persisted throughout the delay period, slowly and irregularly declining toward baseline in the course of it. Figure 3 shows a unit activated for almost the entire duration of delays longer than 1 minute (*7*).

A minority of units (14 percent in MD, 17 percent in prefrontal cortex) was characterized by an inhibition beginning with cue presentation and followed, during the delay, by gradual return to the intertrial firing level. The remainder of the units (28 percent in MD, 18 percent in prefrontal cortex) were apparently unaffected by the events of delayed response trials.

Records of eye movements, obtained concomitantly with unit records, show no evident correlation between such movements and unit activity in the areas explored (*8*).

Natural stimuli, presumably significant to the animal, were tested on a few units. Such stimuli failed to produce excitatory changes comparable to those observed in most units during delayed response trials. The frontal unit illustrated in Fig. 2A is especially interesting in this regard for, while it was slightly activated on every trial at cue presentation and beginning of delay, it was no less consistently inhibited by the tape-recorded cries of other monkeys at feeding time.

Although cerebral regions outside the prefrontal cortex and MD were not systematically explored, records were obtained from 48 cells or fibers in posterior cingulate cortex, corpus callosum, posterior commissure, caudate nucleus, and thalamic nuclei other than MD. In this assorted sample, 27 units did not change firing frequency in delayed response trials, while 9 and 12 were respectively excited and inhibited during either cue or delay. The majority of those activated were found in intralaminar thalamic nuclei (centrum medianum, parafasicularis). Caudate units showed a tendency to inhibition by cue presentation.

The temporal patterns of firing frequency observed in prefrontal and thalamic units during cue and delay periods suggest the participation of these units in the acquisition and temporary storage of sensory information which are implicated in delay response performance. Their function, however, does not seem to be the neural coding of information contained in the test cues, at least according to a frequency code, for we have not found any unit showing differential reactions to the two positions of the reward.

It is during the transition from cue to delay that apparently the greatest number of prefrontal units discharge at firing levels higher than the intertrial baseline. This may be the basis of the d-c negative potential shift that has been reported to occur at that time in the surface of the prefrontal cortex; it also may help to explain the observation that electrical stimuli are maximally disruptive to performance when applied to that cortical area at the end of the cue period and beginning of the delay (*9*).

We believe that the excitatory reactions of neurons in MD and granular frontal cortex during delayed response trials are specifically related to the focusing of attention by the animal on information that is being or has been placed in temporary memory storage for prospective utilization. These reactions are probably an integral component of a basic function of the prefrontal-MD neuronal circuits in active attention. This view is in agreement with evidence obtained by behavioral experiments (*10*) and by studies of the prefrontal syndrome in man (*11*), which indicates a fundamental disturbance of attentive mechanisms in frontal lobe injury. However, the question of how the frontothalamic system may be functionally articulated with other cerebral structures to play the postulated role in attention requires further investigation.

JOAQUIN M. FUSTER
GARRETT E. ALEXANDER
Department of Psychiatry and *Brain Research Institute, University of California School of Medicine, Los Angeles 90024*

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20 May 1971

Ultraviolet Absorption in Lenses

Zigman (*1*) used data on the photooxidation of aromatic amino acids to suggest "a possible chemical basis for lens coloration." His findings may be of some interest with respect to the problem of cataract formation, but his speculations on the significance of such pigments in relation to the function of the lens ignore most of the available literature on the subject.

That melanin-like compounds are formed in the lenses of primates has been known for decades (*2*); Wald measured the absorption of primate lenses in the near-ultraviolet region and assessed their role in reducing chromatic aberration (*3*). From the lenses of a variety of lower vertebrates we extracted a dialyzable, heat-stable substance that accounted for their very considerable absorption in the near-ultraviolet region (*4*). On the basis of chromatographic behavior and fluorescence, we tentatively characterized these lens pigments as pteridines. More recently, Cooper and Robson (*5*) have reexamined squirrel and human lenses; they report the extraction, in large amounts, of a compound that appears identical to ours in all important respects.

The matter can thus be summarized in terms that are now quite general. The lenses of nearly all diurnal vertebrates, whether visibly colored or not, possess ultraviolet-absorbing compounds that make them excellent "cutoff" filters in the spectral region from 390 to 410 nm. The adaptive significance of this feature is almost certainly related to the reduction of chromatic aberration; the wavelength restriction is imposed not at the point where ultraviolet light becomes abiotic, but rather at the point where it begins to impose serious refractive errors. In this context, Zigman's arguments are rather perplexing. He states: "The lens appears to utilize a most ingenious and efficient mechanism for eliminating near-ultraviolet light before it reaches the retina by converting it to fluorescence at a higher wavelength." Were the conversion in fact efficient, it would merely create stray visible light that would constitute noise in the visual image.

The protein-bound complexes produced in Zigman's photooxidation experiments on dogfish lenses contribute relatively little absorption at 365 nm; lenses that are good ultraviolet cutoff filters show much higher absorbance at this wavelength. It is thus unlikely that this class of compounds, even if present in the lenses of diurnal terrestrial vertebrates or surface-living fishes, plays a significant role in their absorption of near-ultraviolet light. Indeed, it is unlikely that dogfish, at their usual depths in coastal marine waters, ever receive significant amounts of ultraviolet light at 340 to 380 nm, the wavelengths employed in Zigman's irradiation experiments.

Thus, although the reaction described by Zigman may occur, its contribution to the ultraviolet-absorbing properties of vertebrate lenses is not great. That such lenses are superb ultraviolet cutoff filters is due to an entirely different class of compounds having low molecular weight and wide distribution.

DONALD KENNEDY
Department of Biological Sciences, Stanford University, Stanford, California 94305
ROGER MILKMAN
Department of Zoology, University of Iowa, Iowa City 52240

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26 March 1971

The comments of Kennedy and Milkman (*1*) confirm the fact that certain partially characterized, fluorescent, aromatic substances of low molecular weight are present in the lens, and that they strongly influence its light transmission properties. Such comments add further emphasis to the idea, stated in my report (*2*), that other aromatic compounds as well as the amino acids in the lenses of diurnal animals could also be photooxidized by near-ultraviolet light to colored or ultraviolet-absorbing compounds. The evidence that pteridines are present in the lens, as suggested by Kennedy and Milkman (*3*) and later by Cremer-Bartels (*4*), is still incomplete. In addition, Cooper and Robson (*5*) have found that the amounts of unbound fluorescent substances extractable from colorless young human lenses tend to decrease at an age when intensification of lens coloration begins. This coloration of human lenses becomes progressively greater with aging, a process that sometimes results in brunescent cataracts.

Although the elimination of chromatic aberration has long been known to be an advantage of colored lenses, an additional emphasis is placed (*2*) on a possible role of the lens as a protective shield for the retina against near-ultraviolet light. Near-ultraviolet light causes certain harmful effects on the retina (*6*) and on other cells, tissues, and organs (*7*).

In my work I used dogfish lenses as model lenses *because* they infrequently encounter ultraviolet light and are not colored. However, lake trout, maintained in shallow water exposed to bright sunlight, were found by McCandless *et al.* to have a high incidence of cataracts (*8*). In my report (*2*) I showed that the absorption of 365-nm light by the isolated dogfish lens increases with coloration from 41 to 70 percent, an amount which I believe is appreciable. Discrepancies between the lens absorption values reported by Kennedy and Milkman (*3*) and Cooper and Robson (*5*) and my measurements can be explained on the basis of differences in instrumentation. In their work a spectrophotometer with a narrow beam of light through the central and densest portion of the lens was used; I used a more energetic and diffuse near-ultraviolet light which passes through the peripheral portions as well.

In my discussion of the efficiency of converting ultraviolet light to fluorescence, as referred to in (*2*), I meant the conversion of a potentially hazardous type of energy into a harmless type. The magnitude of the fluorescence was not discussed. The lens compounds referred to by Kennedy and Milkman (*1*) would also convert ultraviolet energy into visible fluorescence.

In summary, the colored and fluorescent compounds of lenses will need to be isolated and characterized, and further experimental documentation of the relative importance of these compounds will be required before any final conclusions can be formulated.

SEYMOUR ZIGMAN
Departments of Ophthalmology and Biochemistry, University of Rochester School of Medicine and Dentistry, Rochester, New York 14620

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21 May 1971

Adaptation of an Intertidal Fish Is Not Unique

Recently, Graham and Rosenblatt (*1*) have shown that an intertidal clinid fish (*Mnierpes macrocephalus*) has two flattened surfaces in each cornea so that vision may be possible in both media. The authors' claim that the remarkable eye structure is unique among fish cannot be upheld, since it had been found earlier in another amphibious clinid (*Dialommus fuscus*) (*2*). Moreover, this structure was suggested to be an ecological adaptation because of a striking correlation between the ontogeny of the eye and the amphibious life habit.

E. CURIO
Arbeitsgruppe für Verhaltensforschung, Abteilung für Biologie, Ruhr-Universität Bochum, 463 Bochum-Querenburg, Postfach 2148, German Federal Republic

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