

the animal being artificially respired during that period.

The animals were supported stereotactically, the stimulated eye in each case being refracted and fitted with a contact lens to protect the cornea from drying and to bring the retina into conjugacy with the 57 cm distant testing plane. Stainless steel micro-electrodes were introduced into the visual cortex and superior colliculus through an agar sealed skull aperture.

Once localized in visual space, the receptive field of each cell was mapped through the neutralizing refractive correction for that axis in space, using the most commonly optimal stimulus conditions (a flashing 1 sec on, 1 sec off, $1/2^\circ$ diameter, 4.1 cd/m² light spot against a 0.03 cd/m² background). Occasionally, when as described in these results, a cell responded best to other stimuli, e.g., movement of a black edge against an 8 cd/m² background, those more optimal stimuli were used to map the field. The receptive field was then replotted for each of a series of spherical (plus power to induce myopia; minus power to induce hyperopia) refractive errors by centering the inducing lenses on the receptive field axis.

Recording sites were later confirmed by Prussian blue marks localized in frozen sections made of each brain.

The Figure shows, for a photically responsive midbrain cell (in the stratum opticum of the superior colliculus), spike totals integrated over 30 sec periods during which time a black edge was passed through its receptive field from alternate directions once each second at the cell's optimum response velocity of 12°/sec. Figure A shows the actual spike totals resulting from this stimulus procedure as they were recorded over a wide range of eye focus conditions. Figure B shows this same data, after the maintained discharge of the cell was linearly corrected for drift (i.e. based on the spike totals over 30 sec intervals without the moving edge present), using the following model⁷:

$$R = N - \left[S_0 + t \left(\frac{\Delta S}{Q} \right) \right].$$

Figure C represents the maximum case (calculated by the model above) of transient response distortion due to the maintained activity drift of this cell, which could have resulted from taking the data in the particular sequence indicated in the Figure.

The fundamental assumption where such a correction model is applied is, of course, that linearity of the maintained activity drift is essentially constant over the testing period encompassed⁸. In the case of the particular cell illustrated in the Figure, one test applied was to repeat the first focal condition (i.e. perfect sharpness of the retinal image) once again at the end of the entire focal series. As can be seen in Figure B, the consistency of the corrected response (using the linear model) was

within 2% of the original response to that condition measured 12 min previously. This was so, even though the maintained background activity had increased by more than 50% over that same period of time, from 22 up to 34 spikes/sec.

Two conclusions might then be supported from these observations: first, that the gain functions of the transient signal activity and of the background activity need not be rigidly tied⁹, and second, that the 'analyzer(s)' of total spike activity, making up such a channel as described here, may well be doing a similar kind of correction (linear, sinusoidal or of some other more complex form) in order to preserve the quantitative integrity of the transient signal code. Such a correction however would seem to require, as here, a close comparative cognizance of both signal and maintained activity at any particular time.

Zusammenfassung. Die fokalen Reaktionen der photischen Zellen auf durchgehende Anregungen erwiesen sich als quantitativ gleichmässig, dies sogar bei wechselnd gehaltener Aktivität.

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⁷ R is defined as the specific response to the transient stimulus presented (i.e. the moving black edge during a particular focal condition), N is the total number of spikes counted during the sampling interval (i.e. 30 sec here) S_0 is the rate of the maintained discharge just previous to starting the stimulus sequence described, Q is the number of intervals within which stimulus-response counts (one for each focal condition) were made, these intervals all being of equal length, t , and evenly distributed in time, and ΔS being the net increase of the maintained discharge rate over the entire experimental period, i.e., from just before the t_1 interval for the first focal condition to just following the t_Q interval for the last focal condition tested.

⁸ Rather than a linear drift, some cells do show sufficiently cyclic patterns of their maintained discharge that such activity can be described, and thus neutralized, using a basic sinusoidal model of the form:

$$R = N - \left[S_0 + A \sin \left(\frac{2\pi}{T} \cdot t \right) \right]$$

in which A is the sinusoidal amplitude (in spike frequency) and T is the sinusoidal period. t here is elapsed time and all other terms are defined as previously.

⁹ H. SUZUKI and E. KATO, *J. Neurophysiol.* 29, 909 (1966).

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Pineal Body: Neuronal Recording

In recent years interest in the pineal body (PB) has increased considerably. The PB has now been shown to be an endocrine controlling organ¹. It is likely that it controls the peripheral organs of internal secretion by a mechanism which involves the conversion of 5HT (serotonin) to melatonin².

Histological and electron microscopic (EM) studies on the cytoarchitecture of the PB are controversial. KAPPERS³ reported that in the rat, the majority of nerve fibres

enter bilaterally from the superior cervical ganglia via the nervi conarii, while only aberrant fibres were observed coursing up the epiphyseal stalk. However, in other mammals definite habenular innervation has been

¹ J. AXELROD, *Science* 184, 1341 (1974).

² H. WEISSBACH, B. G. REDFIELD and J. AXELROD, *Biochim. biophys. Acta* 43, 352 (1960).

³ J. A. KAPPERS, *Z. Zellforsch.* 52, 163 (1960).

demonstrated⁴. WOLFE⁵ reported that the predominant (90%) type of cell in rat PB is parenchymal glandular (pinealocyte). WURTMAN et al.⁶ demonstrated in several mammals synaptic processes and PELLEGRINO DE IRALIDI et al.⁷ reported that the PB has an orthosympathetic innervation coming bilaterally from the superior cervical ganglia via the transverse sinus. Nerve fibres mainly follow the perivascular space and end free around the capillaries or in loose association with the pinealocytes⁷.

Despite many cytological, neurochemical and neuropharmacological studies, there are only a few studies concerning the electrophysiological properties of this structure, two on EEG activities^{8,9} and one on field potentials¹⁰. Since neuronal elements were observed electron microscopically in rat PB, initial attempts were made to record the spontaneous activity from single neuronal units by using microelectrodes technique.

The electrophysiological experiments were carried out using 30 Holtzman male rats weighing 250–350 g. The rats were anesthetized with urethan (1.2 g/kg) and secured in a stereotaxic instrument. Glass micropipettes (10–30 M Ω) and nichrome semimicroelectrodes of 50 μ m (60–80 K) in diameter were used to record the spontaneous unit activities¹¹. The electrodes were attached to a hydraulic microdrive which permitted penetration in increments of 1 μ m. The PB was surgically exposed, and the electrodes were placed by direct observation. Spike discharges were amplified by Grass P511 AC preamplifier, monitored on Tektronix storage oscilloscope and were recorded on a magnetic tape recorder. Only in the first 200 μ m below

the surface was it possible to observe spike activity (Figure 1).

When micropipette electrodes were used, the spike discharges were accompanied by high voltage, long duration waves (Figure 1, A and B). However, when 50 μ m electrodes were used for recording, only spike activity was observed without the other waves (Figure 1, C and D). No more discharges were observed by advancing the electrodes. Upon approaching the inferior surface of the pineal, however, the base line became more noisy and unstable, irregular spikes of low amplitude (40–80 μ V) and long duration (3–5 msec) appeared. When the electrodes were advanced further and reached the colliculi, the base line activity changed and became less noisy and clear spikes (ratio to noise) became evident.

When a stable spike was detected, the spontaneous activity during 210 sec was recorded and then varieties of input (Photic [210 sec of constant illumination provided by surgical lamp 1.5 m from the animal], Amyg, MFB and Hab stimulation [200 repetitive square wave pulses of 0.2 msec duration every 1.1 sec at 3–5 V] were tested). The average spontaneous firing rate for 43 units is summarized in Figure 2. From the distribution of the frequency histogram (Figure 2), it seems that the neuronal discharges exhibited a wide range of firing rates, of which the greatest proportion demonstrated a low frequency. The responsiveness to the various modalities of stimulation was high (70–80%). Amyg, Hab and MFB stimulation resulted in approximately $1/2$ the responsive units increasing their firing rate and $1/2$ decreasing their firing rate, while photic stimulation resulted in $3/4$ of the units increasing their firing rate. In conclusion, the present studies have been able to demonstrate for the first time that the PB exhibits spontaneous spike discharges which could indicate the existence of several functional neuronal elements. Moreover, these spontaneous activities were altered when a variety of inputs were used. The present experiment also supports the neuropharmacological studies which indicate that the PB has neurotransmitter activities^{12–14}.

Zusammenfassung. Im corpus pineale der Ratte konnte bis zu einer Tiefe von 200 μ m spontane Aktivität einzelner neuronaler Elemente nachgewiesen werden. Diese reagierten auf Photostimulation, Stimulation der Habenula und des Fasciculus medialis.

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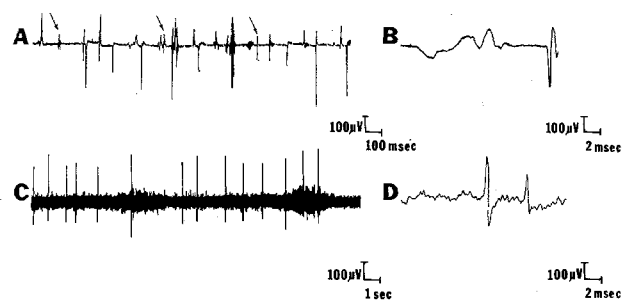


Fig. 1. Spontaneous unit activity recorded from pineal body: A and B glass micropipettes, the arrows indicate neuronal spike activity; C and D recording with semi-microelectrodes (50 μ m).

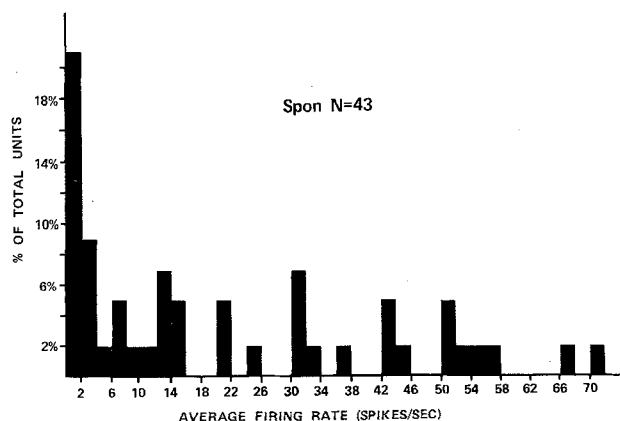


Fig. 2. Frequency histogram of the average firing rates (spikes/sec) of 43 units recorded from the PB.

⁴ G. DAVID and J. HERBERT, *Brain Res.* 64, 327 (1973).

⁵ D. E. WOLFE, in *Progress in Brain Research* (Eds. J. A. KAPPERS and J. P. SCHADÉ; Elsevier, Amsterdam 1965), vol. 10, p. 332.

⁶ R. J. WURTMAN, J. AXELROD and D. E. KELLY, *The Pineal* (Academic Press, New York and London 1968), p. 1–45.

⁷ A. PELLEGRINO DE IRALDI, L. M. ZIEHER and E. DE ROBERTIS, in *Progress in Brain Research* (Eds. J. A. KAPPERS and J. P. SCHADÉ; Elsevier, Amsterdam 1965), vol. 10, p. 389.

⁸ A. N. TAYLOR and R. W. WILSON, *Experientia* 26, 267 (1970).

⁹ S. SCHAPIRO and M. SALAS, *Brain Res.* 28, 47 (1971).

¹⁰ R. MCCLUNG, N. DAFNY and S. J. STRADA, *Soc. Neurosci.* 3, 365 (1973).

¹¹ N. DAFNY and S. GILMAN, *Brain Res.* 59, 243 (1973).

¹² R. J. WURTMAN, J. AXELROD, G. SEDVALL and R. MOOR, *J. Pharmac. exp. Ther.* 147, 487 (1967).

¹³ M. BROWNSTEIN and J. AXELROD, *Science* 184, 163 (1974).

¹⁴ We thank Dr. S. J. STRADA for his helpful comments and suggestions.