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Auditory Specificity in Unit Recordings from Cat's Visual Cortex

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A substantial percentage of cells in the primary visual cortex of the cat can be activated by nonvisual stimuli. Twenty-five cells were studied in detail in five cats and their responses to visual and acoustic stimuli tested. While all units could be activated by visual stimuli, seven of these responded to visual and acoustic stimulation. Analysis with frequency-modulated tones showed that these seven units were responsive to specific parameters of the sound stimuli. Two-dimensional maps done with a small disc on a contrasting background showed that these units have, in addition, visual receptive fields.

Introduction

A number of researchers have provided evidence that multisensory effects can be shown in the lateral geniculate body (11, 18) and in the primary visual areas (3, 6, 7, 9, 10, 14–16, 19) of the cat's cortex. The physiological significance of activity of nonvisual origin in the visual system is not clear: thus, signals could reach the visual system as part of a diffuse activation of the entire brain, or impinge on the visual system only, possibly together with some other specialized locations, to produce activation restricted to the visual system. A further possibility, which would be of considerable theoretical importance, is that the signals may provide specific information of a nonvisual origin to the visual system. If the last possibility is indeed the correct one, it would be likely that the nonvisual signals arriving at the visual locations would display specialized characteristics of the stimulus rather than some generalized presence or absence function.

The present investigation was undertaken to explore directly this possibility. At the same time the question was posed whether such signals of nonvisual origin converge onto cells that display well-organized visual receptive fields. The auditory system was chosen because of the relative ease with which highly precise control of the stimulus parameters can be

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automated. The method for mapping was developed from that devised to display visual receptive fields that has been described (24, 25).

Method

Twenty-five units were studied in five cats. Unit activity was recorded with tungsten microelectrodes directly attached to a solid-state source follower connected to a microdrive (23). A Schmidt trigger was used to generate a standard pulse that was then fed to a computer. The sensitivity of the Schmidt trigger was set so that only spikes that were clearly above noise level would be selected. The units described in the present study were recorded from primary visual cortex (20) in the posterior marginal gyrus, about 0.5–1.5 mm from the medial border, anteroposterior 0 in the HC coordinates; the microelectrodes were inserted no deeper than 2 mm from the surface of the cortex. Surgery was performed under Halothane anesthesia and kept to a minimum. An incision was made in the skin over the skull and a small hole opened in the skull and dura. A small polyethylene catheter was inserted in the radial vein; the trachea was intubated to allow artificial ventilation. The animal was then immobilized with Flaxedil (gallamine triethiodide, 50 mg/hour), placed in a stereotaxic apparatus with hollow ear bars and artificially ventilated (constant-volume pump 50 ml, 20/min). All incisions and pressure points were infiltrated with a long-acting local anesthetic (Zylejectin) and anesthesia was discontinued.[2] Contact lenses were used to protect the cornea and correct for accommodation. In a few experiments, eye movements were monitored during the auditory mapping by a method similar to the one described by Rodieck *et al.* (21).

Each unit recorded was first tested briefly for responsiveness to visual stimuli by moving a black disc on a white background; all units responded to this stimulus, most of them binocularly.

A small general-purpose computer (PDP–8) was used to control stimulus displays and data collecting and processing. A sine-wave generator was used to produce the acoustic signal. The frequency of the generator could be voltage controlled (F voltage) from 0 Hz to 15 kHz; similarly the output amplitude of the generator was controlled by a voltage (A voltage). These two voltage functions were generated by the PDP–8. The output of the generator was fed to an Altec 802D transducer and the sound stimuli conducted to the left ear of the animal through an appropriately dampened hollow ear bar. Twenty-five test frequencies were presented in the following fashion: the frequency of the sine-wave oscillator was (*a*) raised from 0 to test frequency 1 in 300 msec (F on); (*b*) held

[2] When used on human patients this drug has been found to remain active for several days.

steady for 300 msec (F steady); (*c*) brought back to 0 in 300 msec (F off); this was followed by a 300-msec period of 0 frequency (no sound). This procedure was repeated for test frequency 2, 3, 4–25. All of the above was then repeated 25 times. The number of spikes produced by the unit under examination during each F on, F steady, F off, and no sound period were counted and stored separately. The effect of the A voltage was to control the output amplitude of the sine-wave generator in such a way that the same sound pressure was obtained for all test frequencies. The intensity of the sound was set at 100 db (referred to 0.0002 dyne/cm^2) for the first few maps; when possible, units were also mapped at 80 db. Ambient noise was equal to 60 db. All these measurements were done with a B & K sound-level meter from a minimal-volume coupler attached to the end of the ear bar.

At the end of the procedure the computer memory contained 25 sets of four values for each of the 25 test frequencies. A separate total for the F on, the F steady, the F off, and no sound for each of the 25 frequencies was also obtained. The final result then consisted of four histograms (Fig. 1) that are presented one after another. On the *y*-axis, common to all, is the total number of spikes produced in the 25 presentations of each frequency; in the first histogram the spikes were produced while the frequency was swept from 0 to each of the values read on the *x*-axis, in the second, while each frequency was held steady, in the third, while the frequency was swept to 0; the fourth represents the totals of equivalent periods of spontaneous activity collected after each frequency presentation. This fourth histogram is extremely useful in detecting systematic changes in spontaneous activity that could be interpreted as caused by the stimulus. These sums and the individual values were displayed on an oscilloscope for inspection and then stored on digital tape for subsequent statistical analysis. Some of the data were also collected in analog form on magnetic tape for the purpose of obtaining post-stimulus histograms. If the unit proved to be specific to one or more of the test parameters, the visual receptive field of the unit was also mapped.

Results

Of the 25 units thus analyzed, seven showed relatively restricted responses to one of the auditory stimulus parameters. Figure 1 shows one of these units that was mapped five times. The collection and storage of one of these mapping runs requires about 20 min. The five sets of histograms therefore, show the long-term (100 min) behavior of this unit. A number of things are immediately apparent: (*a*) There are slow fluctuations in the level of spontaneous activity expressed as different mean backgrounds. (*b*) The maximal responsivity of the unit is 1175 Hz (test frequency 11).

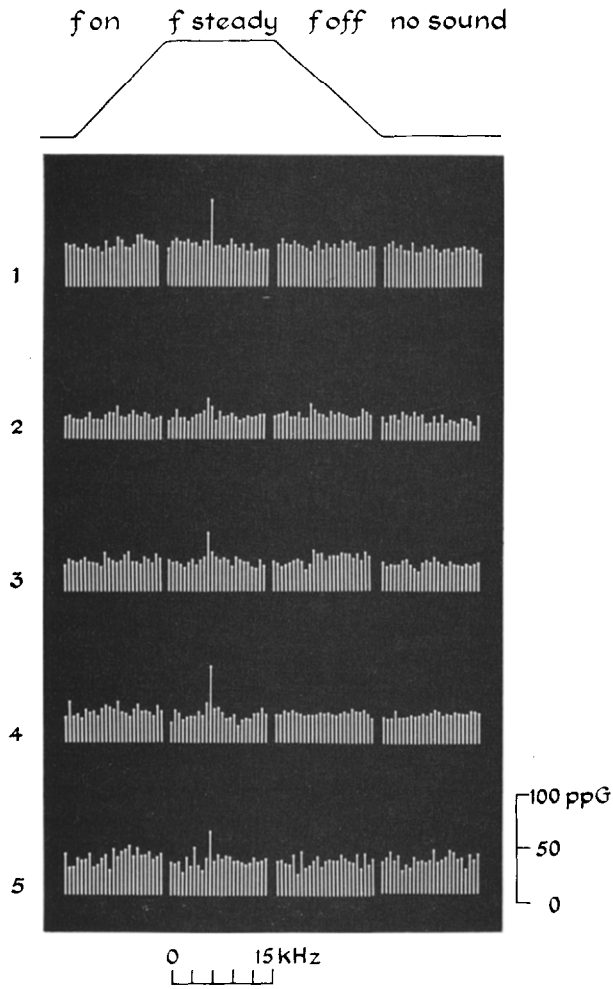

FIG. 1. The five sets of histograms in this figure were obtained from the same unit at about 20-min intervals. Note in the F steady column the peak of activity at test frequency 11 (1175 Hz). On the x-axis the frequency calibration is equal to: 500 Hz at the second mark, 1175 Hz at the third mark, 2750 Hz at the fourth mark, 7000 Hz at the fifth, and 15,000 Hz at the sixth. Cumulative spike count on the y-axis. See text for details.

(c) The point of greatest response does not fluctuate from run to run, even though the size of the response may vary. (d) The unit does not respond to onset or offset of frequency but only to the steady test frequency. This last point is of interest (see also unit 3) because onset frequencies higher than 1175 Hz contains this frequency. Clearly this unit can differentiate between these two conditions. Figure 2 shows four other

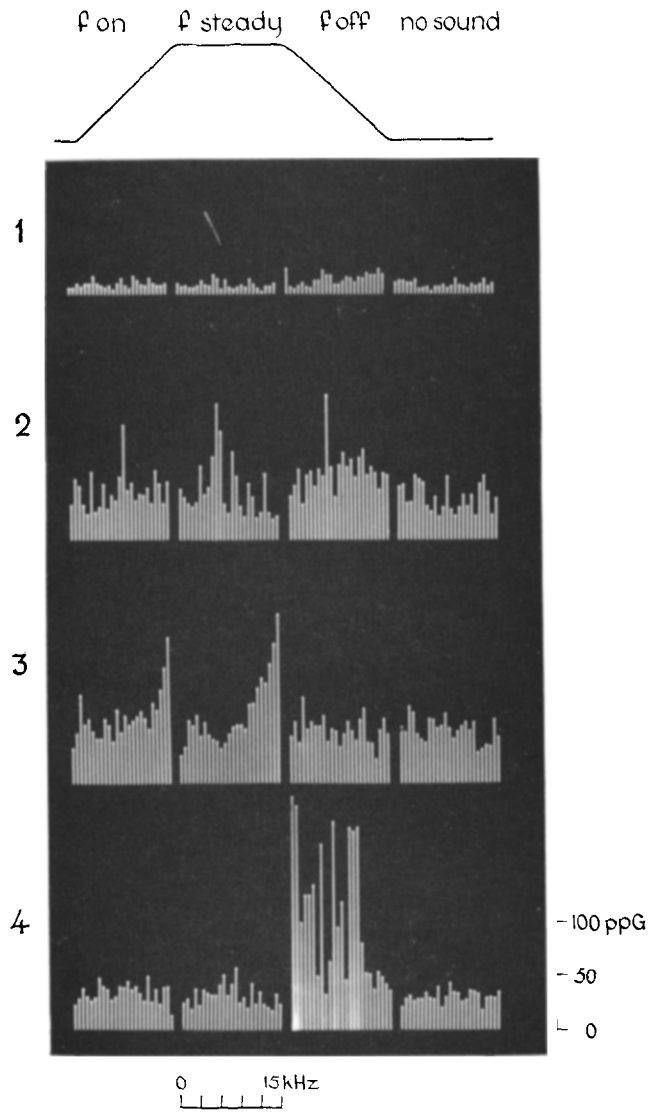

FIG. 2. In rows 1, 2, 3, and 4 are displayed the response histograms to modulated frequencies from four different units. Higher firing rates can be seen to some specific aspects of the stimuli in units 2, 3, and 4.

units. Unit 3 responds best to the higher frequencies, both at onset and steady but not at off; unit 2 shows frequency specificity for onset, steady, and off frequencies. Unit 1, for comparison, is a unit that had no response to sound.

Figure 3 shows two post-stimulus time histograms from the same unit

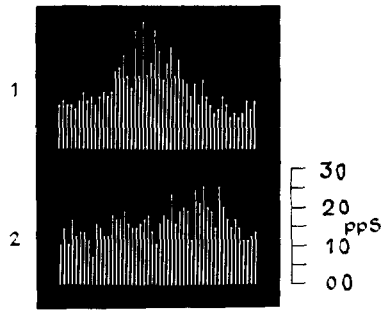

FIG. 3. In row 1 is shown a response histogram to 1175 Hz. Cell activity in pulses per second on the y-axis (time 200 msec total) on the x-axis. In row 2 is shown a response histogram to 2025 Hz. A clear response is visible in 1 but not in 2. Same unit of Fig. 1.

of Fig. 1. In "1" the computer is triggered at the beginning of the steady period for 1175 Hz in "2" at the beginning of the steady period for 2025 Hz; cumulative counts of unit firing are on the y-axis, time on the x-axis. It can be seen that there is a clear response to 1175 Hz with a latency of about 60 msec and no response to 2025 Hz. This latency is comparable to the latencies of click-evoked response in visual cortex units found by Murata, Kramer and Back-Rita (19).

The visual receptive fields of these cells were mapped with a black 0.5 degree disc on a white background (reflectance for the black 3%, for the white 75%), with the disc moving vertically. In general such fields proved to be more diffuse than the receptive fields of cells responsive only to visual stimuli (Fig. 4). In some cases averaging had to be used to increase the signal to noise ratio. Yet there is no question that these units did have, by the definition given by Hartline (8), visual receptive fields.

In interpreting these results the possibility of artifacts must be considered. The possibility of eye movements and pupillary changes were excluded by Murata *et al.* (19) because the preparations were atropinized and curarized. Blood pressure changes were excluded because of their long latency (1–2 sec), slow onset and decay (10 sec), and rapid habituation. The size of these changes was also usually limited to less than 5 mm Hg. Hypothetical visual stimuli accompanying nonvisual stimuli were excluded by trials in absolute darkness. In our experiments the animals were also atropinized and curarized, but it has been reported that even large doses of Flaxedil leave some small slow residual movements of the eyes (21). This aspect needed to be checked and the eye movements for five units (the unit in Fig. 1 is one such) were recorded. The movements measured in these units were less than 0.5 deg, appeared very infrequently and sporadically, and did not have any relation to the frequency that elicited

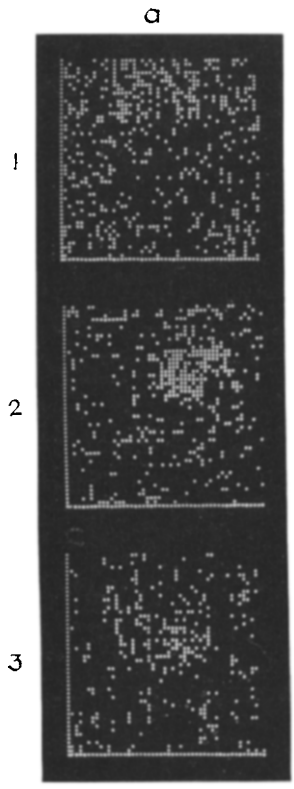

FIG. 4. In rows 1, 2, and 3 the visual receptive fields of units 2, 3, and 4 of Fig. 2 are shown. X-axis and y-axis are equal to 25 degrees of visual angle. The visual axis falls approximately at the center of the display.

response. A few maps were also obtained in the complete absence of any movement. The specificity of any given unit for a different test frequency and the stability of such specificity also speaks against these residual movements as a possible source of artifact. There was no correlation between such residual movements and the responsiveness to auditory stimulation.

Discussion

A feature that distinguishes ganglion cells from geniculate and cortical cells is the greater "irregularity" of the spontaneous activity of the cortical and geniculate units; this has been noted also by other authors (1, 12, 17). It would seem that levels and type of background are influenced by the "state of the animal," i.e., sleep versus nonsleep (1, 12, 13). It was therefore deemed necessary to have a systematic check of the "spontaneous activity" of the units studied for statistical analysis.

Statistical analysis consisted of an analysis of variance applied to the four sets of 25 × 25 values represented in the histograms. Thus, the group size was 25 and the n within each group was 25. After establishing that there was no significant difference between the 25 × 25 background groups but that the null hypothesis could be rejected for one or more of the test groups, a t test was run on the individual values between the group showing auditory frequency specificity and a randomly selected group. For all units that were classified on inspection as frequency specific, the differences observed were significant at the 0.01 level except for the difference shown in 2, Fig. 1, which was significant at the 0.05 level.

The question arises as to the possible physiological significance of the data. It is possible to assume that the activity induced by auditory stimuli, even though correlated with specific stimulus parameters, is not "used" by the visual cortex and should be considered as "noise." If this is the case, a severe burden would be put on the visual information processing mechanisms. What one would expect then is that at some later stage this "noise" would be filtered by some mechanism. In other words, some nonlinear mechanism should be found that would progressively filter, i.e., fire only to aspects of the visual image irrespective of what is going on in the other sensory systems. The evidence seems to be just the opposite: nonvisual stimuli affect the activity of ganglion cells only minutely (22, 23, 25); they affect that of the geniculate cells to a greater extent (18) and very markedly affect cortical cells (19). Even more interaction appears to be present in prestriate cortex (4).

Each sensory system, and the visual system in particular, has to cope with the mobility of its receptor surface as well as of the stimulus in tridimensional space. This mobility is such that, in essence, a given object in visual space will rarely produce identical images on a given retina twice.[3] While retinal images of the same object will be somewhat similar, too much variability would be present to allow some simple recognition mechanism. A variety of schemes have been developed to cope with these difficulties. Thus Jung interpreted the activity induced in visual cortex cells by vestibular stimulation as necessary or at least useful for the correct processing of visual stimuli. While the significance of the presence of auditory information in visual cortex is not as intuitively obvious, these results combined with those of others (2, 14, 19) seem to indicate that intersensory, as well as intrasensory processing are proceeding concurrently. Further research is needed to elucidate the nature of the integration.

[3] Consider, e.g., that a moving object can be projected along three axes or rotated along three axes, or both, with the added complication that translations along the axis are accompanied by considerable changes in the size of the retinal image. In addition, the retina itself can be moved and rotated depending on eye position and body position.

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