

<sup>1</sup> "The Interpretation of Electric Current Flow in Terms of the Electron Theory," *J. Elec., Power, Gas*, February, 1914.

<sup>2</sup> O. W. Richardson, on pages 430-432 of his *Electron Theory of Matter*, refers to the work of Schuster, Jeans, and H. A. Wilson in dealing theoretically with free-electron conductivity under periodic forces. These authors derive a diminution formula which is different from the one used by Thomson. Schuster, applying his formula to the optical data accumulated by Drude, finds that "for all the commoner metals the number of free electrons in a given volume is from one to three times as great as the number of atoms present."

<sup>3</sup> Schuster, whose paper appeared in 1904, does not refer to the work of Hagen and Rubens and of course does not deal with the 4 micron wave-lengths of which Thomson makes so much. The difference between Thomson's estimate and Schuster's estimates of  $n$  does not materially affect the force of the argument I am making.

<sup>4</sup> *Proc. Nat. Acad. Sci.*, 7, pp. 98-107.

<sup>5</sup> *Zeits. Physik*, 47, February, 1928.

<sup>6</sup> Owing to the rate of increase of both  $n$  and the heat of ionization with rise of temperature, according to my theory, the number of free electrons here indicated might involve a contribution of about 3% to the specific heat of silver.

<sup>7</sup> See the paper referred to in my opening paragraph.

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## A DESCRIPTION OF THE ONTOGENETIC DEVELOPMENT OF RETINAL ACTION CURRENTS IN THE HOUSE MOUSE

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Several investigations upon the eyes of lower vertebrates (Chaffee and Adrian and their collaborators, and others) have given us much information as to the nature of the retinal response elicited by the action of light. These studies were made almost entirely employing excised eyes. Technical difficulties make it almost impossible to apply these methods to mammals. All such attempts employing eyes of the highest class of vertebrates have failed since the excised mammalian eye, tested immediately after removal, shows evidence of degeneration.

In a recent communication<sup>1</sup> (Keeler, Sutcliffe and Chaffee, 1928) it was shown that it is possible to obtain from normal intact unanaesthetized adult house mice, action-current responses quite similar to those found in the excised eyes of lower forms, while "rodless" house mice exhibited no changes in potential.

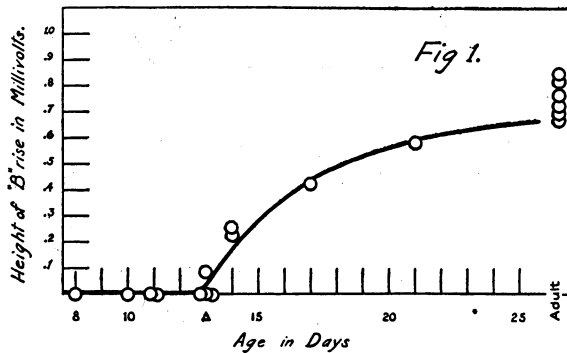
*Apparatus.*—The apparatus employed has been described by us, and in more detail<sup>2</sup> by Chaffee, Bovie and Hampson, 1923. The changes in potential are detected by a delicate Einthoven string galvanometer

in connection with a two-stage resistance-coupled amplifier and are recorded by means of sensitized paper upon a revolving drum.

*Procedure and Results.*—The trimodal curve of potential differences constituting the action-current record of vertebrate eyes, describes admittedly a very complex phenomenon, probably dependent upon several reactions localized in the retina and overlapping in time. The three modes are labeled "A," "B" and "C" upon the response curves of a 21-day-old mouse taken at an intensity of 538 meter candles, shown in figure 2.

The authors decided that a study of the beginnings of reaction in growing mice might shed some light in the direction of the proper interpretation of the nature of the reactions within vertebrate eyes, in general, since the times of onset of the supposed several reactions, if independent, might not arise simultaneously in ontogeny.

It has been shown (Keeler, 1927) that the rod is most probably the secretor of visual purple and that in normal mice these secretors (rods) are



entirely undifferentiated at birth. It was also pointed out that the internal nuclear and external nuclear layers separate about the fifth day after birth and that the rod buds do not grow out until the 7th or 8th day of postnatal development. If then, the action currents depend at least in part upon photochemical changes taking place in visual purple, we should not expect to find normal electrical responses in mouse eyes before the development of the rods, i.e., during the second week after birth. Thus the young mouse should be suitable material for studies into the ontogeny of the Retinal Action Currents.

To the end of determining the point in development of the mouse-eye at which the action currents are first discernible, a series of mice was examined from birth to maturity. In all animals which had not yet opened the eyes the lids were separated with forceps.

The height of the "B" rise was measured in millivolts in the cases where responses were detected. It will be seen from figure 1 that the youngest

mouse to exhibit action currents was 13 days old, while 3 others of the same age gave no response. The height of response increases with age, although it has not reached the adult height even in mice 21 days old.

In order to study more precisely this development, numerous records were taken for the same animal at intensities of light between 0.09 and

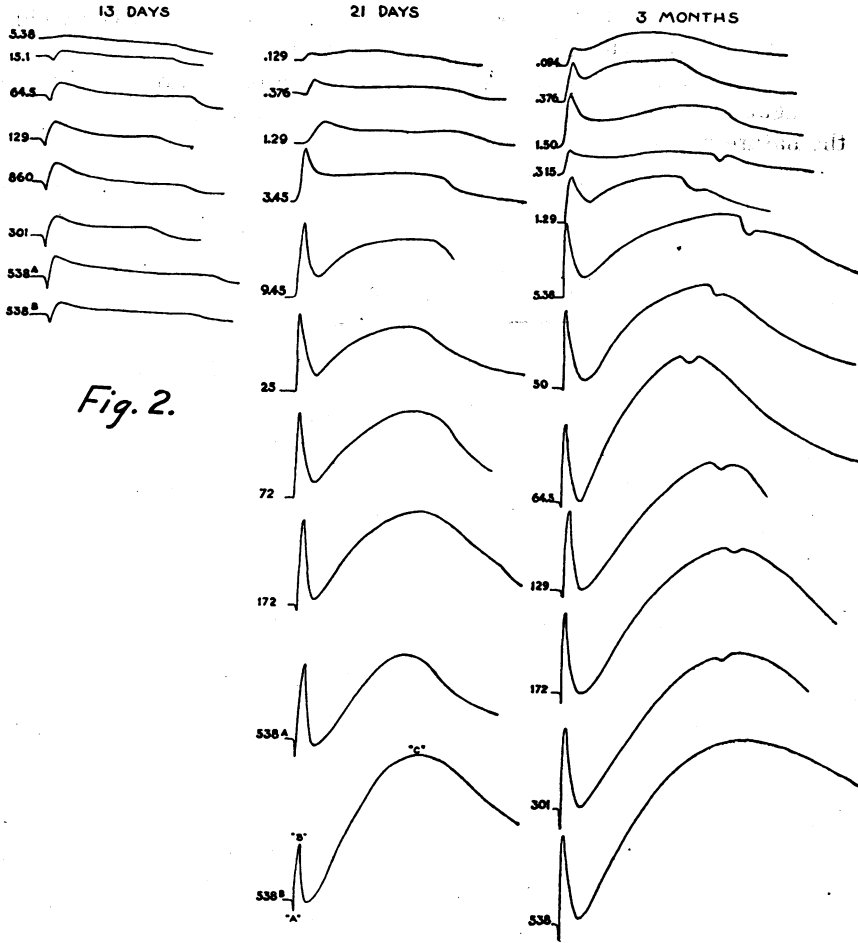


Fig. 2.

540 meter candles. The total increase of intensity for this range is about 6000-fold.

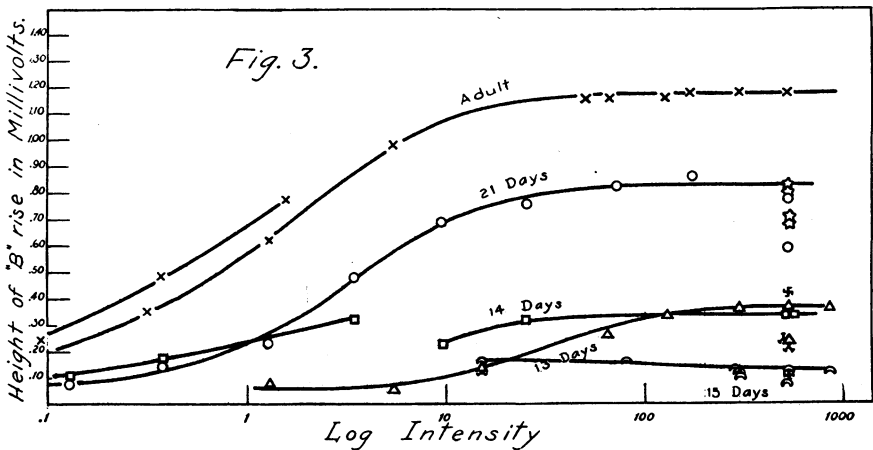
In figure 2 are shown tracings for an intensity series using short time exposures upon animals of 13 days of age, 21 days of age, and adult. The numbers preceding each curve denote the intensity of light employed for stimulation in each case.

It will be noticed at once that the curves obtained for the 13-day-old

mouse differ greatly in form from those of the older animals, yet in all three they increase in height with increase in intensity. In the 13-day-old animal, however, there is present a negative "A" deflection comparable to the "A" found in older animals only at the highest intensities. There is no appreciable "C" rise in the curves of the youngest animals.

In the 21-day-old animals the "C" rise becomes very prominent although not nearly so great as in the adult mouse. The valley ordinarily made in the "C" curve by the turning-off of the light is quite noticeable in the records for adult mice. This is commonly referred to as the "off effect."

At all ages the height of the "B" rise, the depth of the "A" deflection, and the height of the "C" (when present), increase with increase in intensity.



An explanation of the meaning of the various curves is not attempted in the present communication. As, however, the most obvious and constant feature of these curves is the "B" rise, we have used its height as a measure of the response as has been done in earlier papers.

For the present we can do no more than give a bare description of the results, hoping that these will aid in a future analysis.

In figure 3 are charted several intensity series taken upon animals of ages varying from 13 days old to adult. The record for the eye of the animal at 15 days of age is probably that of a defective eye, whereas the other records are considered those of normal-eyed mice.

The records were taken in order from low to high intensities with intervals of darkness of from 3 to 5 minutes between exposures. After the taking of the first series in the case of the 13-day-old mouse and the adult,

a second series of extremely low intensities was obtained. These curves are of the same general form as those obtained from lower animals such as the frog and lizard.

The effect of adaptation or supersensitization is seen in the curves for the 13-day-old, 21-day-old and adult. That is to say, when an eye has once been tested and then allowed to remain in the dark for a long time, if another record then be made at the same intensity the latter response will be larger than the former. For example, the stars in figure 3 represent the height of "B" rise at the highest intensity for adult mice without adaptation. The cross mark above represents the increased response after a certain amount of dark adaptation acquired during the time of running through the series of nine tests shown by cross marks.

If one plots for older animals, the logarithm of the height of the "B" rise against the logarithm of the intensity, a sigmoid curve is suggested.

It is hoped to make a more extensive study of the action currents in the mouse, employing curare to anaesthetize the motor end plates with the hope of separating the adaptational effect from the basic reaction.

*Summary and Conclusions.*—The ontogeny of action-current responses has been studied in the intact unanaesthetized house mouse, obtaining the following results:

1. The age at which the first potential differences are visible was found to be the 13th or 14th day.

2. In young mice the reaction is quite different from that found in the adult, consisting of a deep, wide, negative "A" deflection followed by a low wide "B" rise. The "C" rise is not found even in the records taken with stimulation of 538 meter candles intensity.

3. As the animal grows, the reaction gradually takes on the adult form, although even at 21 days of age it is obviously inferior in size to that of the adult.

4. In mice from 21 days of age on, there is no "A" deflection at the lower intensities, but at the highest intensities it is present, increasing in size with the increase in intensity. This increase in size of the "A" deflection with increase in intensity is found also in the youngest animals where the "A" rise is present at all intensities.

5. The effect of adaptation is seen in these records, in that an eye stimulated after short and long exposures to darkness differ greatly in size, the more adapted giving the greater response.

6. If the height of the "B" rise of any age be plotted against the logarithm of the intensity the result is a sigmoid curve.

7. Adapted eyes show a smaller "C" rise than unadapted eyes.

<sup>1</sup> Keeler, Sutcliffe and Chaffee, 1928, *Proc. Nat. Acad. Sci.*, 14, No. 6, pp. 477-484, June, 1928.

<sup>2</sup> Chaffee, Bovie and Hampson, 1923, *J. Opt. Soc. Amer.*, 7, No. 1.