Adequate stimuli are sound fields along the body, vibrations under the body, touch, and other mechanical stimuli. Vibration under the head does not evoke responses from this system except at very high amplitudes. The somatic frequency-sensitivity curves cover an octave or more on either side of the auditory curves and lack the sharp peak at the best frequency which is characteristic of the auditory system. These findings will be expanded and documented below.

It is desirable to be able to distinguish between responses mediated by the two systems. This can be done by severing the spinal cord to permit study of the VIII nerve system and by destroying the ears to permit study of the somatic system. The irreversible nature of these procedures makes them inappropriate for some experiments. Since it was found that the area of the midbrain responding to somatic stimulation was larger than, and included, that giving responses via the VIII nerve (see below), it was possible to examine spinal-system responses free from contamination by auditory activity. But for the same reason it was not possible, by judicious choice of the recording site, to isolate the VIII nerve system from contamination by the spinal system; other criteria for its isolation had to be developed.

The VIII nerve system was isolated by using a preparation in which the columellae on both sides of the snake were vibrated directly. Two vibrating probes were used (Fig. 2B); the hypodermic needle of each was tied to the end of one columella. For this, the quadrate and squamosal bones had to be partially reflected and the columellae had to be dissected free from the quadrates and surrounding connective tissue. This operation reduced the sensitivity of the auditory system to head vibration by 20 dB, and to air-borne sound by 15 dB. If, after this rather drastic surgical procedure, the quadrate and columella were allowed to return to their normal configurations, sensitivity was largely restored. Damage done to the inner ear by the operation is therefore deemed not to be serious. The response of the spinal system was unaffected by the manipulations described above. The threshold displacement for bilateral columella vibration in four snakes tested was 0·4–2·0 Å, for sinusoidal stimulation at the best frequency. The ratio of this figure to the threshold for response to whole-head vibration in the same snakes prior to dissection, was 0·5. The mechanical loss in converting vertical displacements of the head to displacements of the columella was therefore of the order of 6 dB.

Responses to columella vibration were found in roughly the same area of the midbrain as responses to vibration of the head. Both yielded the same frequency response and both were eliminated by destruction of the ear. These observations are documented below and are taken to suggest that columella vibration and head vibration result in the same mechanical and neural events. A possible reservation is that a natural stimulus might involve inner ear sensory structures not stimulated by columella vibration; the crude ear-destruction experiments could not be used to evaluate this possibility. Nonetheless, in what follows, I shall consider columella vibration and head vibration to be equivalent stimuli. Since head vibration does not stimulate the somatic system, it can be used to achieve the isolation of the VIII nerve system from the spinal system in intact snakes.

Frequency response

The frequency-response curves for the two systems are presented in Fig. 4. The graphs show intensity required to achieve criterion responses as estimated visually on the oscilloscope. The threshold criterion was a 25–50 μV response to approximately 50% of the stimuli. Repeatability of curves obtained in this manner was *c.* 3 dB at each point. Curves have also been constructed by averaging stimuli at two intensities within 5 dB of threshold and extrapolating to zero response. This method is extremely time consuming and curves thus obtained have the same shapes as curves obtained by the visual method. Visually evaluated curves were often displaced upward in intensity by 2–3 dB. For these reasons construction of curves by the averaging method was not used here. The frequency axes of these graphs are linear rather than traditionally logarithmic. This accentuates the difference between spinal system and VIII nerve system at high frequencies, and de-emphasizes the difference at low frequencies. This was desired because of the major and consistent differences between the two systems at high frequencies. The frequency response of the VIII nerve system alone, in a preparation with severed spinal cord, is given in Fig. 4A. This can be contrasted to the response of the spinal system alone (Fig. 4B); curves for either system, in the different species used for these figures, were similar, so cross-species comparison is valid. The VIII nerve system curve is narrow and peaked at the best frequency, *c.* 250 Hz in this specimen. For different snakes and different species, the best frequency has been observed in the range of 200–400 Hz. Temperature affects both absolute sensitivity and frequency response (see Hartline, 1971). The curve for the spinal system extends to higher and lower frequencies and lacks a distinct peak. Different individuals of the same species showed different maximum sensitivity considering either system alone. Thus, the maximum sensitivity shown in figures 4A and B cannot be directly compared. Such a comparison can be made, however, in Fig. 4D. The auditory system has 20 dB greater sensitivity; this is representative of the snakes sampled critically. The minor differences in the shapes of response curves for the VIII nerve system when local sound to body or head, head vibration, or body vibration were the stimuli, and when the recording locus was the same (as is the case in Fig. 4A), probably reflects different mechanical properties of sound and vibration pathways for these stimuli. The general shape of the curve for the auditory system was independent of recording locus, individual, and species. Whether there are small but significant differences in frequency-response curves for different species was not explored.

Fig. 4C illustrates that there are only minor differences in frequency response of the VIII nerve system in a spinalized snake for head vibration and columella vibration, illustrating the similarity of these two stimuli. The curves for columella vibration and for head vibration are nearly identical. Loss of sensitivity of the VIII nerve system caused by exposure of the columella is also illustrated. No response of the spinal system was observed in snakes whose cords were still intact when the columellae were vibrated. Furthermore, in snakes whose ears were destroyed, head-vibration amplitude required to give spinal-system responses was beyond the range of normal stimuli to the auditory system (Fig. 4B). Both head vibration and columella vibration failed to produce responses when the ears were destroyed. These observations are fundamental in the identification of head vibration as a pure auditory stimulus.

A more complicated frequency-response curve results if the electrode is placed in the auditory area of the mid-brain and sound stimuli are delivered when both ears and spinal cord are intact (Fig. 4D). The response curve for head vibration is similar to the pure auditory response of Fig. 4A. The points in Fig. 4D, representing threshold to sound, follow this curve below 500 Hz, but not above (nor at 50 Hz). This is understood if the response of the spinal system to sound, plotted on this figure for a different electrode position in the same snake, is considered. It is evident that the high-frequency deviation of the sound curve is due to contamination of the auditory response by somatic response.

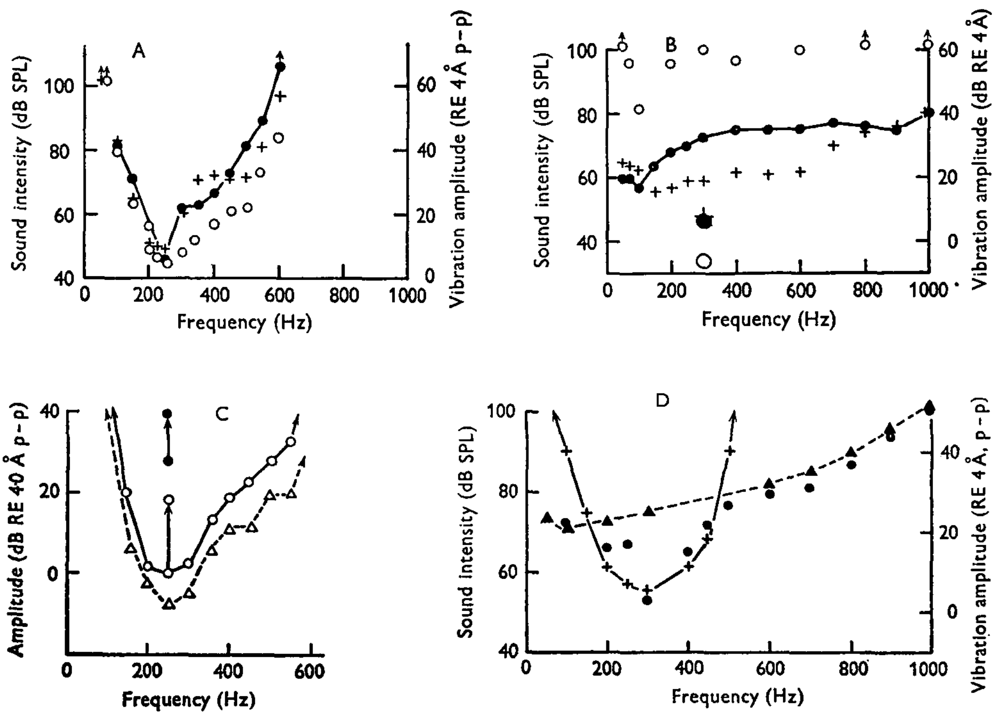


Fig. 4. Frequency/response curves for auditory and somatic systems. These are threshold curves, where the criterion was a 25–50 μV response occurring for *c.* 50 % of the stimuli, evaluated visually. Sound levels are given relative to 0·0002 dyne/cm^2, r.m.s. (SPL). Stimuli: general-field air-borne sound, ●; vibration under head, ○; vibration under body excluding head, +.

(A) Response of the auditory system in *Crotalus viridis* with the spinal cord destroyed. The origin of the vibration axis was chosen to provide coincidence for sound and vibration curves at the points of peak sensitivity. Note the sharp peak of sensitivity at 250 Hz ('best frequency') and the rapid decline of sensitivity at higher and lower frequencies.

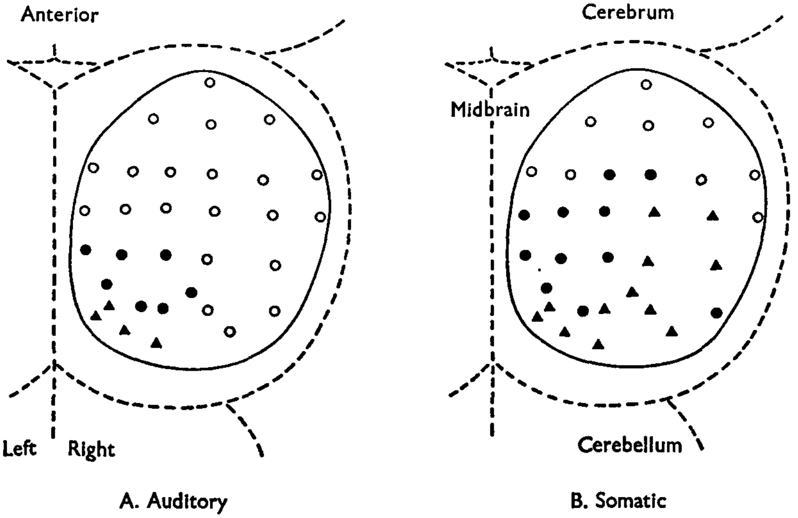
(B) Response of the somatic system in *C. cerastes*; inner ears were destroyed bilaterally. The larger symbols show this snake's 'best frequency' response of the auditory system. In general, the somatic system is not as sensitive as the auditory system, and lacks the distinct 'best frequency' characteristic of the latter. Its frequency range, however, is greater than that of the auditory system.

(C) Response of the auditory system to columella vibration: ○, head vibration before operation exposing columellae (arrow indicates new threshold after the operation); △, bilateral columella vibration. Threshold change for air-borne sound before and after the operation is shown by the arrow and ●. The operation exposing columellae for direct vibration by vibrating probes involved partially reflecting quadrates and squamosals, and disconnecting columellae from the connective tissue. This figure shows the similarity between frequency/response curves for head vibration and columella vibration and is taken as evidence that head vibration stimulates the auditory system. *C. viridis.*

(D) Composite frequency response. *C. viridis* with both systems intact. After ● and + curves were determined with the electrode in an auditory region of the midbrain, the electrode was moved to the region of the midbrain which gave only somatic-system responses, and the ▲ curve was determined for air-borne sound. Note that the closed circle curve follows the open circle curve (head vibration, which stimulates only the auditory system) at low frequencies, but follows the open triangle curve (somatic system) above 500 Hz and perhaps at 50 Hz. This illustrates contamination of auditory-system responses by spinal-system responses in snakes with intact spinal cords.

Anatomical distribution of midbrain responses

The above section establishes that the two systems can be distinguished from each other by their different absolute sensitivities, different frequency-response curves, and by the absence of spinal-system response to head vibration. In particular, the spinal system alone responds to sounds of 700 Hz and the auditory system alone responds to head vibration. These criteria were used to construct maps, in a single animal, of anatomical regions of the tectal surface below which either spinal- or auditory-system responses were present (Fig. 5). The area sensitive to auditory input is more restricted than that sensitive to spinal input; the spinal response area includes the entire auditory response area.



A. Auditory B. Somatic

Fig. 5. Somatic and auditory response areas. These are dorsal views of the right tectal surface. (A) Penetration sites where no response ○, slow potential response ●, spike response ▲, was obtained for auditory-system stimulus (head vibration, 10 Å p-p amplitude, 300 Hz). (B) Same penetration sites. The symbols have the same significance except that the spinal system alone was stimulated (air-borne sound, 80 dB SPL, 700 Hz). Areas outside the solid lines were not tested. These maps show overlap of the area yielding somatic-system responses ('somatic area') and that yielding auditory-system responses ('auditory area'). Note that the auditory area is completely contained in the somatic area. In the auditory area, spinal-system responses were obtained more superficially than auditory-system responses. *C. cerastes.*

Spatial distribution of sensitivity

It is reasonable to expect that sound delivered to a limited part of the surface of the snake's body (locally applied sound) would stimulate the spinal system if the sound were sufficiently intense. This is demonstrably the case. It is more interesting that the auditory response can also be elicited by local delivery of sound along the body as shown in Fig. 6. Since the broken line shows the extent of sound spread from a point of local stimulation, sound spread cannot account for all of the auditory sensitivity along the body. Details of spatial sensitivity are different for different individuals, and in addition there may be species-related differences; but these were not studied systematically. The general feature, that there is substantial sensitivity to sound delivered to the body excluding the head, remains for all specimens tested. The question then arises: does the same mechanism mediate the responses of the auditory system to head (columella) vibration, to general sound, and to sound applied locally to the body?

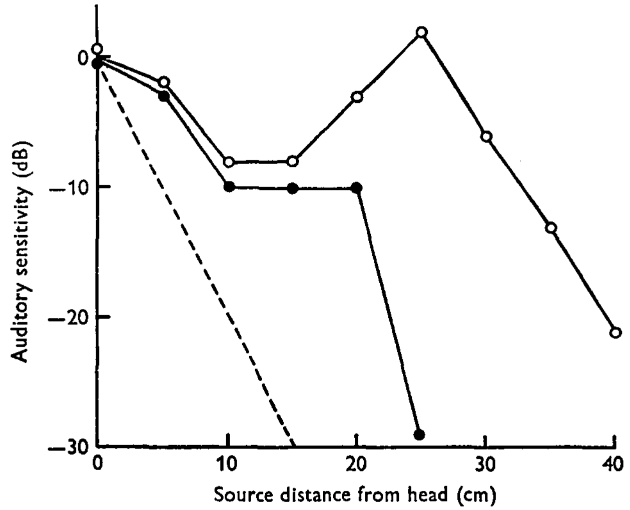


Fig. 6. Auditory sensitivity to body sound. Sound was applied locally at the distance from the head indicated on the abscissa, for two species of snakes (spinal cords severed): *C. viridis*, ●; *C. cerastes*, ○. The ordinate is the difference between threshold intensity for local sound delivery to the head and local sound delivery at the indicated distance. The ordinate thus reads sensitivity, increasing toward the top of the graph. The broken line shows sound scatter. Read abscissa as distance of microphone from sound source and ordinate as sound intensity measured.

VIII nerve system: common basis for response to vibration and sound delivered to head or body

It is a well-known phenomenon that, if noise is present, the response of an animal's auditory system to test tones is reduced (Hawkins & Stevens, 1950). The analogous experiments have been carried out in snakes and the result supports the conclusion that, for snakes, locally applied sound, general-field sound, and head vibration all stimulate the same sensory pathway (for the auditory system). From Fig. 7A it is seen that continuous general-field sound noise or head-vibratory noise causes diminution of the responses to concurrent sound or vibration stimuli (the spinal cord was severed to eliminate contribution by the somatic system to sound responses). Further, noise effecting 50% reduction in either response produced 50% reduction in the other, regardless of the source of noise. Use of a local sound source along the body in place of the general-field source gave the same results. If one accepts, as the basis for this masking, the classical explanation that neurones which would give responses to stimuli are unavailable because they are responding to noise, the parallel conclusion is that in snakes most neurones which respond to local or general sound also respond to vibration, and vice versa. Although this assumption about the mechanism of masking is reasonable, it is not verified for snakes. Furthermore, not all units may be affected in the same way by noise. A small proportion of unaffected units would pass unnoticed since a spatial average, the slow evoked response, is being taken. One can assert,

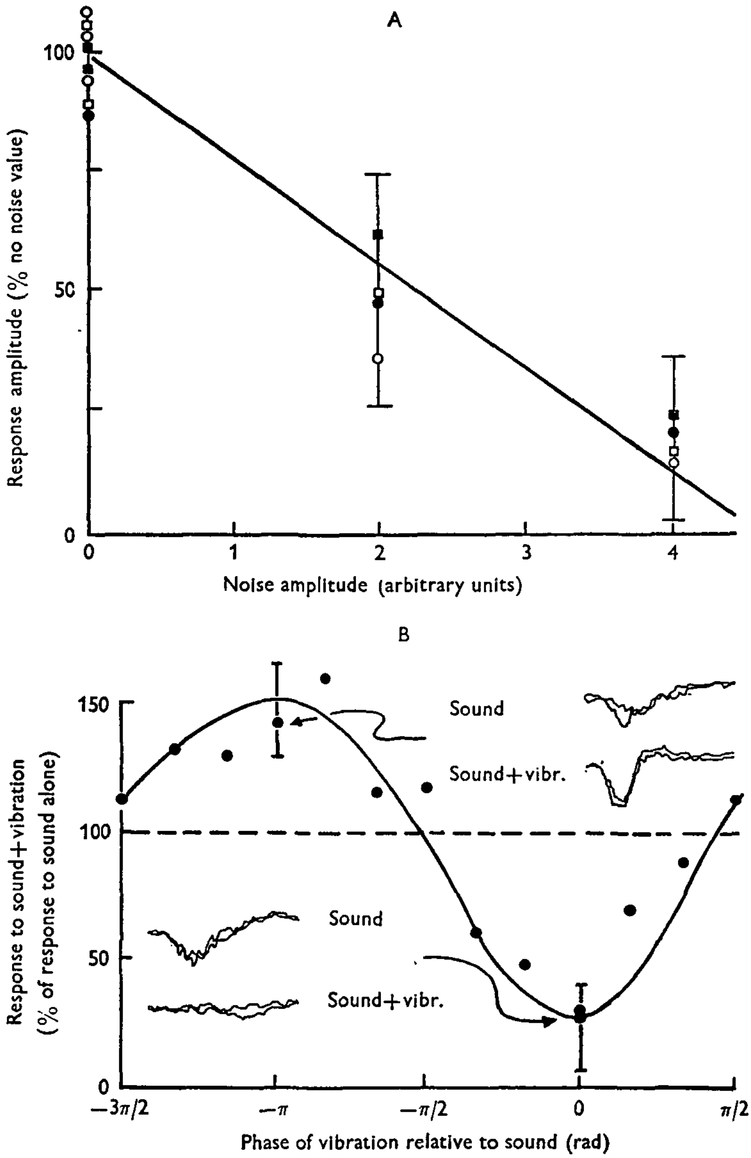


Fig. 7. Identity of auditory responses to sound and to vibration.

(A) Masking of sound or vibration stimuli by sound or vibration noise in the auditory system (spinal cord severed). Vibrations (stimuli or noise) were presented under the head, whereas sounds were not localized. ●, sound noise with sound stimulus; ○, sound noise with vibration stimulus; ■, vibration noise with sound stimulus; □, vibration noise with vibration stimulus. Sound stimulus was a 300 Hz tone of 100 msec duration at 57 dB SPL and the vibration stimulus was a 7 Å p-p, 300 Hz tone of 100 msec duration. Each point was based on two measurements of the response to the stimulus under the specified noise condition.

(B) Cancellation of auditory response to sound by simultaneous vibration stimulus. Sound was delivered locally to the middle of the snake. The amplitude of head vibration was adjusted to produce the best cancellation at the phase arbitrarily labelled 0 radians. Data used to calculate the points at 0 and $-\pi$ are shown. For each data point the mean amplitude of the two responses to sound plus vibration was expressed as percentage of the control (sound presented alone). Sound stimulus: 300 Hz, 74 dB SPL, 100 msec; vibration stimulus: 300 Hz, 12 Å p-p, 100 msec. The smooth curve was drawn by hand; theory predicts a sine wave. This demonstrates that responses to sound locally applied along the body are mediated by the same mechanical analyser which mediates responses to head vibration. Sine waves were generated by a Hewlett Packard model 203 A variable-phase function generator. $n = 10$ for all averages.

however, that the major population of auditory neurones handles information concerning both sound and vibration.

An elegant demonstration that the same sensory end-organs respond to head vibration and to local sound stimulation, in a spinalized snake, was inspired by experiments of von Bekesy (von Bekesy, 1932; see also Lowy, 1942). He demonstrated that the mechanisms leading to sensation of sound in the air and sound via bone conduction in humans are identical by finding, for any bone-vibration tone, an intensity and phase of air-borne sound such that the subject reported no sensation of sound when both stimuli were presented concurrently. If, for snakes, the mechanical analyser of sound (presumably a set of hair cells) subserves both local sound delivered to the body and head vibration, it should be possible, for a given local tone stimulus, to find a vibration of phase and intensity such that no motion would occur at the analyser. Consequently, either stimulus alone would evoke a response, but the combination of the two would evoke none. This result is clearly shown for one snake in Fig. 7B. Not only was annihilation of the response achieved at one phase (phase = 0 radians), as expected, but intermediate interactions and even enhancement (phase $= -\pi$) were noted at different phases.

The results of this experiment closely followed predictions at all phases, eliminating the possibility that some complex 'recovery' or masking phenomenon could be invoked to explain annihilation at phase 0. If vibration alone was used as stimulus, a response similar to that elicited by sound alone ('control') was seen. In order to explain these results by neural mechanisms, one would have to postulate that the phase information for oscillations arriving at two sensors is preserved in such a way that nervous activity could cancel in the central nervous system. This possibility seems sufficiently remote to be ignored.

In the same preparation responses to louder sound, delivered either locally or generally, were diminished by a head vibration of appropriate intensity and phase. The annihilation was not as complete as that shown in Fig. 7B; this is not unreasonable, as one would expect that, if the two types of stimulus arrived at the analyser through different mechanical pathways, each would be subject to different harmonic distortion. Responses to harmonics would persist after the fundamentals had been effectively cancelled out. The intensity of sound employed in Fig. 7B was chosen so that energy in the harmonics would not be great enough to produce a response. The results of this series of experiments (performed in three snakes including one colubrid and two crotalids) is reinforced by those of the masking experiments, and together they justify the assertion that there is a mechanical path through which sound energy incident on the snake's body is transmitted to its ear.

VIII nerve system: mechanical pathway

Any sound presented near the snake must cause small sympathetic vibrations of the substrate. Thus there is a possibility that the mechanical path invoked above is the substrate itself, and that sound delivered along the body is only effective inasmuch as it causes vibrations of the substrate at the head. The results presented in Fig. 8 show that vibrations reaching the head of the snake through the substrate, due to local sound stimulation, are not sufficiently strong to cause a response. In this experiment

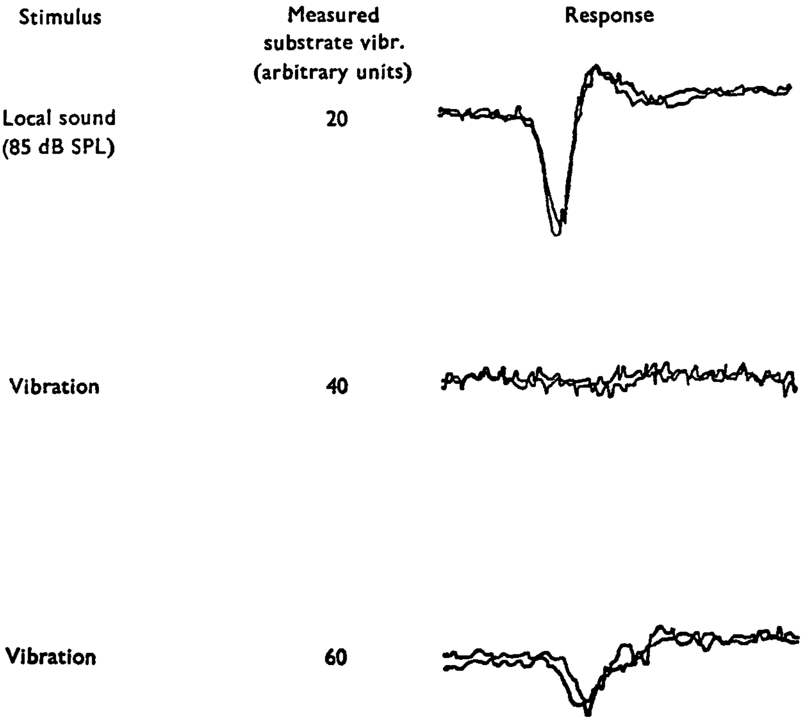


Fig. 8. Control for sympathetic vibration. The response of the auditory system to local sound and to head vibration is shown. The piezoelectric element of the platform was used as a measuring transducer ('measured substrate vibration' is the voltage in millivolts induced by displacement of the platform, as measured by a high-impedance amplifier; this is proportional to displacement). A vibrating probe was placed with its needle in the centre of the platform to deliver vibrations. Duplicate averages ($n = 10$) are shown for each stimulus (frequency = 300 Hz). The figure illustrates that substrate vibrations induced by sound stimuli (top line) are not sufficient to cause the response elicited by sound. Sound energy is therefore conducted to the ear through the snake's body.

the vibrating platform was used as an uncalibrated 'vibration detector'; a high-impedance amplifier monitored voltage induced across the piezoelectric ceramic by vibrations of the platform. As measured by the output of this vibration detector, the amplitude of substrate vibration caused at the head by suprathreshold sound applied at the middle of the snake's body would not itself have caused a response of the auditory system. It is then necessary to look for mechanical paths in the snake itself which couple the body to the ear.

Role of the lung

The lung–airsac system, in these snakes, extends from 2–10 cm posterior of the head to 2–10 cm anterior of the anus, and is an obvious candidate for a role in transmission of sound from one end of the snake to the other. Intensities of sound inside and outside the snake were measured for local application of sound near the posterior end of the airsac (Fig. 9A). Sound intensity at 200 Hz fell 32 dB from the point of focal stimulation to the head, if measured by a microphone outside the snake. The intensity inside fell only 8 dB over the same distance (13 dB counting the initial 5 dB

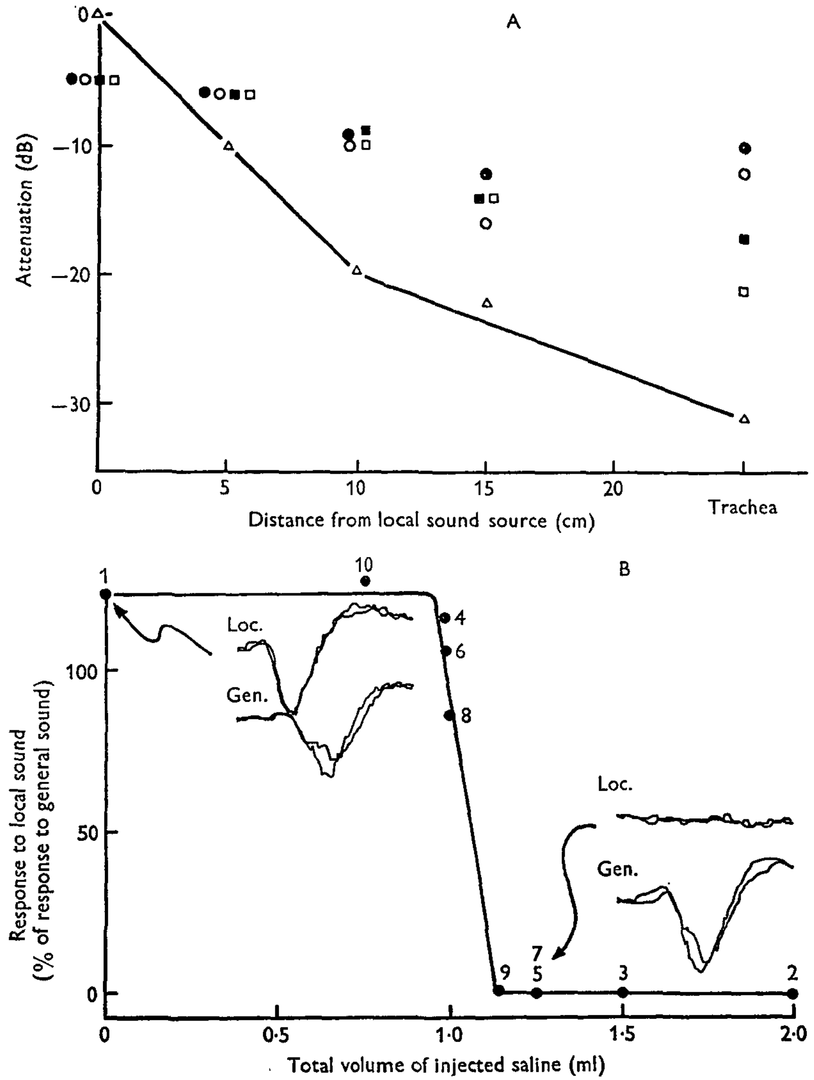


Fig. 9. Role of the lung in the auditory response.

(A) Sound intensity was measured with a hypodermic microphone probe (see text) outside the snake at 300 Hz, △; and inside the snake at 100 Hz, ●; at 200 Hz, ○; at 300 Hz, ■; at 400 Hz, □. The measurements were made on a freshly killed specimen. Points at 25 cm were measured with the microphone probe inserted into the trachea. All others were measured by inserting the probe through the body wall into the lung-airsac at a distance from the local sound source which is indicated along the abscissa. The source was near the posterior end of the airsac. This figure illustrates that the air passages conduct sound from the body to the region of the head.

(B) Auditory responses (spinal cord severed) to sound delivered locally, posterior to a U in the snake's body, are compared to responses to general-field sound. For each point the mean amplitude of the two averaged responses ($n = 10$) to locally applied sound was expressed as a percentage of the mean of two averaged responses to general-field sound. Saline was either injected or withdrawn from the airsac at the U, and total saline in the airsac is plotted on the abscissa. The order in which points were taken is given by the number adjacent to each point. The response to general-field sound was unaffected by saline injection whereas the response to locally applied sound diminished abruptly between 1·0 and 1·2 ml saline. This illustrates that the integrity of the airsac system is required for responses to sound delivered locally to the body.

attenuation measured for the snake's body wall) as measured by a microphone probe inserted into the airsac.

The integrity of this air path is necessary for normal reception by the auditory system of sound or vibration incident on the body (Fig. 9B for sound). A snake with severed spinal cord was bent into a U, and sound was applied posterior to the U. The auditory response was measured as saline was injected into the airsac at the U via a hypodermic syringe. Control responses to general-field sounds showed no change in amplitude as saline was injected, a result expected since the anterior half of the airsac and the sound-receiving apparatus at the head were intact. Injection of saline presumably filled the air space until there was no connexion between the point of local sound delivery and the anterior portion of the airsac. As illustrated by the figure, the volume of injected saline at which the air path became occluded was very sharply defined. Addition of 0·2 ml was sufficient to effect 90 % reduction in response. Withdrawal of 0·2 ml subsequently restored the response to its previous level. Such an occlusion and restoration was repeated several times. This experiment indicates that the lung–airsac system plays a substantial role in the transmission of mechanical energy from the body to the ear.

DISCUSSION

The classical suggestion

I have shown that the central nervous systems of snakes of at least three families are responsive to sound and to substrate vibrations. The classical theory assigning a role to the mandible–quadrate–columella path in sensing vibration is supported by the remarkable sensitivity of the auditory system to vibrations under the head. However, the notion that this specialization has led to insensitivity to air-borne sound is not confirmed. In the frequency range of maximum sensitivity the snake responds to stimuli within 20 dB of the behavioural thresholds reported for humans or cats (for a discussion of relation between evoked potentials and human sensation, see Rosner & Goff, 1967). Fig. 10A compares the snake's auditory system with the auditory systems in other animals.

Cochlear microphonics

As Wever & Vernon (1960) pointed out, the deficiency of snake hearing lies not in its absolute sensitivity, but in its restricted frequency range. They found 0·1 μV cochlear microphonic responses to sounds of intensities below 75 dB SPL in the frequency range 50–800 Hz for *Pituophis melanoleucas*. My data for *Pituophis* indicate a narrower frequency range at this intensity: 250–450 Hz. For this species, sample size was small in both studies, but I feel that the results show a real difference between hearing as indicated by cochlear microphonics and by evoked brain potentials.

Wever & Vernon argue convincingly that air-borne sound causes the cochlear microphonic responses and my studies corroborate that finding. My results suggest in addition that cochlear microphonics will result if air-borne sound is delivered along the body of the snake, or if the substrate is vibrated. Wever & Vernon explored the contribution of bone vibrations to cochlear microphonic responses and concluded that the quadrate acts as a sound-receiving surface, much as does the tympanum in tetrapods. By using a vibrating probe I have found that vibrations delivered by firm contact of the hypodermic needle with the skin over the quadrate or with the skull itself are approximately as effective stimuli as is vibration of the whole head. I can neither confirm nor deny the special role of the quadrate proposed by these authors. I can assert, however, that the quadrate and indeed the entire mechanical path subserving the response of the auditory system to sound at the head is not the only path for sound reception.

Auditory response: role of head vs. body

The body has a role in receiving sound (Fig. 6). The relative importance of the body and of the head for reception of sound energy is not easy to establish. Several snakes with spinal cords intact or destroyed were compared in auditory thresholds when sound was delivered to the entire body and when it was delivered locally to the head. Variation between individuals was large; differences in threshold ranged from less than 2 dB (corresponding to 0·2 or less contribution of the body) to 15 dB (corresponding to 0·8 contribution of the body). The reasons for the wide variation are not understood. The state of inflation of the lung, body configuration, and similar factors seem to be involved. Certainly under some circumstances the body is important as a sound receiver. With such a system the snake could gather sound from a source which was shielded from its head by objects in its environment.

I have not established how sound pressure in the lung causes responses of the ear. One possibility eliminated by the following observations is that sound in the lung is translated by mechanical elements into vertical displacement of the head, which is conducted to the ear by the same mechanism underlying responses to actual substrate vibration. Loud sounds (100–120 dB SPL) were applied along the body, and the resulting vibration of the head was measured with the same optical system as used for calibration of the vibrating platforms. If linear extrapolations to lower sound intensities can be made, sounds along the body and indeed at the head do not cause enough vertical head displacement to explain the observed responses. Evidently there is a more direct effect of sound on the ear which may involve the quadrate–columella path or a mechanism such as was suggested by Smith (1968) for vibration sensitivity in the salamander. Since anatomical disruption of the quadrate–columella path leads to 15 dB loss of sensitivity to sound, it seems likely that these elements play a role in sound reception as well as vibration reception.

A role such as is played by the snake's body, in particular the lung, in gathering auditory and vibratory energy has not been described, to my knowledge, in any other vertebrate excepting fish. Studies in man show a 50 dB attenuation of sound energy in the path from the air passages to the ear (von Bekesy, 1960). Frogs have tectal units which respond to both sound and vibration, but the body has not been implicated as the source of vibratory stimulus (Potter, 1965). Cetaceans, notably porpoises, have sound sensitivity over portions of their heads not usually associated with audition (Bullock *et al.* 1968). Some earless lizards, whose auditory anatomy is superficially similar to that of snakes (primarily the Chamaeleonidae, which have a well-developed airsac system and no external ear) might be of interest for comparison with snakes (Toerien, 1963).

Only in fishes with swim bladders is there a demonstrable role of the body in reception of sound. In some fishes, the swim bladder may convert 'far-field sound' into 'near-field sound' which is received by the ear; in others, the Weberian ossicles conduct vibrations from the swim bladder to the ear (Enger & Andersen, 1967). It seems unlikely that the similarities of fishes and snakes with respect to audition is anything but coincidental. Snakes have independently evolved what seems a unique system for transmitting sounds and vibrations from the body to the ear. These findings may add to the discussions of the evolution of airsacs in various reptiles (George & Shah, 1956, 1965; Brattstrom, 1959).

Responses to vibration

The sensitivity of snakes to vibration is certainly remarkable. Even though the vibrating probes and platforms were calibrated to within 3 dB and required only 30 dB of extrapolation on the basis of piezoelectric linearity, it would be unwise to assert that the figure of 1 Å cited here represents an absolute physiological limit of

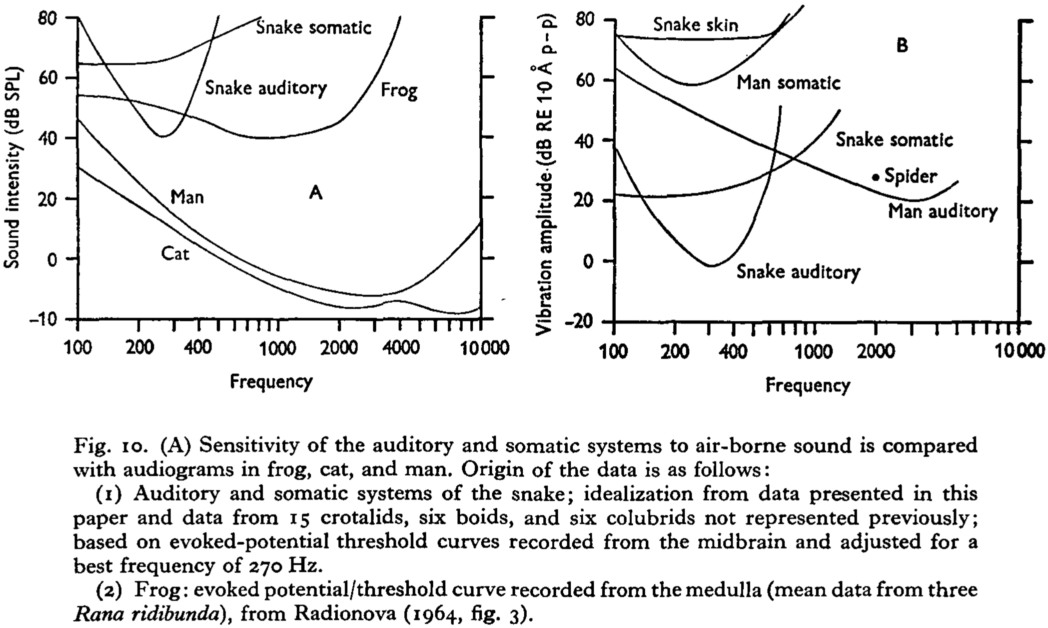


Fig. 10. (A) Sensitivity of the auditory and somatic systems to air-borne sound is compared with audiograms in frog, cat, and man. Origin of the data is as follows:

(1) Auditory and somatic systems of the snake; idealization from data presented in this paper and data from 15 crotalids, six boids, and six colubrids not represented previously; based on evoked-potential threshold curves recorded from the midbrain and adjusted for a best frequency of 270 Hz.

(2) Frog: evoked potential/threshold curve recorded from the medulla (mean data from three *Rana ridibunda*), from Radionova (1964, fig. 3).

(3) Cat: behavioural thresholds from Miller, Watson & Covell (1963, fig. 8).

(4) Man: composite of data on behavioural thresholds from Licklider (1951, fig. 5).

(B) The sensitivity of the auditory and somatic systems of the snake to substrate vibration is compared with thresholds for a snake mechanoreceptor, human auditory system, and human somatic system. Origin of the data is as follows:

(1) Auditory and somatic systems of the snake; idealization of data from fifteen crotalids and six colubrids in addition to those previously cited; evoked potential/threshold curves recorded from the midbrain and adjusted for 300 Hz best frequency (auditory).

(2) Snake, isolated skin: threshold curves for single vibration mechanoreceptor from Proske (1969); 0·5 μ was assumed to be the maximum sensitivity. The curve rises 20 dB by 50 Hz.

(3) Man, auditory system: psychophysical data from von Bekesy (1948, 1960); threshold curve for hearing of skull vibration (1960, fig. 6-34) modified for skin attenuation from figures 6-6 and 6-7 (1960); the result gives threshold vibration for a 1 cm^2 vibrator pressed with 1 kg force against the forehead. Corrections for frequencies above 800 Hz were not presented by von Bekesy but were estimated by extrapolation of his data.

(4) Man, somatic system, psychophysical thresholds from von Bekesy (1939); a vibrating rod was held between two fingers. The single solid circle represents the threshold of the peripheral leg nerve of the spider to vibration of the tip of the leg (Walcott & van der Kloot, 1959).

sensitivity. Certainly the nervous system of the snake can respond under laboratory conditions to vibrations of this magnitude. But, in singular environment, a snake may encounter noise both in the vibration domain and in the sound domain, either of which would reduce the snake's effective sensitivity by masking. In quiet surroundings there might be units more sensitive than the limits found for slow potentials. Spikes have been recorded from units in response to 1 Å vibrations; others with lower thresholds may be found in more extensive examinations. The sensitivity of the snake's auditory system can be compared to sensitivity of other non-tactile vibratory sense organs. Spiders sense 25 Å vibrations in their webs (Walcott & van der Kloot, 1959). If direct bone vibrations at these frequencies is the stimulus, humans require 10 Å displacement of the skull for sensation of sound; if a vibrator is applied to forehead skin with 1 kg force, this figure rises by *c.* 30 dB (von Bekesy, 1939, 1948, 1960; see Fig. 10B). It is remarkable that the snake's vibration threshold is so close to the 1 Å tympanic excursion usually cited as the threshold for human sensation of sound. The sensitivity of snakes to vibration is extraordinary.

The description of peripheral vibration receptors (Proske, 1969) provides a plausible explanation for the origin of responses to sound and vibration mediated by the spinal cord. The frequency-response curves of these receptors are similar in shape to some but not all of those found in this study. A similar shift toward higher frequency of the upper frequency limit with elevation of room temperature was noted in Proske's study and in this one. But whereas the lower frequency limit shifted upward with increasing temperature in Proske's receptors, it remained fixed, as measured by slow potentials, in the few cases that I have measured carefully.

It would be helpful to compare the absolute thresholds of Proske's vibration receptors to the sensitivity found in my study. But Proske did not use a stimulus of known amplitude, nor, by virtue of their point application, would his stimuli be directly comparable to mine even if the amplitude was known. Proske believes (personal communication) that the point stimulation threshold was on the order of 0·5–1·0 μ; the threshold for isolated Pacinian corpuscles is in the same range (Sato, 1961). Threshold somatic response to body vibration was elicited by 10–100 Å vibrations in my study. This is at least two orders of magnitude smaller than the 1 μ thresholds of Proske or Sato for vibration-sensitive mechanoreceptive units. Spatial summation and differences in threshold criteria may account for this discrepancy, but further comparison is needed. A comparison of vibration sensitivity in the snake and in other animals is given in Fig. 10B.

Biological function

It is of biological interest to compare responses of the auditory system and responses of the somatic system, keeping in mind the question: what additional information does the snake get out of having two systems sensitive to sound and to vibration? It is clear that, at its best frequency, the auditory system provides information about stimuli of lower amplitude, whereas the somatic system has a greater frequency range. Using the evoked potential as an assay, it is noted in Part II that the somatic system has a greater dynamic range than the auditory system. But the evoked potential is limited in its utility in ascertaining what intensity information is available to the animal (Rosner & Goff, 1967). It is reasonable to suggest that the auditory system is specialized for sensitivity and serves to alert the snake to the presence of faint sources of sound or vibration. The somatic system, with its greater frequency range and lower sensitivity, might give the snake information about closer sources of disturbance, for instance, approaching prey or predator. My study has been concerned primarily with slow evoked responses. These indicate that sound and vibration are effective stimuli for two sensory systems. My results fail to show that a neural distinction is drawn between sound and vibration in either system alone. It is possible that extensive unit studies would show that discrimination is made but is lost to the observer who monitors summed activity of units, processes and support tissue. There may be ways to resolve the apparent ambiguity between energy sources. Referring to Fig. 4, suppose that a snake sensed a threshold stimulus at 250 Hz. Then, if the stimulus were pure sound, the auditory system would be activated at 25 dB above threshold (compare 45 dB SPL auditory threshold to 70 dB SPL somatic threshold). But, if the source were pure vibration (open circles), the auditory system would be activated at 15 dB above threshold (as above for sound; this example assumes that the sets of curves for Fig. 4A and B would be found in the same individual). Thus information about the energy source would be available to the snake if it could measure and compare the amplitude of a disturbance as reported by the two systems.

To decode information from the two systems in this manner would require that information about stimulus intensity be available via each system in overlapping intensity ranges. It would also require that the nervous system be capable of comparing the responses of the two systems as to intensity content. Although this is conjectural, such a rationale might explain why the snake has evolved two sensory systems which respond to overlapping sets of stimuli, and why neither system alone need draw the distinction between air-borne sound and substrate-borne vibration.

This problem of 'ambiguity' may best be approached with behavioural questions in mind. Do sounds and vibrations occur in the snake's environment of amplitudes such that there is ambiguity? If they do, is the biological end served by the somatic and the auditory systems enhanced by eliminating the ambiguity? At present we need more knowledge about levels of relevant sound and vibration signals in the snake's world, and about irrelevant or 'noise' signals. We must know to what extent the snake uses information about sound and vibration. Manning's experiments (1923) and aversive conditioning used to train snakes (Crawford & Holmes, 1966) did not make use of stimuli or situations in which the snake's capabilities would be tested.

Many problems posed by this study need supporting data from behavioural studies. The failure of investigators to find that snakes can hear is not because snakes lack neural access to information about sound; more likely it is due to failure on the part of the investigators to present sounds in a context which could give them relevance and meaning to the animal, or by their failure to motivate it to show that it heard In spite of the absence of corroboration from behavioural studies, I believe that the responses to sound and to vibration reported here in species of three families will also be found in other species The sound detecting system and the vibration detecting system are functional in snakes, and will prove important to our understanding of them. Furthermore, a detailed study of the vibration sensors, both auditory and somatic, is likely to contribute to our understanding of the fundamentals underlying vibration sensitivity in other animals.

SUMMARY

1. Snakes possess two sensory systems which respond to both air-borne sound and substrate vibration as shown by extracellular slow evoked potentials recorded in the midbrain. One involves the VIII cranial nerve and inner ear (designated 'auditory system'); the other requires an intact spinal cord and probably originates in skin mechanoreceptors (designated 'somatic system').

2. In species of the families Colubridae, Crotalidae, Boidae, the auditory system has a typical U-shaped frequency-threshold curve, similar to those found in other animals, but restricted to a narrow frequency range, *c.* 150 Hz to 600 Hz. The U-shaped curve has a distinct minimum threshold or best frequency. Frequency-threshold curves for sound and head vibration have only minor differences.

3. The auditory system is not remarkably sensitive to sound. It is about 20 dB less sensitive than the human auditory system for air-borne sound between 200 and 400 Hz. It is remarkably sensitive to head vibration: at the best frequency, 1 Å peak-to-peak amplitude is suprathreshold.

4. The auditory system responds not only to stimuli at the head but to sound and vibration delivered to the body alone. Responses to body stimulation by sound are caused by the same sensory end-organ that responds to head vibration. The role of the body in picking up sound for the auditory system can be substantial; thus the lung plays an important part in snake hearing, a novel situation among land vertebrates.

5. The somatic system is not as sensitive to sound or to vibration as is the auditory system over most of the latter's frequency range. The somatic system has a relatively flat frequency-threshold curve which lacks a distinct best frequency. The frequency range extends both above and below the range of the auditory system, 50–1000 Hz. The somatic system is insensitive to vibration of the head.

6. Evoked slow potentials fail to show that either spinal or auditory system distinguishes between vibratory energy from the air and from the substrate. It is proposed that intensity information from the auditory system could be compared by the snake's brain with intensity information from the snake's somatic system in order to determine the relative amounts of air-borne sound and substrate vibration in an unknown natural stimulus.

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