

also in the frog the density of the neurotubules at the level of the spinal roots proved to be lower in dorsal root fibres than in ventral root fibres. However, in the frog equal numbers of neurotubules were found in motor and sensory fibres immediately distal to the spinal ganglia. We have now found considerably higher tubular densities in rat saphenous nerve fibres than in MGN fibres of comparable sizes. This fact suggests an even more pronounced difference in the content of neurotubules between motor and sensory fibres of rat peripheral nerves, with lower values for motor nerve fibres than those presented for MGN in Table I; for it has to be taken into account that muscle nerves like the MGN contain a considerable percentage of sensory nerve fibres which could not be excluded by our sampling technique.

Zusammenfassung. Es ergab sich, dass die Neurotubulsdichte in den Axonen eines Hautnerven (Ratte, N. saphenus) klar höher ist als in gleich dicken Fasern eines Muskelnerven (N. gastrocnemius med.). Ein weiterer Befund leistet einen Beitrag zur Erklärung dieses Gegensatzes: Die Neurotubulsdichte in den peripheren Neuriten primärer sensibler Neurone unmittelbar distal des Spinalganglions (L_5) ist signifikant höher als in den zentralen Neuriten in Höhe der Hinterwurzel.

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Visual Cell Coding: Factoring Dioptric Responses from Maintained Discharge

Maintained discharge, common throughout the visual system, has long fascinated and frustrated investigators¹⁻³. Although such activity is now generally accepted as physiological, and indeed vital, to the normal function of that sensory system (see the current review of LEVICK⁴), its very presence complicates the deciphering of transient event signals moving in those pathways.

While complex models have been explored for the analysis of maintained activity in the visual system⁵, certain forms of transient information can at times be extracted through very fundamental models, even in the presence of very high density 'noise' (e.g. 30 spikes/sec or more) generated by the conducting neurone. The relative success of such reduced factoring models depends, of course, on the regularity of the maintained discharge, and is illustrated here in relation to one of the most fundamental of transient signals in the visual pathways: the ongoing assessment of image focus on the retina⁶.

The responses cited are from amongst a cumulative sample of more than 300 neurones within the rabbit mesencephalon and visual cortex now studied. The animals were maintained under light urethane anesthesia (6.0 ml/kg body wt. of a 20% solution in saline, a dosage level found from earlier work to be no more detrimental to cell responsiveness than 'encéphale isolé' techniques). This was supplemented with 3.3 mg/kg body wt./h of gallamine triethiodide to prevent eye and body movements,

¹ H. K. HARTLINE, *J. cell. comp. Physiol.* 5, 229 (1934).

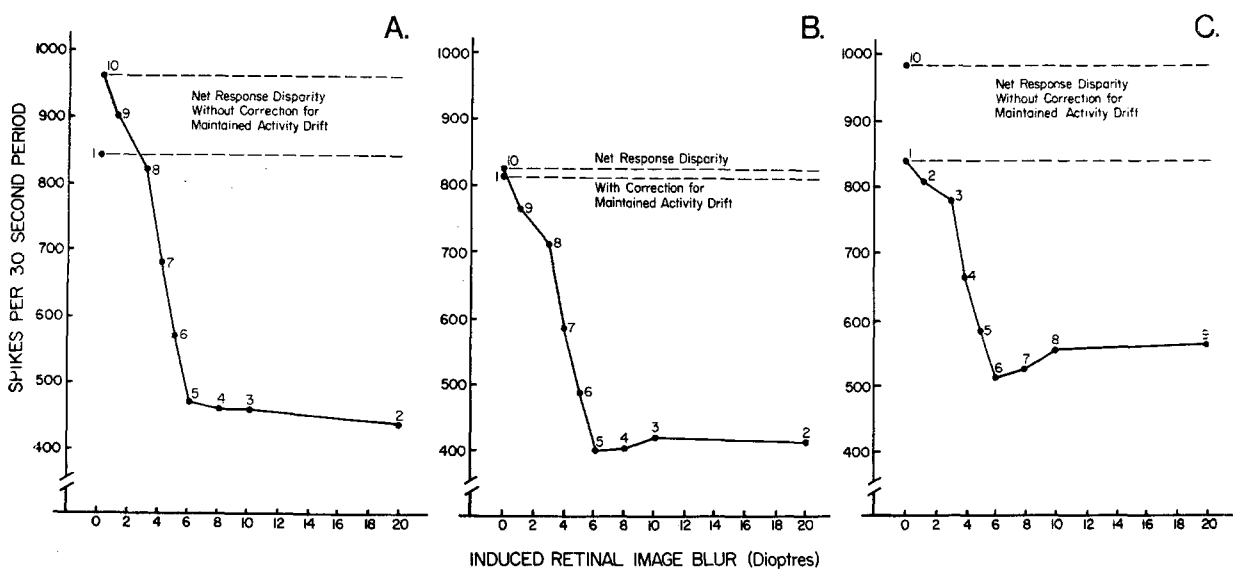
² E. D. ADRIAN, *J. Physiol., Lond.* 91, 66 (1937).

³ R. GRANIT, *Acta physiol. scand.* 1, 370 (1941).

⁴ W. R. LEVICK, *Handbook of Sensory Physiology* (Springer-Verlag, New York 1973), vol. 7, part A, p. 575.

⁵ H. B. BARLOW and W. R. LEVICK, *J. Physiol., Lond.* 202, 699 (1969).

⁶ R. M. HILL and H. IKEDA, *Arch. Ophthal.* 85, 592 (1971).



Responses of a midbrain cell to a black edge moving across its receptive field once per sec, integrated over 30 sec periods. The test sets for each focal condition were spaced 90 sec apart, their order of presentation being indicated by the numbers next to the points. A) shows the actual spike totals recorded, i.e. without correction for maintained activity drift; B) shows the same data, corrected for maintained activity drift (see text); and C) shows the maximum case of transient response distortion expected, calculated on the assumption that the data could have been collected in the particular order indicated.

the animal being artificially respired during that period.

The animals were supported stereotaxically, 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, $\frac{1}{2}^\circ$ 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_0 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).

¹⁰ This work was supported by a grant from the USPHS National Eye Institute. We thank T. G. GAST and A. A. LEE for their assistance.

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).