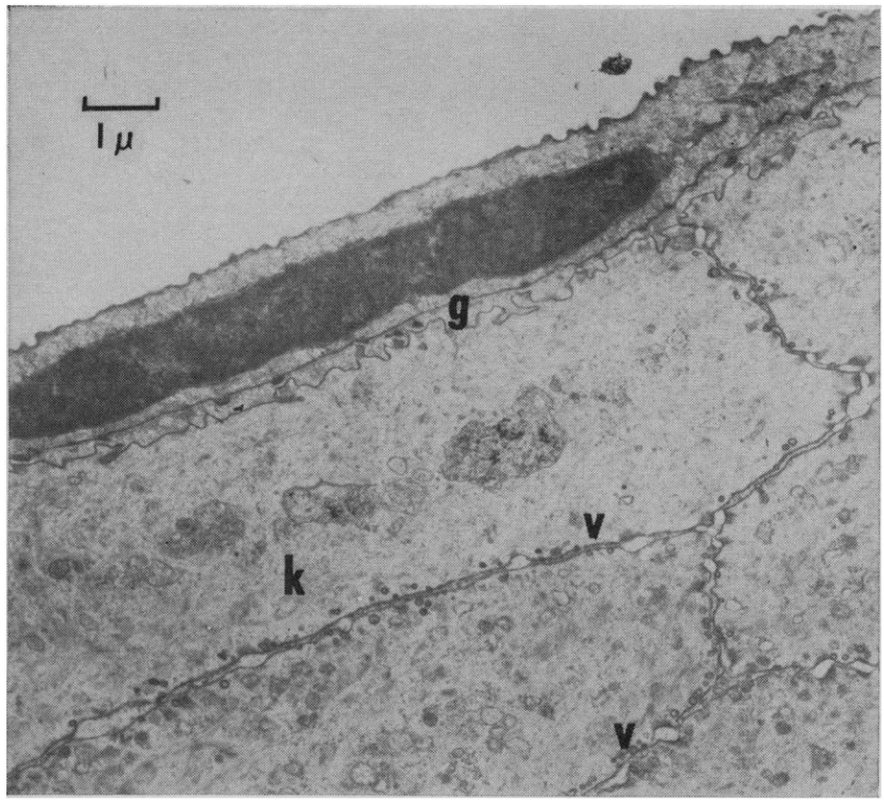

Fig. 3. Outer layers of the epidermis of *N. pictus*, fixed in glutaraldehyde and osmium and stained in uranyl acetate and a lead preparation. The outer keratinized layer of cells (*stratum corneum*) is shown separating from the underlying layer (*g* is intercellular gap) to form the cocoon. Filaments of keratin (*k*) and remnants of intracellular organelles are visible. Notice the small vacuoles (*v*) close to the intercellular gap.

The lethal limits of water loss of previously hydrated desert-dwelling frogs lies between 40 and 50 percent of the body weight (*2*). Thus a *C. alboguttatus* weighing 18 g can afford to lose approximately 7.2 g of water, and an *N. pictus* weighing 9 g, 3.6 g of water. These estimates exclude the water stored in the urinary bladder which may be reabsorbed to replace water lost, and which in desert-dwelling frogs may amount to 50 percent of the body weight (*2*).

Therefore the total amounts of water these frogs can afford to lose is 16.2 g and 8.1 g, respectively. Should conditions as vigorous as those in the experiments prevail, and if the surface area of the cocoons is assumed to be the same as that estimated for the frogs, then the rate of water loss from the cocoons would be 0.027 g/hr for a *C. alboguttatus* weighing 18 g and 0.013 g/hr for an *N. pictus* weighing 9 g. With the exception of water lost from the lungs, *C. alboguttatus* would reach the lethal limit of water loss after 600 hours, and *N. pictus* after 623 hours. Thus, the cocoons contribute significantly to the water economy of the frogs, but some additional factor must suppress evaporative water loss as these frogs may spend periods of 3 months or more underground. This additional factor is presumably moisture in the soil (*2*).

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Frequency Sensitivity of Single Auditory Neurons in the Gecko Coleonyx variegatus

Abstract. *Although acoustic communication is not pronounced in reptiles, analysis of single auditory neurons in the medulla oblongata shows that the cochlea is a frequency analyser. Auditory neurons of the lizard* Coleonyx variegatus *respond to acoustic stimuli over a range of less than 0.1 to 17 kilohertz and are maximally responsive between 0.8 and 2.0 kilohertz. The frequencies to which they are most sensitive differ from neuron to neuron, ranging from 0.11 to 4 kilohertz. Some neurons have an inhibitory area which greatly overlaps the response area, so that inhibitory areas do not seem to sharply tune the response area at this level of the auditory tract. The inhibitory area is responsible for producing in some neurons a phasic response and nonmonotonic relation between sound intensity and number of impulses. The response pattern shows a tendency to change from tonic to phasic in more advanced auditory centers. This may serve to code rapid changes in the acoustic stimuli.*

Acoustic communication is a prominent feature in many amphibians (*1*). Frishkopf and Goldstein (*2*) have demonstrated in the eighth nerve of frogs two types of neurons distinguished by different frequency sensitivities. In the midbrain auditory system of frogs, however, Potter (*3*) has demonstrated units with various shapes of response areas (area above threshold curve of a single neuron). Compared to amphibians, the reptilian inner ear is anatomically more specialized for hearing. The basilar membrane is elongated and differentiated in width along its length. The hair cells also show considerable differentiation in number and distribution along the basilar membrane (*4*). Despite these developments, acoustic communication is considered to be rudimentary or absent in most reptiles except for the crocodilians, lizards of the family Gekkonidae, and a few turtles (*1, 5*). The central auditory physiology of reptiles, even the vocal forms, has received almost no attention. The majority of the studies of reptilian hearing have used cochlear microphonics or behavioral responses as indexes of sensitivity. We now report the properties, in terms of frequency sensitivity, of auditory neurons in the medulla oblongata of a gecko.

The banded gecko, *Coleonyx variegatus*, a desert species from western North America, was chosen for the study. In contrast to most geckos, this species has a relatively restricted vocal repertoire. This lack of vocal development is surprising in light of the auditory sensitivity in this species, which is among the most sensitive of the lizards so far studied (*6*). No mating call is reported, though individuals produce a characteristic "squeak" when handled. This sound is also produced by males during territorial combat (*7*). The predominant fundamental frequency of this sound is from 1 to 1.5 khz, and many harmonics are present in our recordings. Studies of cochlear microphonics (*8*) and midbrain evoked potentials (*9*) indicate that the ears of this species are most sensitive to sounds of 0.4 to 0.8 khz, though the evoked potentials also show a second region of sensitivity around 1.5 khz.

In our experiments, animals anesthetized with nembutal were mounted upside down on a small platform in a soundproof room. Sound stimuli were presented through a loudspeaker located 90 cm in front of the head. Temperature was maintained between 22° and 25°C. A small hole was made in the basioccipital bone just medial to the round window. A glass micropipette electrode filled with 3*M* KCl was inserted into the medulla through the hole, while a 50-msec pure-tone pulse with a 10-msec rise-decay time was delivered. Responses of 57 auditory neurons were studied.

Responses to acoustic stimuli were obtained chiefly in two regions, in the ventromedial portion of the medulla (olivary complex) and near the dorsolateral surface (probably in the nucleus magnocellularis dorsalis which is equivalent to the ventral cochlear nucleus in mammals). In the former location neurons were often found which showed a phasic response (for example, a few impulses were discharged only at the onset of the stimulus), while in the latter they were chiefly tonic. Responses of single neurons were obtained to sounds from below 0.1 to 17 khz at 100 db, referred to 0.0002 dyne/cm^2 root mean square. The lowest threshold found was 27 db, at frequencies between 0.8 and 2.0 khz (Fig. 1). Cochlear microphonic measurements show the minimum threshold at 18 db sound pressure level at 0.5 khz (*8*). The best frequencies (that to which the neuron is most sensitive) of the neurons ranged from 0.11 to 4.0 khz; no neurons with a best frequency above 4.0 khz were located. The shape of the response area of the neurons, which was not noticeably different for the two areas of the brain stem, was not sharply cut off above the best frequency as is found in mammals (*10, 11*). This may be due to the lack of a traveling wave along the basilar membrane, as the anatomy would suggest (*4*), or it may be due to the multiple innervation of primary auditory neurons to the hair cells as is the case in the external spiral fibers in mammals, or it may be due to both. The Q values, which indicate the sharpness of the response area (best frequency divided by band width at 10 db above minimum threshold), ranged between 0.6 and 3.7. These values are lower, on the average, than the values calculated over the same frequency range for primary auditory neurons in the cat (*11*). Adequate comparative data for other animals are not available.

In the majority of the tonic neurons studied, the number of impulses increased monotonically as the stimulus intensity was increased over a dynamic range of 50 to 60 db. However, a number of the phasic neurons showed a nonmonotonic relation between sound intensity and number of impulses in response to stimuli at a certain frequency; that is, the number of impulses increased with increasing stimulus intensity until it reached a maximum value, after which an increase in stimulus intensity resulted in a decrease in number of impulses. In order to study the neural mechanism involved in creating the phasic response pattern and the nonmonotonic spike-count function, and in order to study the funneling effect which narrows the response area around the best frequency, we measured inhibitory areas with a pair of tone pulses (*12*). A conditioning tone pulse of 30 msec was delivered 10 msec before an excitatory sound of 30 msec. The rise-decay time of these pulses was 10 msec. Frequency and intensity ranges of the conditioning tone pulse which inhibited completely the response to the excitatory sound were measured. The excitatory stimulus was usually the best frequency of the neuron being studied, and the intensity was set slightly above

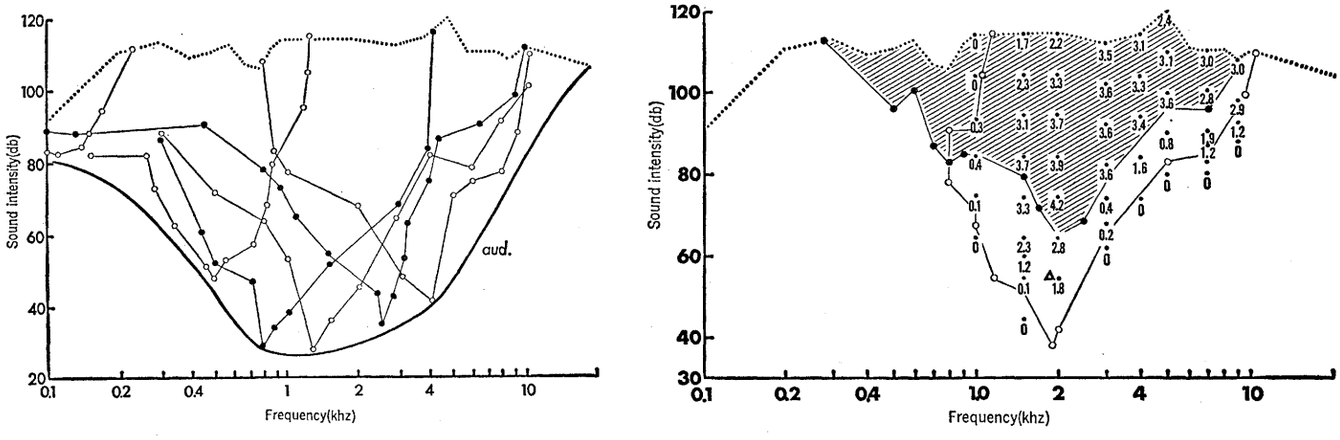

Fig. 1 (left). Response areas of six single auditory neurons. The curve labeled *aud.* is the audiogram suggested by the response areas of all the neurons studied, and the threshold curves of the multiunit evoked potentials (*db* refers to 0.0002 dyne/cm^2). Fig. 2 (right). The response and inhibitory areas of a neuron which showed a phasic response and a nonmonotonic spike-count function. The response area is the region above the threshold curve indicated by the open circles and solid line. The inhibitory area is the shaded area above the solid circles and solid line. The numbers in the response area are the average number of impulses discharged in response to a 50-msec stimulus of the frequency and intensity indicated by the dot immediately above the number. A triangle indicates the excitatory sound used when the inhibitory area was measured.

threshold so that the response was easily inhibited by any inhibitory stimulus.

An inhibitory area of a neuron which showed a phasic response and a nonmonotonic spike-count function is shown in Fig. 2. The inhibitory area greatly overlaps the response area. Inhibitory stimuli from the area outside the response area (for example, 0.6 khz) did not evoke a response from the neuron, but inhibited the response to the excitatory stimulus. Stimuli from the shaded portion within the response area were not only inhibitory but were themselves excitatory while suppressing the response to the second stimulus. Measurement of the recovery curve of the neuron showed an inhibitory period immediately following the discharge of impulses to the first stimulus. In other words, the phasic response pattern can be said to have resulted from an inhibitory bombardment immediately following an excitatory bombardment. The nonmonotonic spike-count function of the neuron is understandable in light of this inhibitory area overlapping the response area. A decrease in the number of impulses with increasing intensity of a single stimulus can be seen clearly in the inhibitory region overlapping the response area of the neuron. In the region of the nucleus magnocellularis dorsolis, the spike-count functions were usually monotonic when the intensity of the stimulus was below 100 db. The nonmonotonic spike-count function must be produced by an inhibitory effect from other neurons, as discussed for mammals (*13*).

In the medullary auditory neurons, the inhibitory area often covered most of the response area. Inhibitory areas tightly sandwiching a response area from both sides of the best frequency were found but were rare. Neurons with narrow response areas were not found in this sample. At this level in the auditory system, both the response and inhibitory areas of single neurons scarcely show indication of the funneling, or sharpening effect around the best frequency. But, as in the case of mammals, there was a general tendency for the response pattern to shift from tonic to phasic as higher centers became activated. This phasic response pattern might serve to code rapid changes in the stimulus.

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Receptive Fields in the Cat Retina: A New Type

Abstract. *A new type of receptive field of cat retinal ganglion cells is described and termed the "suppressed-by-contrast" type. The firing rate of these cells is suppressed by a variety of visual stimuli. However, it has not been possible to find a stimulus that increases the firing rate above the maintained level.*

The two common types of receptive field organization of cat retinal ganglion cells were first described by Kuffler (*1*). The "on"-center type increases its firing rate when there is an increase in the ratio of the luminance of a central region to that of a surround region of the visual field. The "off"-center type increases its firing rate when there is a decrease in this ratio. Thus both types have the same spatial form, but a stimulus that excites one inhibits the other, and vice versa.

Until recently no new types have been described in the cat retina, although other types of receptive field organization have been described in the cat lateral geniculate nucleus and striate cortex (*2*) and in the retinas of other animals (*3*). However, Stone and Fabian (*4*), by concentrating on the small ganglion cells of the area centralis, found 16 units whose organization was different from the center-surround type. Four of the units had receptive fields that produced an on-off response to a small spot of light anywhere in the receptive field. One of these four on-off units was direction-sensitive, two units had diffuse receptive fields, and the remaining ten did not appear to have a surround. More recently Spinelli (*5*) studied the response of ganglion cells to a flashing light in a sequence of positions in the visual field and interpreted his findings as new types of receptive field organization. However, Barlow *et al.* (*6*) have criticized this interpretation, arguing that spurious factors, such as the effect of stray light, are responsible for the response patterns obtained by Spinelli.

During a study of the maintained activity of retinal ganglion cells (*7*), two units were found that differed radically from those previously described. They both had the same response properties and were studied extensively with a variety of stimuli. They appear to represent a new type of receptive field organization here termed the suppressed-by-contrast type. The units were recorded extracellularly by the use of tungsten electrodes in the intact eye. One cat was decerebrate, the other anesthetized with nitrous oxide.

The location of each of these receptive fields was initially difficult to find. Yet when it was found and the effective visual stimuli discovered, the response was clear-cut and reproducible. Each unit had a receptive field estimated with small spots of light to be about 1.5° to 2.5° in diameter. Both were found medial to and above the area centralis. When a white disk (visual angle, 2°) before a gray background was moved into the center of the receptive field, the maintained firing was suppressed and remained so until the disk was removed. Upon removal of the disk there was no off-response characteristic of the off-center type of unit. The firing rate simply returned to the previous rate. When a