preted as meaning that the process of light adaptation is more pronounced in the night-phase eye, resulting in a lower concentration of photosensitive materials than is present in the day-phase eye light-adapted to the same extent. Why this difference in the effect of light should exist must be left to future investigation. The differences in response to flicker, described elsewhere (Jahn and Wulff[3]), can be explained in a similar manner.

The usual migration of proximal and distal retinal pigment under the influence of light is sufficiently well known not to require further discussion (Parker[4]).

Conclusions. 1. The distribution of retinal pigment is similar in the dark-adapted day-phase and dark-adapted night-phase eyes. 2. The distribution of retinal pigment is similar in the light-adapted day-phase and light-adapted night-phase eyes, as well as in the illuminated and non-illuminated eyes of the same animal. 3. The diurnal variations in visual function, described elsewhere, are, therefore, independent of retinal pigment migration and originate in the physiological mechanism of the visual process.

13419

Influence of a Visual Diurnal Rhythm on Flicker Response Contours of Dytiscus.*

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A physiological diurnal rhythm is present in the compound eye of the predaceous diving beetle, *Dytiscus fasciventris.* This diurnal rhythm results in two distinct functional states of the eye which are referred to as the night phase and the day phase. These physiological states may be identified by several characteristics which are enumerated elsewhere (Jahn and Wulff[1, 2]).

The measurement of subjective flicker fusion frequency at various intensities of stimulating light has proven to be an excellent index of the physiological state of photoreceptors. The purpose of this

4 Parker, G. H., *Ergebn. der Biol.*, 1932, **9**, 239.

* Aided by a grant from the Rockefeller Foundation for Work in Cellular Physiology.

1 Jahn, T. L., and Wulff, V. J., submitted for publication, 1941.

2 Jahn, T. L., and Wulff, V. J., submitted for publication, 1941.

investigation is to measure the flicker fusion frequencies of the Dytiscus compound eye during the night phase and day phase by means of the objective method of determining from the electroretinogram when fusion of the individual electrical responses occurs.

Materials and Methods. Prior to use as experimental material specimens of *Dytiscus fasciventris* were kept in the laboratory in aquaria under conditions simulating those of the natural environment.

The method of recording the potential from the eye was similar to that described previously (Jahn and Crescitelli[3]). The electrical leads were made from the corneal surface of the eyes of the beetle mounted in the dark chamber. One eye only was exposed to the stimulating light. The recording device consisted of a condenser-coupled high-gain amplifier, a cathode ray oscillograph and a camera. Just previous to experimentation the animals were maximally light-adapted, and progressive dark adaptation occurred during the course of the experiment as the intensity of the stimulating light was decreased. The flicker consisted of a 1 to 1 ratio of light and darkness of variable frequency, which could be adjusted in steps of 4 cycles per second. The maximum intensity of light was 10,000 foot-candles.

Results. A. Measurement of flicker fusion frequency at high intensity. The results of the high intensity (10,000 foot-candles) flicker response experiments during the day and night phases are shown in Fig. 1. As determined in this manner the ability of the day-phase eye to distinguish flicker (as indicated by the ERG) is not lost until the flicker frequency is increased to almost 60 stimuli per second.

In the light-adapted night-phase eye fusion was observed at 40 stimuli per second, a frequency which is significantly lower than the fusion frequency of the same eye during the day phase. Comparison of the magnitude of the response of the day- and night-phase eyes to the same flicker frequencies, records B and D, and records C and E, tend to emphasize this difference.

B. Flicker response contours for the day- and night-phase eyes. In these experiments each of the 3 beetles used was subjected to only 2 investigations; one during the day phase and one during the night phase. In each experiment the flicker fusion was determined over an intensity range beginning with 10,000 foot-candles and decreasing gradually to threshold value. The intensity was controlled with Wratten neutral filters.

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[3] Jahn, T. L., and Crescitelli, F., *J. Cell. and Comp. Physiology*, 1938, **12**, 39.

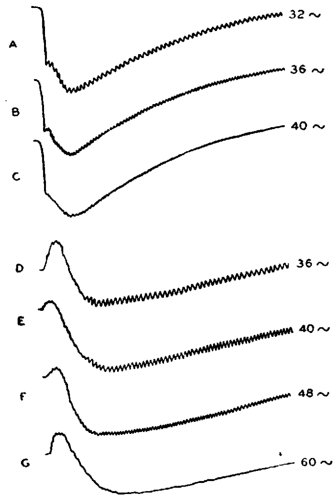

FIG. 1.

Flicker responses of the night- and day-phase eyes. Records A through C are from the night-phase eye; records D through G from the day-phase eye of the same animal. The intensity of the stimulating light was 10,000 foot-candles for all records. The amplifier was operated at a constant intermediate gain and a 2.9 second time-constant. Refer to text for further details.

The responses of the eye to flicker were recorded on constantly moving sensitized paper. At each intensity records were taken of frequencies immediately above and below the critical fusion frequency. When the records indicated a smooth base line (compared to the control) it was assumed that the eye was not able to distinguish the flicker. The curves of Fig. 2 demonstrate the relationship between flicker fusion frequency (in cycles per second) and the logarithm (base 10) of the light intensity. Each point on the graph represents the average value from three experiments on 3 beetles.

These curves illustrate that the flicker response of the day- and night-phase eyes differ over most of the intensity range. At the high intensity end the flicker fusion of the light-adapted night-phase eye is considerably lower than that for the light-adapted day-phase eye. As one approaches the low intensity portion of the graph the two curves approach and finally cross each other, indicating that the flicker fusion at low intensity is higher for the now partially dark-adapted night-phase eye than for the partially dark-adapted day-phase eye.

Discussion. From experiments published elsewhere (Jahn and Wulff[1]) it is known that, in the maximum dark-adapted condition, the night-phase eye is approximately 1000 times more sensitive to light than is the day-phase eye (threshold measurements). This difference in sensitivity is entirely unrelated to any differential pig-

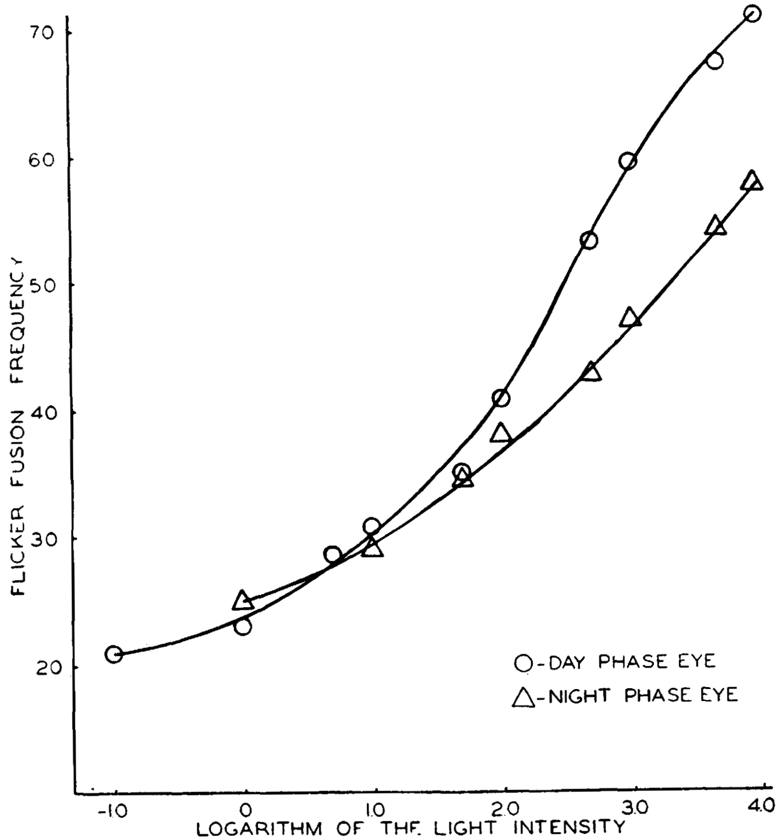

FIG. 2.

Flicker fusion response contours of the day- and night-phase eyes. The frequency (in cycles per second) at which fusion occurs is plotted against the logarithm (to the base 10) of the light intensity. The amplifier was operated at the highest gain which would permit a smooth base line and at a time constant of 0.1 second. Refer to text for further details.

ment distribution (Jahn and Wulff[2]) for the retinal pigment has precisely the same distribution in both the dark-adapted day- and night-phase eyes. Hence, this difference in sensitivity indicates a basic difference in the functional states of the eyes.

Although the results of the two types of experiments reported in this paper are not directly comparable, they both demonstrate the fact that at high intensities the flicker fusion frequency for the day-phase eye is greater than for the night-phase eye. On the basis of the established fact that flicker fusion frequency is a measure of the subjective sensitivity of the eye to light (Ferry-Porter law), this observation means that the intensity perception of the light-adapted day-phase eye is considerably greater than that of the light-adapted night-phase eye. In other words, the light-adapted day-phase eye is more sensitive to light than is the light-adapted night-phase eye. Since the retinal pigment distribution of both of the light-adapted eyes is identical, the basis for this difference in sensitivity must lie in the physiological mechanism of the eye.

This profound reversal of sensitivity relations of the night- and day-phase eyes from the dark-adapted state to the light-adapted state can not be satisfactorily explained at present. It is certain, however, that the reversal is brought about by light and that light adaptation is much more pronounced in the night-phase eye than in the day-phase eye.

Since the dark-adapted night-phase eye is considerably more sensitive to light than is the dark-adapted day-phase eye one would expect that, as the dark-adapted state is approached, the flicker fusion frequency of the night-phase eye would gradually become greater than that of the day-phase eye. The curves of Fig. 2 corroborate this expectation. At high intensity, where the eyes are maximally light adapted, the spread between the curves is large. As the intensity is progressively decreased the eyes become more dark-adapted, and the sensitivity of the night-phase eye increases more rapidly than that of the day-phase eye with the result that the curves approach and finally cross each other. Beyond the crossing point the curves again separate, the night-phase curve now higher than the day-phase curve. The threshold sensitivity of the eyes prevented carrying the experiment to lower intensities.

In general, these flicker experiments indicate that the day-phase eye and the night-phase eye of the beetle, *Dytiscus fasciventris,* represent physiological states which are so different that they may be considered functionally as two distinct photoreceptors.

The objective method of measuring flicker fusion frequency is quite different from the subjective methods ordinarily used (Hecht,[4] and Crozier[5]). At present no data are available which can demonstrate the exact relationship between these methods, but it is assumed that the flicker contour curves obtained by the two methods follow parallel courses. This assumption is based on various demonstrations (Granit,[6] and Therman[7]) that the magnitude of certain components of the electroretinogram are closely related to certain visual functions.

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[4] Hecht, Sebig, *Phys. Rev.*, 1937, **17**, 239, and earlier publications.

[5] Crozier, W. J., *J. Gen. Physiol.*, 1941, **25**, 75, and earlier publications.

[6] Granit, R., *Documenta Opthalmologica*, 1938, **1**, 7.

[7] Therman, P. L., *Acta Societatis Scientiarum Fennicæ*, New Series B, 1938, **2**, No. 1.

Conclusions. 1. The flicker fusion frequency-intensity relations differ for the light-adapted day- and night-phase eyes. 2. This difference is marked in the high intensity range and decreases as the threshold intensities are approached. 3. In view of data published elsewhere the reversal of sensitivity relationships indicates that the process of light-adaptation is much more pronounced in the night-phase than in the day-phase eye. 4. The flicker response contour and other relationships confirm the conclusion, made elsewhere, that the diurnal rhythm present in the eyes of these beetles results in two physiological states which are so different that they may be considered functionally as separate and distinct photoreceptors.

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Sexual Behavior of Intersexual Domestic Fowl.*

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This investigation concerns the behavior of intersexual birds, produced by the injection of estrogens into the egg on or before the fourth day of incubation. The males, as a result of this treatment, develop into intersexes of varying degrees of femininity, as indicated by behavior patterns and plumage.[1] The females are essentially normal except for the occasional occurrence of anomalous oviducts and the greater frequency of right oviducts.[2] The use of intersexual individuals permits the beginning of an analysis of the various components of sexual behavior, which, in this instance, is attempted from a psycho-analytical viewpoint.

The birds were kept in pens measuring 8′ x 17′ and containing from 5 to 9 birds of both sexes. The males were arbitrarily classified on the basis of plumage characters into 4 intergrading classes

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1 Domm, L. V., PROC. SOC. EXP. BIOL. AND MED., 1939, **42**, 310; Domm, L. V., *Anat. Rec.*, 1940, **78** (suppl.), 144.

2 Domm, L. V., *Anat. Rec.*, 1940, **78** (suppl.), 145.