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Final Report AFOSR F44620-67-C-0030

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Sensory Properties of Some Units in the Tectum of the Frog

Histological studies have revealed more or less distinct alternating cellular and plexiform layers in the optic tectum of the frog (Ramon, P. Bibliog. anat. 1896, 4. Cited from S. R. y Cajal, Histologie du Systeme Nerveux de l'Homme et des Vertebres, Vol. 2. Maloine 1911; Larsell, O., J. comp. Neurol. 1929, 48). Starting from the inside, the first layer is a single row of columnar cells lining the optic ventricles and recognized as ependymo-glial cells. The ependyma is immediately followed by three thickly packed neuronal layers numbered from inside to outside, 2, 4, and 6 and separated by two thin plexiform sheets numbered, respectively 3 and 5. This region is considered the principal cellular or granular layer of the frog's tectum. The seventh layer is again a plexiform sheet composed of a thick band of medullated fibers which separates the granular zone from the superficial neuropil formed by layers 8 and 9 according to Larsell (J. comp. Neurol., 1929, 48), or 8 to 15 according to P. Ramon (Bibliog. anat. 1896, 4). These authors studying the fine structure of the frog's tectum have observed that the optic axons end in the superficial neuropil which occupies the more superficial half of the frog's tectum. Lettvin, Maturana and co-workers (J. gen. Physiol. 1960, 43), studying the function of retinal ganglion cells, have described four major groups of optic fibers that reported to the superficial neuropil of the frog's tectum. They have also shown (in Sensory Communication, ed. by W.A. Rosenblith, New York, Wiley, 1961) two kinds of cells in the granular layer that receive impulses from the optic fibers. One of these cells detects novelty in visual events ("newness" neurons), and the other one is concerned with continuity in time responding to the same object in the visual field ("sameness" neurons).

In the present study we have examined the discharge of units that lie deeper in the granular layer, close to the ependyma, and which seem to belong to layer 2 according to the terminology. These units respond in an interesting way to sensory stimuli.

In the course of this study we used the American frog, Rana pipiens. Frogs were paralyzed with tubocurarine (Squibb) injected in the lymphatic

sacs, pinned on a cork board and regularly moistened with water. In order to expose the tectum the bone of the top of the skull, the dura mater, and the arachnoid were removed. Mineral oil was added to prevent drying. The recording electrode consisted of a metal-filled micropipette with gelatinized platinum black tip (Geateland, R.C., et al., Proc. Inst. Radio Engin., 1959) of 1μ to 5μ in diameter. After amplification, signals were monitored on a cathode-ray tube and a loudspeaker and recorded.

During each penetration, once the electrode had been placed on the granular layer, a variety of natural stimuli were tested for a possible influence on the activity of each unit. Natural stimuli used more commonly were somatic (light and brief touch, prolonged pressure or air blown over the surface of the body), visual (movements of various objects, such as the hand or a black or white 1 x 1-inch card, before the eyes, light flashes or sudden changes of the room illumination), acoustic (voices or claps) and vibrational (tapping the table or the microscope framework). Receptive fields were measured in the somatic and visual spheres. In the visual field one method was coarse and consisted of identifying the part of the visual field in which movements of an object provoked a response.

As the electrode, placed deeper than the fourth layer of optic terminals (Maturana, H.R. et al., J. gen. Physiol. 1960, 43) penetrated through the granular layer, it began to record from tectal elements of this region. These units responded only to visual stimuli, and the great majority behaved like the "newness" and "sameness" neurons described by Lettvin and co-workers (in Sensory Communication, ed. by W.A. Rosenblith, New York, Wiley, 1961). If, once the ependyma had been reached (as determined by an increase in resistance, measured by noise level), the electrode was pulled back very slowly, immediately it began to record again spike activity. When this point was reached, it could only mean that the tip of the electrode had been placed on the second layer of the tectum. That is, the neuronal layer that lies immediately above the ependymo-glial region.

In the present study 120 units placed in this particular area were examined. Each one of these units showed convergence involving three kinds of stimuli: somatic, visual and vibrational. None of these elements seem to respond to voices or claps. The most frequent response to a brief stimulus of any sort, such as movements of an object, touch or vibration, was a

short burst of spikes followed in some cases by a pause. When prolonged stimuli were applied, the response was generally an initial acceleration followed by a decline to the pre-stimulus rate, even if the stimulus was not removed. The time taken for this return usually varied between some m sec. to 20 sec. Six units did not respond in this way. In these units somatic and vibrational stimuli always evoked a slowing of the spontaneous activity and the visual one an acceleration.

Responsiveness to somatic stimuli was widespread, covering one-half to all the skin surface. Analysis of the field size indicates a predominance of elements whose somatic fields covered all the skin surface (103 units). Unilateral fields were found to be ipsilateral in 10 units and contralateral in 7 units.

The distribution of the sensitivity throughout the field was not always uniform and sometimes units were reliably accelerated by weak stimuli in one-half of the body, or in a localized small area of the field, and gave only weak responses in the other regions. Moreover, a few number of elements were excited by touching one side of the body and inhibited by touching the other side.

In the visual modality responsiveness to stimuli was also widespread. Each of these units sees all the four quadrants of the visual field. Therefore, wherever the hand or the target was moved, there was a burst of impulses followed by a decline or a pause if the object was kept still for some seconds, or if it was removed. As in the somatic field, the distribution of the sensitivity was not uniform and, sometimes, there was a place in the visual field where movements of the object gave a strong response, while in other regions only weak discharges were obtained. Units were not especially sensitive to contralateral visual stimuli. In 20 elements both contralateral and ipsilateral visual fields were investigated. Seven units were excited from both fields, eleven from the contralateral field and only two from the ipsilateral side. Other visual stimuli, such as a flash of light or a sudden change in the room illumination were also effective in a great number of cases. That is, individual elements in the frog's tectum showed a great convergence to different stimuli. However, such a description does not show the most interesting aspects of these convergences. When a stimulus had been found which activated a unit,

repetitive presentation of such stimulus was associated with a gradual attenuation of the response. The response to the first stimulus was always brisk, but the response gradually became less vigorous with successive presentations of the stimulus. If after the response has weakened in this way, the stimulus was withdrawn for sometime and then re-presented, a response was usually elicited once again. The time course of attenuation varied from one unit to another. In most cases the response was reduced or had disappeared after three or four stimuli. In some cases, however, there was a slow attenuation during successive trains of stimuli. Generally, the response to the first stimulus became smaller, and then they attenuated more rapidly with each succcssive train.

Generally, a unit which had failed to respond after repeated presentation of a given stimulus could be made to respond to another stimulus to which it was sensitive, or to stimulation of another region of the somatic or visual field. Return of the response after attenuation could be obtained after a pause of 20 sec. or more, or if another kind of stimulus was interposed.

Tectal units showing convergence involving different kinds of stimuli were observed before in the tectum of cats (D. Jassik-Gerschenfeld, Nature, 208, 1965) and rabbits (Horn, G. and Hill, R.M., Nature, 202, 1964). Attenuation of the response to a brief stimulus as a result of repeated presentation has also been reported in the tectum of rabbits (Horn, G. and Hill, R.M., Nature, 1964, 202) and cats (Huttenlocher, P.H., J. Neurophysiol., 1961, 24). Groups of fibers such as those found in the frog optic nerve and superficial neuropil of the tectum (Maturana et al., J. gen. Physiol., 1960, 43) that responded to a restricted class of stimuli and to which it seems possible to assign a specific perceptual role, have not been found in this region of the tectal granular layer of the frog. The particular behavior of the units described in this study with any stimulus which loses its novelty strongly suggests a great sensitivity to change. These responses might be presumably concerned with detection of sudden changes in the frog environment.

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13. ABSTRACT

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