

that which had to be removed from the control dogs in order to reduce their arterial pressures to 50 mm Hg. The results, summarized in Table II, show that the volume of blood which could be removed from the burned dogs was significantly lower than that of the control dogs. The sum of the local fluid accumulation in the burned legs plus the bleeding volume was in every case, however, equal to or greater than the bleeding volume of the corresponding control.

Because of the difficulty in caring for dogs with such severely burned legs, three of the burned dogs were killed immediately after the bleeding, and the remaining two were sacrificed on the third and fifth days. Only part of the withdrawn blood was reinjected into the controls, 21 to 29.5 ml/kg of body weight being withheld. All survived indefinitely.

Conclusions. It was not found possible to produce a progressive decline in arterial pressure, leading to death in lightly anesthetized

dogs by means of deep muscle burns alone. A prodromal state of shock was produced, however, since the resistance of these dogs to bleeding was significantly less than that of control dogs similarly anesthetized but not burned. Since the volume of blood which had to be removed from the burned dogs in order to lower their mean arterial pressure to 50 mm Hg, plus the volume of edema in the legs, was as large as or larger in each case than the bleeding volume of the corresponding control dogs, it is concluded that the accumulation of fluid at the site of the burn is the principal factor responsible for the prodromal stage of shock in the burned dogs. Association of the extensive muscle destruction with restriction of movement and with prolonged moderately deep anesthesia converts the prodromal stage into outspoken shock with death of the dog even when the accumulation of fluid at the site of the burn is quite small.

14678 P

Functional Polarization in Retinal Development and Its Reestablishment in Regenerating Retinae of Rotated Grafted Eyes.*

L. S. STONE.

From the Department of Anatomy, Yale University School of Medicine, and the Osborn Zoological Laboratory, Yale University.

The retina of adult salamander eyes always degenerates and is replaced by regeneration from surviving peripheral cells when the eye is grafted,^{1,2,3} even repeatedly,⁴ or when its blood supply is temporarily interrupted.⁵ If

the optic nerve is cut without interfering with the blood supply the retina survives and the nerve immediately regenerates.⁵ This offers unusual opportunity to test the functional quadrants of the retina.

When Sperry first reported⁶ reversed visuomotor responses in salamanders after optic nerve regeneration in eyes rotated *in situ*, I examined the effects of various types of rotation on vision in 100 grafted adult *Triturus viridescens* eyes in which a new functioning retina could be tested.

Normal visuomotor responses in salamanders are demonstrated when the animal moves toward, snaps at and follows a lure approaching any of the 4 quadrants in the field of vision. The animal also automatically moves

* Aided by grants from the John and Mary R. Markle Foundation and the Fluid Research Fund of Yale University School of Medicine.

¹ Stone, L. S., and Zaur, I. S., *J. Exp. Zool.*, 1940, **85**, 243.

² Stone, L. S., and Ellison, F. S., *Proc. Soc. Exp. Biol. and Med.*, 1940, **45**, 181.

³ Stone, L. S., and Cole, C. H., *Yale J. Biol. and Med.*, 1943, **15**, 735.

⁴ Stone, L. S., and Farthing, T. E., *J. Exp. Zool.*, 1942, **91**, 265.

⁵ Stone, L. S., and Chace, R. R., *Anat. Rec.*, 1941, **79**, 333.

⁶ Sperry, R. W. (Abst.), *Anat. Rec.*, 1942, **84**, 20.

head and body in the same direction with a rotating black and white drum only if it passes posteroanteriorly through the field of vision of an eye^{7,8,9} (clockwise for a left eye and counterclockwise for a right eye). These compensatory movements are not elicited when the drum moves anteroposteriorly through the vision field of either eye.

The right or left eye was rotated 180° *in situ* and fixed in place after cutting conjunctival and muscular attachments. The optic nerve and blood supply was left intact to preserve the original retina. The results were the same as in similar experiments by Sperry. All quadrants of the original intact retina were functionally reversed. After removing the normal eye on the opposite side the animals tended to swim and walk in circles toward the eyeless side. The head usually proceeded in the same direction when the animal came to rest. To a rotating drum the head and body movements were elicited only when the drum passed from the original posterior to the original anterior pole, but they were reversed—a direction opposite to that of the moving field. When the lure was brought into the fields of each of the 4 retinal quadrants the animal reversed its reactions and sought the lure in the opposite direction. After the eye was rotated back to normal position again, normal visuomotor reactions were restored.

When the eye was excised and reimplanted upside down (180° rotation of all quadrants) return of vision through the new retina showed complete reversal of all quadrants as in the case of rotated eyes retaining their original retinae. The results were the same as those reported by Sperry in rotated eyes whose optic nerves were later cut and allowed to regenerate.

When the left or right eye was excised and grafted to the opposite side so that dorsal and

ventral quadrants were normally oriented, the anterior and posterior poles were then reversed (180° rotation). After vision returned in the new retina the swimming, head movements, and reversed reactions to the rotating drum were the same as in the case of rotated eyes mentioned above. Reactions to the lure were completely reversed and abnormal only in the rotated anterior and posterior quadrants.

When the right or left eye was excised and grafted on the opposite side, upside down, the dorsal and ventral quadrants were reversed, leaving the anterior and posterior quadrants normally oriented. Head and body movements, swimming, and reactions to the rotating drum were the same as in animals with one normal eye, since the anterior and posterior quadrants were not reversed. To the lure, reactions were reversed only in the rotated quadrants, the dorsal and ventral.

These experiments indicate that the functional pattern is different in each of the 4 retinal quadrants and that each is re-established in the regenerated retina and properly connected with the optic tectum to function according to its orientation.

In an attempt to determine the stage in development at which the retina becomes functionally polarized, the optic vesicle and early cup were excised, rotated 180° and reimplanted in embryos from the closure of the neural folds to late tail bud in *Amblystoma punctatum*. Vision tests during the larval and adult life of these hosts demonstrated functionally normal eyes. When the eye was excised, rotated 180°, and reimplanted at the time retinal layers were beginning to differentiate, vision tests later showed complete reversal of all retinal quadrants. Experiments on intermediate stages are now under way to determine the exact developmental period at which the retinal quadrants become functionally established. A 400-foot colored motion picture film has been made recording these experiments.

⁷ Sperry, R. W., *J. Exp. Zool.*, 1943, **92**, 263.

⁸ Sperry, R. W., *J. Comp. Neur.*, 1943, **79**, 33.

⁹ Sperry, R. W., *J. Neurophysiol.*, 1944, **7**, 57.