physiological action of adrenaline.[11] The latter offers most interesting possibilities in the dual sympathetic and parasympathetic controls of the body of which cardiac regulation is an example. It strongly suggests a reciprocating chemical control built upon physiological variation of the hydrogen ion concentration. Specifically, a rising cH increasing the parasympathetic inhibitory action might be supported by a diminishing intensity of sympathetic excitatory action, and a fall in cH would be associated with a converse reciprocal interaction. Central neuroreciprocal action between the excitatory and inhibitory cardiac centers would be complemented by an outlying chemical reciprocation.

On the assumption that carbon dioxide can substitute for eserine and related compounds for producing experimental effects in those systems of the body where acetylcholine is normally deposited, it is deemed advisable to reinvestigate many of the fundamental researches in neurohumoral physiology. In the light of normal and pathological fluctuations in acid-base equilibrium and the practical applications which may arise, this course is imperative. The valuable studies of Cannon and Rosenblueth[12] and their associates on the five stages of stimulation where physostigmine has such profound effects is but a single example. Will carbon dioxide produce comparable effects to those of physostigmine on these phases of stimulation? Is an increasing muscle cH a possible explanation of the fifth stage? These are merely illustrations of the many questions that may be raised to test the application of the acid neurohumoral mechanism of activation in the body.

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Influence of Intensity of White Light upon Pupil Diameter of the Human and of the Rabbit.

I. H. WAGMAN AND L. MATTHEW NATHANSON. (Introduced by J. M. D. Olmsted.)

From the Division of Physiology, University of California Medical School, Berkeley.

Hecht and Pirenne[1] attempted to measure the minimum visual threshold of the nocturnal long-eared owl by comparing the inten-

[11] Andrus, E. C., *J. Physiol.*, 1924, **59**, 361.

[12] Cannon, W. B., and Rosenblueth, A., *Am. J. Physiol.*, 1937, **119**, 221.

[1] Hecht, S., and Pirenne, M. H., *J. Gen. Physiol.*, 1940, **23**, 709.

sity of monochromatic light necessary to cause a pupillary constriction of 0.5 mm in the dark adapted owl with the intensity necessary to do the same in the human, thus assuming that the relationship between thresholds for intensity discrimination and pupillary constriction is the same in both species. Their data for the human pupil were taken from measurements on 6 subjects made by Reeves in 1918 and 1920.[2]

Reeves' data, although unique, cannot be taken as too accurate at low intensities because of too few measurements. Reeves took as the first point on his curve the size of the pupil after 15 minutes in the dark. He assumed this to be its size at the visual threshold which was assigned an arbitrary value of –6 log intensity units. At his next point, –3.8 log intensity units, the pupil already shows a distinct contraction. One cannot be sure at what point in the curve the pupil starts to contract, and consequently any reasonably accurate judgment cannot be made as to the relationship between visual threshold and threshold for pupillary contraction.

Reeves' work is here repeated more carefully, using as subjects both the human and the rabbit, and comparison is made between their pupillary thresholds. If Hecht and Pirenne are justified in their assumptions, then the data here obtained may offer information regarding the visual threshold in the rabbit gained by an objective method.

The method used is to be described in detail elsewhere. It is a modification of the infrared photographic method described by Gullberg, Olmsted, and Wagman,[3] and enables the pupil diameter to be measured under any condition of light or dark adaptation, as well as the subjective visual threshold. The subject was dark adapted for a period of time ranging between 20 and 30 minutes. With the human (6 subjects) at the end of this time, the subjective visual threshold was measured and a series of photographs taken with this light in the eye. With the rabbit (10 subjects) the first photographs were taken at a brightness of 6.14×10^{-5} foot-lamberts, a brightness which was found not to affect the dark adapted pupil. The intensity of light was then increased in definite steps and a series of photographs was taken at each intensity at intervals of 10, 20, 30, 45 and 60 seconds. Sixty seconds are enough to insure complete adaptation at each intensity. Periods of rest in the dark between changes of intensity were found to be unnecessary, since

[2] Reeves, P., *Psychol. Rev.*, 1918, **25**, 330; *J. Opt. Soc. Am.*, 1920, **4**, 35.

[3] Gullberg, J. E., Olmsted, J. M. D., and Wagman, I. H., *Am. J. Physiol.*, 1938, **122**, 160.

the state of light adaptation readily changed its level at each intensity (*cf* Hecht and Schlaer[4]).

The field of light, which was 16.6° visual angle, was centrally fixated for the human. For the rabbit, the spot was adjusted so that it appeared to be central in position. The rabbit was rigidly held in place after adjustment by means of a specially constructed holder. No anesthetic was necessary with this device, which held the rabbit securely and quietly in position in a comfortable manner with no previous struggling. The head of the human subject was held in place by a chin rest and upright bar and eyepiece.

The pupil diameter was measured at nine intensities over a range of about 9 log units (from 2.5×10^{-7} foot-lamberts to 105.5 foot-lamberts) for the human, and eight intensities over a range of about 7 log units (from 6.14×10^{-5} to 206.6 foot-lamberts) for the rabbit.

If the light is kept in the eye, the pupil dilates slightly following its initial rapid constriction. This dilatation is followed by a secondary constriction. There is always a continual small fluctuation in the pupil, no matter what the state of adaptation (Reeves[2] and Laurens[5]). The changes, however, are small enough to be ignored.

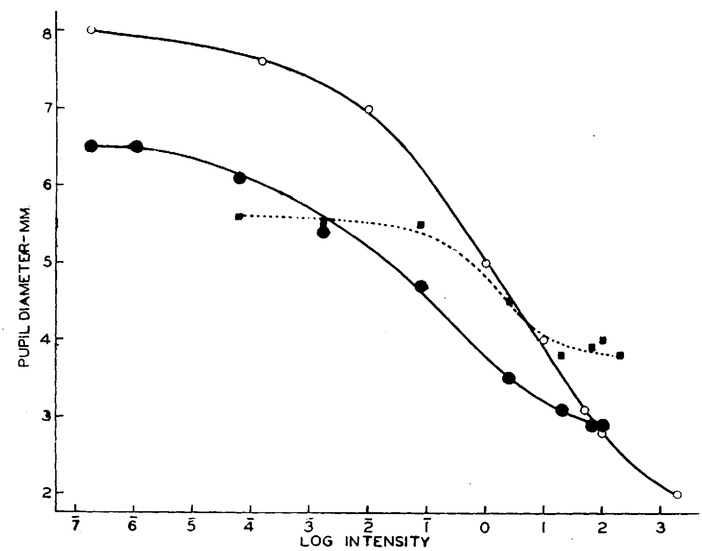

FIG. 1.

Curves showing the relationship between the intensity of white light and the pupil diameter for both the human subject and the rabbit.

● The present measurements on humans.

○ Reeves' measurements (1918, 1920) on humans.

■ The present measurements on rabbits.

[4] Hecht, S., and Schlaer, S., *J. Gen. Physiol.*, 1936, **19**, 965.

[5] Laurens, H., *Am. J. Physiol.*, 1923, **64**, 97.

The times in which the pupil closed to the minimum with various intensities were always the same.

It was found here that the pupil in both humans and rabbits reached its minimum in about 5 seconds, and thereafter fluctuated closely around that value (*cf.* Laurens and Reeves). It cannot be said whether or not pupillary size after a given exposure time longer than 5 seconds is more representative of the state of adaptation than its size after any other length of exposure. Accordingly, the pupillary sizes determined after 10, 20, 30, 45 and 60 seconds' exposure to a certain intensity were average to give the value representative of that intensity. The same curve is always obtained when the measurements are taken for any one of these intervals.

The first point in our data for the human subjects (the filled in circles of Fig. 1) is taken at the average of all the threshold values (–6.74 log I) determined subjectively by means of the adapting instrument. The range of these threshold values for the 7 subjects was from –6.28 to –7.13 or 0.85 log units.

The average pupil diameter with the threshold light in the eye is the same as that found after 20 minutes in darkness. From the curve it is evident that the pupil does not start to contract until the brightness is raised by one log unit or until it is 10 times greater than the threshold brightness.

We have arbitrarily placed the first point of Reeves' data (open circles, Fig. 1) at the same place as our own average threshold value, instead of at –6.0 log units which he arbitrarily assigned. No practical difficulties are encountered in comparing his curves with ours although his measurements were in milli-lamberts instead of foot-lamberts. Since the curves in their upper halves run parallel courses, the pupils measured by Reeves would probably show the start of contraction at the same point as ours do. If we take a constant amount of pupillary contraction (*i. e.,* 0.5 mm as Hecht and Pirenne did) to make comparisons, the similarity between the two curves is more striking. Thus our data show that a 0.5 mm contraction occurs at –3.75 log units, which is 2.99 log units more, or 1000 times more than the average threshold value. Reeves' curve shows that a 0.5 mm contraction occurs at about –3.35 log units, which is 3.39 log units more than our average threshold values. Since the latter is merely a guess when applied to Reeves' data, the agreement is surprisingly good. The difference between 3.39 and 2.99 or 0.40 log units is well within the normal variation of subjective thresholds as measured by us and by Hecht and Mandelbaum.[6]

[6] Hecht, S., and Mandelbaum, J., *J. A. M. A.*, 1939, **112**, 1910.

This similarity between the two sets of data holds for any pupillary constriction up to about 3 mm. We think that the discrepancy from then on is not real, since the brightness measurements made by Reeves do not seem to be accurate at the higher intensities. Although he is not specific, he does say the pupils were measured at brightnesses obtained from direct sunlight or reflections from a white surface. Furthermore, his last point at 2000 milli-lamberts (or 3.3 log units) was obtained from one subject, the one having the second smallest pupil. Since light of this intensity is painful, measurements are extremely difficult to make in such a bright light.

Our results agree with those of Reeves in showing that the pupillary constriction for the human is very slight above an intensity of approximately 100 foot-lamberts.

The average curve for the 10 rabbits is the dotted curve in Fig. 1. The pupil does not start to constrict until an intensity of about −1.5 log units is reached, which is about 4 log units or 10,000 times greater than the intensity necessary to cause a just perceptible contraction of the human pupil. A contraction of 0.5 mm in the rabbit occurs at −0.40 log units or at an intensity of 3.35 log units or about 2200 times greater than the intensity necessary to do the same in the human. We prefer to use, as did Hecht and Pirenne, this latter method of comparison since the determination of the point where the pupil just starts to contract is much more inexact. In any event, the error is less than 1.0 log unit, within the order of variation found in subjective measurements on humans.

If Hecht and Pirenne's assumption is correct that the relationship between absolute threshold and a constant amount of pupillary constriction is constant for different species of animals, then our results show that the rabbit's absolute threshold is 2,200 times greater than man's and 22,000 times greater than the owl's.