"Attention" Units in the Auditory Cortex

Abstract. In the course of examining single unit responses from the cortex of unrestrained and unanesthetized cats, we have come upon a population of cells that appears to be sensitive to auditory stimuli only if the cat "pays attention" to the sound source. We have described these responses, since they have not been previously reported and since they illustrate an important difference between the information which can be gleaned from experiments of this type and that obtained in the usual "acute" microelectrode experiment.

Cortical units that seem to be sensitive to auditory stimuli only if the subject "pays attention" were encountered in a series of experiments carried out on the auditory cortex of seven cats. The recording technique has already been summarized (*1*) and was as follows. Animals were prepared under anesthesia, with a small hollow plastic peg screwed into the skull over the cortical site to be examined. Several days later this peg was used to hold a hydraulic micropositioner containing a tungsten microelectrode (*2*). At the end of each recording session the holder and electrode were removed, and the cat was returned to its cage. The cats were studied for many hours during each of four to six recording sessions carried out over a period of 7 to 14 days. In each recording session the units were examined for periods of up to several hours, during which time the cat was free to move its head, groom, sleep, and so on.

Electrode sites were verified by marking the brain through the lumen of the peg with India ink, perfusing the cat with 10-percent formalin, and removing and photographing the brain. In this series of experiments it was not possible to measure the depth of the electrode accurately at the time of recording. All units, however, were located 5 mm or less beneath the cortical surface. From previous work (*2*) it is known that the electrodes used are capable of recording both from cell bodies and from myelinated fibers, but it was not possible to distinguish one from the other in these studies. Loud-speakers located near the cat's head were used to deliver the auditory stimuli. The frequency range from 50 to 50,000 cy/sec was adequately covered.

The following extracts from the protocol illustrate the peculiar behavior of these cells.

Cat 17. This unit studied for 1 hr 35 min showed little spontaneous activity. It could not be reliably driven by clicks, tones, or noise from the loud-speaker on repeated tests, although a new tone or noise might evoke responses during the first few presentations. When the experimenter entered the experimental room he discovered that a variety of natural stimuli could evoke responses provided the cat appeared to be paying attention to them. The unit responded briskly, for example, to (i) voice, (ii) squeaks emitted by squeezing a toy rubber mouse [Fig. 1], (iii) scratching fingernail on table nearby, (iv) hissing, (v) tapping the table. It responded regularly and consistently to clicks from the loud-speaker whenever the experimenter pretended to tap the loud-speaker in rhythm with the clicks but without actually making any sound. Passively closing the cat's eyes with the fingers did not stop the response when it was present. Discharge rate seemed to vary with the intensity of the stimulus and response frequently outlasted the stimulus by periods of up to about one second.

Cat 18. This unit was spontaneously active but could not be driven by clicks, tones, or noise from the loud-speaker. Keys jingled by the experimenters outside the room in which the cat was isolated evoked responses when the animal looked toward the door, but not otherwise. The experimenter then entered the room, picked up a small piece of paper between each thumb and forefinger and held his hands to the right and left of the cat about 12 inches away from its ears. When the paper was rustled in the right hand no response occurred until the cat looked toward it, whereupon a large burst of firing occurred so long as the sound was produced. If now the paper in the left hand was rubbed, nothing happened until the cat turned its head in that direction, whereupon again the unit responded to the sound. If the noise was made to alternate between left and right hands, responses occurred only to the sound produced by the hand toward which the cat was looking. Holding the hands out of sight did not change the result: so long as the cat looked in the proper direction the responses occurred. The unit was studied in this way for many minutes.

Six units of the sort just described were seen in four cats. At least nine other units, somewhat less intensively studied, should probably also be included, for they responded poorly or not at all to clicks, tones, or noise from the loud-speakers but responded well to sounds produced near the animal. Since the total number of units thus far studied is more than 100, about 10 percent can therefore be called attention units. As for the remaining 90 percent, it is not our purpose to discuss the behavior of these units in detail here, but it should be pointed out that some of them responded reliably for long periods to stimuli presented by means of the loud-speakers, regardless of the behavioral state of the animal (alert, asleep, and so on). Furthermore, one well-studied unit (in cat No. 24) was exquisitely responsive to 53-kcy/sec sound, from which we infer that our failure to drive other units with tones was not due to failure to generate high-frequency sounds. Finally, it has proved impossible to discover the stimuli adequate for driving many of our cortical units, a fact we cannot readily explain.

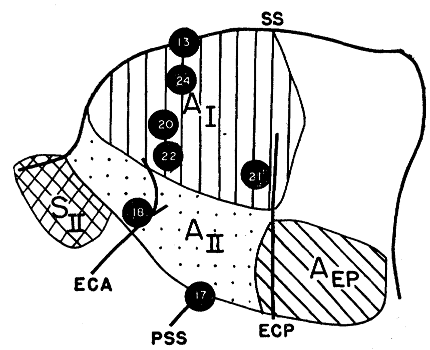

Fig. 2. Schematic drawing of the left auditory cortex of the cat, showing the location of electrode tracks in seven cats. A_I, A_{II}, and A_{EP} are the main auditory cortical areas.

The cortical loci thus far explored include A_I and A_{II} and their rostral and inferior borders with adjacent cortex (Fig. 2). Five punctures (cats Nos. 13, 20, 22, and 24) in approximately the center of A_I yielded no attention units, while three others (cats Nos. 13 and 24) did. In cats Nos. 17 and 18, where most attention units were found, cortex just in or just out of A_I and A_{II} seems to have been entered. The material, however, is still too scanty for us to settle the question of just where attention units occur in and near the auditory cortex.

We have in four punctures (three cats) encountered both attention units and conventional responders in a single electrode penetration. In three separate penetrations in cat No. 17, however, we encountered only attention units, or units not driven by the loud-speaker stimuli. These facts would make it appear that attention units are both interspersed among conventional responders and collected in isolation apart from

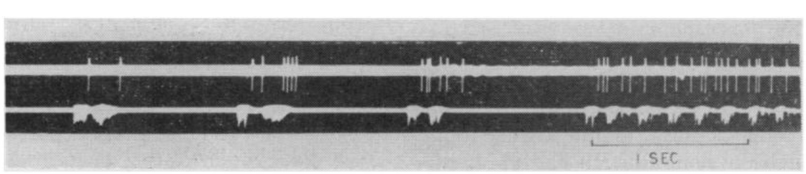

Fig. 1. Response of an auditory cortical unit in cat No. 17. Lower line shows response of a microphone located near the cat's ear; the deflections seen there were produced by squeaks emitted when a toy mouse was squeezed. The upper line shows the unit responding to the squeaks to which the animal was paying attention; this unit almost never responded to clicks, tones, or noise from a nearby loud-speaker.

them, but, again, this problem cannot be considered as settled.

According to Erulkar, Rose, and Davies (*3*), 34 percent of the units isolated in auditory cortex cannot be driven by sounds, and, in fact, only about 14 percent are reliably and securely activated by acoustic stimuli. The cats used by these workers were under light general anesthesia, and so it may be presumed that the attention units under discussion here were included in their class of nonresponders. It is not easy to understand why the auditory cortex, in the anesthetized or intact cat, should be populated with so many cells that fail to respond to auditory stimuli. Perhaps these cells become activated only when certain other conditions are simultaneously met. Thus, from our data one may conclude that the neural processes responsible for attention play an important role in determining whether or not a given acoustic stimulus proves adequate. Unfortunately attention is an elusive variable that no one has as yet been able to quantify. It may be that studies in which cortical unit activity is examined during the course of conditioning and learning will illuminate these matters.

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References and Notes

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Distribution of Radioactivity in Wheat Plants Grown in the Presence of Strontium-90

Abstract. Thatcher wheat grown in soil to which Sr^{90} had been added showed that accumulation of radioactivity in the kernels was about one-tenth the accumulation in leaves and stems. Experimental milling of the kernels gave brans with the largest amounts and flours with the least amounts of activity, the Sr^{90} concentrations being related practically linearly to the weights of total ash in the various milling products.

Because of the current interest in the possible contamination of plant products by strontium-90 from fallout from nuclear explosions, a study was made of the distribution of Sr^{90} absorbed from the soil by wheat plants (*1*). Single plants of the Thatcher variety were grown in individual pots in the greenhouse. Each pot contained 450 g of Saskatchewan Oxbow loam soil, the analysis of which showed 19.2, 6.5, 1.9, and 0.1 milliequivalents of exchangeable Ca, Mg, K, and Na, respectively, per 100 g of soil. The soil moisture was kept at its field capacity of 35 percent by daily watering throughout the period of growth of the plants. At various stages of growth, an aliquot of 1, 2, or 3 ml of a solution of $SrCl_2 \cdot 6H_2O$ (0.1 mg/ml) with Sr^{90} activity of about 2.5×10^6 count/min ml was added to the soil in each pot. The plants were harvested at maturity and separated into kernels, heads, leaves, and stems. Some of the kernels were reserved for milling studies. The remaining fractions, each containing 5.0 mg of added inactive strontium chloride as carrier, were wet-ashed with concentrated sulfuric acid and perchloric acid.

After practically all the excess mineral acids had been evaporated off, each residue was taken up in water, neutralized, and made slightly basic before the strontium was precipitated as strontium phosphate. The precipitate was collected by centrifugation, transferred to a sample pan, and dried, and the activity was counted. Standard samples were prepared in the same way by wet-ashing fractions of nonradioactive wheat to which known quantities of Sr^{90} were added. From such standard samples, the Sr^{90} activity originally introduced into the soil was ascertained, and the uptake of Sr^{90} by various parts of the wheat plant was calculated. The results, summarized in Table 1, indicated that under the conditions of these experiments, the accumulation of Sr^{90} in the kernels was only a few thousandths of 1 percent of the amount added to the soil, while the uptake by the leaves or stems was about ten times as high as the uptake by the kernels. This is in agreement with findings of other workers (*2*) that Sr^{90} taken up from the soil by various types of plants generally appeared in high concentration in leaf tissues and in low concentration in seeds.

It is of interest to determine what portion of the Sr^{90} in the wheat kernels would appear in flour, the product consumed by man. Two crops of kernels from these experiments, each weighing about 7 g, were experimentally milled to give flour, shorts, and bran. The mill used was one similar to that described by Geddes and Frisell (*3*). The radioactivity and ash of the three milled fractions from each crop were measured. The flours contained 9 and 16 percent, the shorts, 29 and 31 percent, and the brans, 62 and 53 percent, respectively, of the total activity of the two crops. Though the flour fraction had the highest weight, it contained the least radioactivity. The largest portion of the activity was found in the bran. This is not surprising since the bran has the highest level of mineral matter, as is indicated

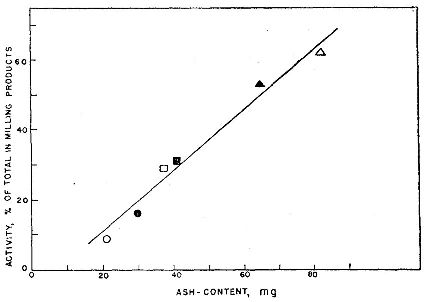

Fig. 1. Relationship between total ash and Sr^{90} concentration in milling products of Thatcher wheat. Circles, squares, and triangles represent flours, shorts, and brans, respectively—open symbols, crop 1; closed symbols, crop 2.

Table 1. Uptakes of Sr^{90} by various parts of Thatcher wheat.

Duration of Sr^{90} in soil before harvest (days)	Av. uptake of added activity (10^{-3} percent)			
	Kernels	Heads	Leaves	Stems
73*	2.9	2.3	30	14
73†	2.2	1.4	19	10
44‡	1.6	2.0	21	38
29‡	1.1	2.5	9.5	33

* 1 ml of Sr^{90} solution added per plant.
† 2 ml of Sr^{90} solution added per plant.
‡ 3 ml of Sr^{90} solution added per plant.

by its ash content. Actually, there was a direct relationship between Sr^{90} activity and total ash in the milling product—namely, the higher the total ash, the greater the Sr^{90} concentration (Fig. 1). One of the criteria of a high-grade patent flour is its low ash content. The results given here would indicate that one may reasonably expect that possible contamination by Sr^{90} from uptake of fallout debris should be lower for higher-grade flours.

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References and Notes

1. This work was supported by the Saskatchewan Research Council and the National Research Council of Canada.
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