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Reciprocal Action of the Constrictor and Dilator Pupillae During Light Adaptation.

J. E. GULLBERG, J. M. D. OLMSTED AND I. H. WAGMAN.

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

It has been shown by infrared photographic measurements that dilation of the pupil during dark adaptation is the result of 2 mechanisms, namely, the passive elasticity of the iris tissue, and the actual contraction of the dilator pupillæ.[1] The maximum pupil diameter during normal dark adaptation is reached when the added effect of these 2 mechanisms just balances the "residual tone" of the constrictor pupillæ.

After cutting the sympathetic, the maximum pupil diameter is less than normal, and is now determined by the balance between the passive elasticity of the iris on one hand, and the "residual tone" of the constrictor pupillæ on the other.

To complete the study of reciprocal innervation of the iris musculature of the rabbit, we observed the rate of both dark and light adaptation of the eye, before and after cutting the third nerve, and before and after paralyzing the constrictor mechanism with atropine.

The photographic method used to determine the size of the pupil during light adaptation is basically the same as the method to measure the rate of dark adaptation previously described.[1] The method is so designed that even under bright light conditions the photographs are taken by illumination with an infrared source of light. There is, therefore, no need for a change in technic nor for any adjustment in the transition from virtual darkness to the condition of an intensely illuminated field if the camera can be made "blind" to the stimulus light.

The middle density infrared filter made for the Xenon F 1.5 lens was used over the lens without an appreciable increase in the exposure time of the previously described method of illumination of the eye. If the stimulus light is made relatively free of the far red and infrared components, it is possible to have the same photographic conditions for light and dark adaptation.

The stimulus light must have the qualities of high intensity combined with stability and uniformity over the considerable area

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

which must be illuminated. For this purpose the best standard lamp is the tungsten ribbon filament, 6-volt, 108-watt bulb. This was used with an aspheric condenser in the lamp housing of Bausch and Lomb. Such a lamp throws an image of great uniformity in the form of a rectangle which has sufficient width to allow for minor head movements without change in the stimulus intensity. Care was taken to control the voltage. The far red and the infrared portions of the radiations were removed from the source by a combination filter consisting of a parallel-sided glass cell, 32 mm in depth, filled with the saturated solution of nickel ammonium sulphate, and a standard glass heat absorbing filter disc, of 2 mm thickness. This combination filter removes some of the blue violet end of the spectrum in addition to eliminating the red and infrared parts, but the residual is still very effective in pupillomotor action.

After a series of photographs had been taken during complete dark adaptation, as previously described,[1] the stimulus light was thrown into the eye, and photographs were taken as quickly as possible, until the pupil reached a constant diameter. The action is very rapid, the average time for completion being from 5 to 10 seconds (Fig. 1). Reeves[2] obtained similar results with the normal

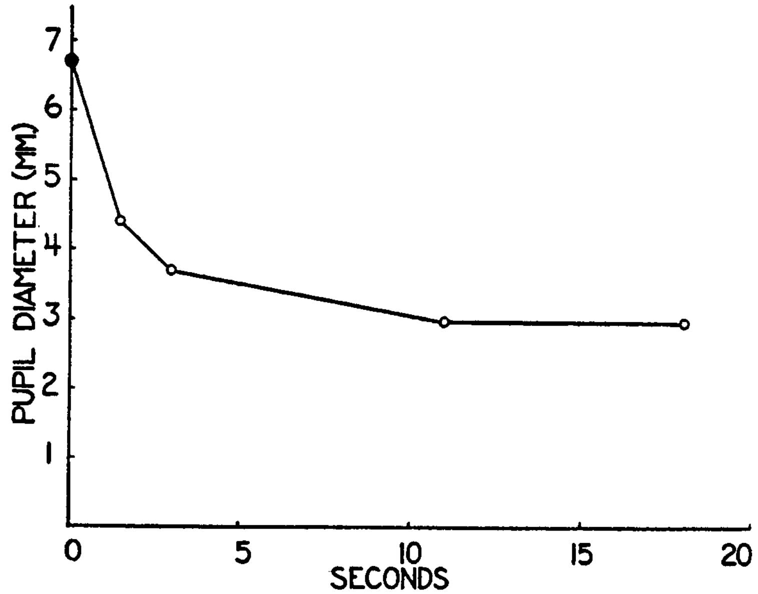

Fig. 1.

Curve showing rate of pupil constriction during light adaptation of the normal rabbit's eye.

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[2] Reeves, P., *Psych. Rev.*, 1918, **25**, 330; *J. Franklin Inst.*, 1918, **185**, 753.

human pupil. He found that it reached its minimum in less than 5 seconds, and the greater part of the constriction occurred within the first 2 seconds.

After the third nerve was cut, the pupil was permanently dilated to a greater maximum than during dark adaptation in the normal eye. No detectable response was obtained when the intense light was thrown into the eye with the third nerve cut. The same result was also observed after the direct application of 3 drops of a 2% solution of atropine sulphate to the normal eye.

It seems from our results that after cutting the third nerve, the elasticity of the iris plus the active contraction of the dilator pupillæ can now have its full effect. There is no longer any "residual tone" of the constrictor to overcome since this muscle is completely relaxed. The pupil, under these conditions, therefore, reaches the maximum diameter of which it is capable, and remains so during dark adaptation and during light adaptation as well.

As there is reciprocal action on the part of the 2 muscles of the iris, an intense light in the eye should cause a relaxation of the dilator even when the third nerve is cut or paralyzed. Such may be the case, but any constriction of the pupil that might take place under these circumstances is not detectable by the photographic method used, presumably because the range of movement of the feeble dilator muscle fibers is exceedingly slight when near or at their shortest length.

It has been found that when both the sympathetic and third nerves are cut, the iris assumes an immobile position in which the diameter of the pupil is only ¾ of the maximum which is reached when the third nerve alone is cut.[3, 4, 5] "Residual tone" has had to be postulated for the constrictor muscle in order to account for the increase in pupil diameter when atropine is instilled into the dark adapted eye after the sympathetic alone is cut. So here, with the third nerve cut, "residual tone" must be postulated for the dilator muscle in order to account for the greater diameter of the pupil when the sympathetic is intact than when it is cut. Again, as in the case of the constrictor, this "residual tone" is independent of the working of its antagonist in its reciprocal action.

Our experiments show that, while dilation of the pupil can be brought about by relaxation of the sphincter alone, relaxation of the dilator plays no appreciable part in constriction. This agrees with

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[3] Parsons, J. H., *J. Physiol.*, 1901, **26**, 366.

[4] Parsons, J. H., *Roy. London Ophth. Hosp. Rep.*, 1906, **16**, 20.

[5] Brücke, H. V., *J. Comp. Neur.*, 1931, **53**, 225.

the work of Poos[6] and Ten Cate,[7] who showed that constriction takes place by contraction of the sphincter alone, in contrast to the claim of Behr[8] that the normal constriction of the pupil to light takes place by an active innervation of the sphincter and simultaneous inhibition of the dilator.

Summary. The differences in pupil diameter in the dark adapted rabbit's eye can be summarized as follows: 1. It is smallest when the sympathetic is cut. This state represents an equilibrium between the elasticity of the iris and the "residual tone" of the sphincter. 2. It is slightly larger when both the sympathetic and the third nerves are cut. In this condition, elastic tissue only holds the pupil open. 3. It is still larger in the normal eye when there is an equilibrium between the "residual tone" of the sphincter on the one hand and the elasticity of the iris tissue plus the active contraction of the dilator on the other. 4. It is at its greatest possible maximum when the third nerve is cut or atropine is instilled into the normal eye. Here the "residual tone" of the dilator and the possible slight contraction of this muscle is added to the action of the elastic tissues of the iris.

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Oxidative Assimilation of Lactic Acid by *Escherichia coli.*

C. E. CLIFTON AND WILLIAM A. LOGAN.

From the Department of Bacteriology and Experimental Pathology, Stanford University, California.

Barker,[1] Geisberger,[2] and Clifton[3] have shown that the oxidation of simple substrates by washed suspensions of actively respiring, non-proliferating cells does not proceed to completion, but instead, a portion of the substrate is apparently assimilated by the cells. For example, the oxidative assimilation of acetate by *Escherichia coli* may be represented[3] as

$$2\ CH_3COOH + 3\ O_2 = (CH_2O) + 3\ CO_2 + 3\ H_2O$$

According to this equation three-fourths of the oxygen required for the complete combustion of the acetate is consumed with the

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[6] Poos, F., *Klin. Monatsbl. f. Augen.*, 1927, **78**, 874.

[7] Ten Cate, J., *Arch. Neerl. de Physiol.*, 1921, **6**, 258.

[8] Behr, *Graefe-Saemisch Handbuch der ges. Augenheilkunde*, 1924, **3**.

[1] Barker, H. A., *J. Cell. Comp. Physiol.*, 1936, **8**, 231.

[2] Geisberger, G., *Beiträge zur Kenntnis der Gattung Spirillum Ehbg.*, Dissertation, Utrecht, 1936.

[3] Clifton, C. E., *Enzymologia*, 1937, **4**, 246.